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QUANTIFYING COAT COLOR PHENOLOGY OF SYMPATRIC SNOWSHOE HARES
AND WEASELS

BY

BRANDON MURRAY DAVIS

Thesis

presented in partial fulfillment of the requirements
for the degree of

Master of Science
in Wildlife Biology

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APPROVED BY:

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CHAPTER 1

CONCEPTUAL OVERVIEW

Camouflage has intrigued naturalist for decades (Wallace 1867, Cott 1940) and continues to fuel research questions on animal coloration (Stevens and Merilaita 2009). Animals across taxa have evolved various forms of camouflage to prevent predation or facilitate it.

For animals whose camouflage changes to match the local or seasonal environment, the time it takes to change color varies. For example, some animals such as cephalopods can change color in seconds, whereas snowshoe hares (*Lepus americanus*) can take weeks to change color. Snowshoe hares are one of approximately 21 animals that undergo seasonal changes in coat color to match snow (Mills et al. 2018, Zimova et al. 2018). However, as the climate warms and snow duration decreases animals in winter white coats become conspicuous on snowless ground, leading to a phenological mismatch between the animal's color change and the background it is evolved to match (Mills et al. 2013). Furthermore, there are fitness cost to camouflage mismatch, as camouflaged mismatched snowshoe hares have increased mortality compared to camouflaged snowshoe hares (Zimova et al. 2016).

Natural selection has shaped winter coat color to match local snow duration (Mills et al. 2018). For instance, across species there are clines in winter white coat color based on snow duration and ephemerality (Mills et al. 2018). In snowshoe hares, snow can affect the initiation and rate of the coat color molt (Kumar 2015).

Given the adaptive value of seasonal camouflage against snow and the effect of snow on the coat color molt (Kumar 2015), one may predict that co-occurring species subjected to the same environmental conditions should share convergent molt phenology. Animals in different

trophic levels, however, such as snowshoe hares and weasels have different selective pressures that may affect their phenology and winter coat color (Davis et al. 2019). We are aware of only one study that has investigated the phenology of sympatric coat color changing species (Hewson 1957).

Overall, this thesis examines phenology of sympatric coat color changing species, elucidating interspecific variation in the phenology of a trait that is directly linked to climate change. As the climate warms and snow regimes change, species specific differences in coat color phenology may affect the capacity of different seasonal coat color species to persist.

Adaptation is an additional way animals may persist amidst climate change. One route of adaptation is through phenotypic plasticity, a common phenomenon in which a genotype produces more than one phenotype in response to various environmental cues (Atkin et al. 2005, Turcotte and Levine 2016). Various biotic and abiotic cues can induce phenotypic plasticity (Turcotte and Levine 2016). For example, two abiotic factors that vary seasonally, temperature and light influence the number of eggs that enter diapause in annual fish (Furness 2015). Here we investigate the effect of snow and temperature on coat color molt.

In chapter 1 of my thesis I quantify coat color phenology of sympatric species in Montana: snowshoe hares, short-tailed weasels (*Mustela erminea*), and long-tailed weasels (*Mustela frenata*). At our study site in Montana, all animals molt white. Therefore, I explore how snow and temperature affect the phenology (timing and rate) of the fall and spring coat color molts for each species. In West Virginia, where snow duration is transient, winter coat color phenology of sympatric snowshoe hares, long-tailed weasels and least weasels (*Mustela nivalis*) has diverged. In chapter 2 of my thesis we use a combination of field methods to discover that snowshoe hares molt white while both weasel species remain brown in winter in West Virginia,

illustrating an interspecific polymorphic response in winter coloration among sympatric species. Chapter 1 of this thesis may be used as a model of phenotypic plasticity in coat color phenology of sympatric species in areas with regular annual snowfall. Chapter 2 of my thesis, however, where snow is transient may provide a glimpse of what the future holds for coat color changing species, as the winter coat color has diverged between species.

In addition to my main chapters on coat color phenology, I have been involved in a number of other projects that are in various stages of progress. One of these includes a collaboration within our lab to quantify the accuracy of coat color scoring from remote camera photos, an innovative method that will allow quantification of coat color phenology, mismatch, and potential adaptation across species globally (Appendix A). I also planned to quantify mortality cost of camouflage mismatch in weasels. Weasels, however, are elusive predators that are difficult to study in the field and I was unable to identify individual weasels or record predation events from remote camera photos. Therefore, Eben Sargent, an engineer, and I developed a device that mimics weasels' rapid movement using brown and white short-tailed weasel pelts on snowy and non-snowy backgrounds to quantify mortality cost. After six months of field testing we developed a prototype, the *Waltzing Weasel*, and even photographed a predation event (Appendix B). We plan to continue this project as a senior thesis to an undergraduate student in the wildlife program. Finally, I contributed to a group project within the Mills lab that we published in the journal *Science* (Mills et al. 2018). Although I do not include Mills et al. (2018) as an appendix, our results fall within the conceptual umbrella of my thesis. In Mills et al. (2018) we georeferenced 2713 samples of known winter white coat color, across eight species to identify geographic clines, including regions of all brown winter morphs, all

white winter morphs, and polymorphic regions with sympatric winter brown and winter white individuals (Mills et al. 2018).

This research, which constitutes my thesis, reflects the work of many. Therefore, I use the collective “we” throughout the thesis.

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CHAPTER 2

DIFFERENCES IN SEASONAL COAT COLOR PHENOLOGY FOR SYMPATRIC SPECIES ACROSS TROPHIC LEVELS

ABSTRACT

Seasonal coat color is a convergent trait providing camouflage for species across taxa. We show that details of coat color phenology differ across sympatric snowshoe hares (*Lepus americanus*) and short-tailed weasels (*Mustela erminea*). We detected species specific differences in the rate of the coat color molt, while molt initiation dates were similar across species. Furthermore, the rate of the coat color molt for short-tailed weasel's varied, with faster molts in the fall compared to spring. We also found that colder temperature and more snow increase the probability that snowshoe hares and short-tailed weasels are white, whereas warmer temperature and less snow increase the probability that each species is brown. Our results highlight phenotypic plasticity in the rate of the coat color molt between sympatric short-tailed weasels and snowshoe hares. As climate-induced mismatch increases, persistence of coat color changing species depends on adaptation via natural selection on molt phenology.

INTRODUCTION

Seasonal changes in the environment shape the evolution of animal phenology (i.e. timing of biological events) (Gwinner 1973, Stenseth and Mysterud 2002). Many animals in northern latitudes have evolved phenologic traits to cope with highly seasonal environments (Blix 2016), including hibernation, seasonal migration, and the seasonal coat color molt.

As the climate warms and environments change rapidly, however, phenologies do not always keep pace, resulting in a phenological mismatch (Visser and Both 2005, Mills et al. 2013). For example, the date of egg laying in the great tit (*Parus major*) has not advanced over a 23 year period (Visser et al. 1998). However, the average spring temperature over the 23 year period has increased, advancing both vegetation phenology and the abundance of great tits prey resulting in a phenological mismatch between food requirement versus availability (Visser et al. 1998). If and how animals adapt amidst rapid environmental change is of utmost importance given climate models predict changes over the next century (Thomas et al. 2004, Urban 2015, Mills et al. 2018).

One route of adaptation is through phenotypic plasticity, the ability of a genotype to produce different phenotypes under different environmental conditions (Atkin et al. 2005, Fusco and Minelli 2010, Turcotte and Levine 2016). Various biotic and abiotic cues can induce phenotypic plasticity (Turcotte and Levine 2016). For instance, two abiotic factors that vary seasonally, temperature and light, influence the number of eggs that enter diapause in killifish (*Nothobranchius furzeri*) (Furness 2015).

Seasonal coat color molt is a visually striking trait directly linked to climate change (Mills et al. 2013, 2018). Approximately 21 species of mammals and birds undergo seasonal changes in coloration, molting white in winter to match snow (Mills et al. 2018, Zimova et al.

2018). Initiation of the coat color molt is driven by photoperiod (Lyman 1943), while temperature and snow appear to modify the initiation and rate (Rothschild 1942, Rust 1962, Zimova et al. 2014, Zimova et al. 2018, Kumar 2015).

Temperature has been shown to affect the rate of the coat color molt across species both in the lab (Rothschild 1942, Rust 1962) and in the field (Watson 1963, Flux 1970, Zimova et al. 2014, Kumar 2015). For example, once the fall brown to white molt initiated, the rate of completion of the fall molt in captive short-tailed weasels (*Mustela erminea*) was affected by experimental temperature treatments (Rothschild 1942). In spring, warm temperatures can accelerate the white to brown molt in snowshoe hares (*Lepus americanus*) (Zimova et al. 2014) and short-tailed weasels (Rothschild 1942).

The seasonal coat color trait is shaped by natural selection to track snow duration (Hall 1951, Hewson and Watson 1979, Zimova et al. 2014, Mills et al. 2018). For example, the most important covariates in a global model that predicted the probability of a coat color changing individual being white were snow cover duration and two climate variables affecting snow seasonality and transience (Mills et al. 2018).

Because snow and temperature are tightly correlated, most field studies have considered both factors together. For example, individuals monitored over multiple years molted slower in snowier and colder springs [mountain hare (*Lepus timidus*) (Watson 1963, Flux 1970, Clinging 1982), snowshoe hare (Zimova et al. 2014), and rock ptarmigan (*Lagopus muta*) (Watson 1973)]. However, Kumar (2015) successfully disentangled the effect of snow from temperature and found direct effects of snow on molt initiation and rate in snowshoe hares.

As the climate continues to warm, white animals become conspicuous against snowless backgrounds (snowshoe hares; Mills et al. 2013, least weasels (*Mustela nivalis*); Atmeh et al.

2018) and experience increased mortality (Zimova et al. 2016, Wilson et al. 2018). In the absence of an adaptive response, mortality costs could result in strong population declines by the end of the century (Zimova et al. 2016) and have already contributed to recent range contractions for snowshoe hares (Burt et al. 2016, Diefenbach et al. 2016, Saultaire et al. 2016).

Adaptation can occur via natural selection (Vander Wall et al. 2013, Mills et al. 2018), behavioral plasticity (Zimova et al. 2014, Kumar 2015) or by phenotypic plasticity (Scoville and Pfrender 2010). The winter color morph (brown versus white) is determined by genetic variation at a single gene (Jones et al. 2018), making the coat color trait subject to selection. Camouflage mismatched snowshoe hares, however, show no behavioral plasticity (Zimova et al. 2014, Kumar 2015). Despite the influence of photoperiod on the initiation of the coat color molt, snowshoe hares show some phenotypic plasticity to adjust coat color phenology in response primarily to snow (Zimova et al. 2014, Kumar 2015). However, phenotypic plasticity in other coat color changing species has rarely been investigated (but see Hewson 1973 for ptarmigan).

Given the adaptive value of seasonal camouflage against snow, one may predict that co-occurring species subjected to the same environmental conditions should share convergent coat color phenology (i.e. initiation date, rate of color change). Abiotic factors such as snow and temperature may have a similar effect on coat color phenology of sympatric species.

Animals in different trophic levels, however, have different selective pressures that could affect coat color phenology. Specifically, different selective pressures may result in differences in the initiation and rate of the molt, as well as winter coat color (Davis et al. 2019). Weasels, for example, have different life-history traits compared to snowshoe hares (i.e. weasels – have high metabolism, are both predator and prey, use tunnels and the subnivean; snowshoe hares – have lower metabolism, are a prey animal, live above ground) (Brown and Lasiewski 1972, King and

Powell 2007, Zub et al. 2009, Zub et al. 2011). These life history differences may also affect the role of snow and temperature in driving plasticity in the molt phenology.

Although many studies have quantified coat color phenology of a single species [snowshoe hares (Mills et al. 2013, Zimova et al. 2014, 2016, Kumar 2015), least weasels (Atmeh et al. 2018), Arctic fox (*Vulpes lagopus*) (Moberg 2017), and ptarmigan (*Lagopus sp.*) (Montgomerie et al. 2001)] only one study has investigated sympatric species, finding that rock ptarmigan and mountain hare have similar month of initiation and rate of the coat color molt (Hewson 1958).

The central aim of this study is to quantify coat color phenology of sympatric snowshoe hares, long-tailed weasels (*Mustela frenata*), and short-tailed weasels. Specifically, our research questions are: do sympatric species exhibit the same seasonal coat color phenologies, and how does snow and temperature affect the coat color molt for each species? We predicted that the rate of both the weasel and snowshoe hare coat color molt would be accelerated by colder temperatures in the fall and warmer temperature in the spring. Given strong selection for camouflage against snow, we also predict that the initiation of the weasel and snowshoe hare coat color molt should change every year to exactly match when snow arrives. Alternatively, differences in the rate of the molt between weasels and hares could be due to the life history differences.

Coat color phenology in snowshoe hares has been estimated by tracking and photographing radio-collared animals on a weekly basis (Mills et al. 2013, Zimova et al. 2014, 2016). However, such approaches are not easily applied to weasels. Therefore, we used remote-cameras to photograph and quantify phenology of all sympatric coat color changing species. In so doing, our study also adds monitoring of coat color phenology to the list of ecological

questions that can be evaluated by remote cameras (e.g. animal activity (Rowcliffe et al. 2014), species diversity (Steenweg et al. 2017), and density (Villette et al. 2017).

METHODS

i. STUDY SITE

We quantified coat color phenology in a 24-km² area referred to as Richmond Ridge (Lat. = 47.32822°, Long. = -113.53244°) on Lolo National Forest in Seeley Lake, Montana (for study area description see Griffin et al. 2005). Richmond Ridge is part of the Swan Range in a temperate boreal coniferous forest where dominant tree species include Western Larch (*Larix occidentalis*), Douglas-Fir (*Pseudotsuga menziesii*), Subalpine-Fir (*Abies lasiocarpa*), Lodgepole Pine (*Pinus contorta*), Ponderosa Pine (*Pinus ponderosa*) and Engelmann Spruce (*Picea engelmannii*). Common predators of snowshoe hares and weasels in the area include lynx (*Lynx canadensis*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), American martens (*Martes americana*), golden eagles (*Aquila chryseatos*), great horned owls (*Bubo virginianus*), barred owls (*Strix varia*), northern goshawks (*Accipiter gentilis*), and red-tailed hawks (*Buteo jamaicensis*).

ii. REMOTE CAMERAS

Field work took place each fall (September – December) and spring (February – June) from fall 2016 – spring 2018. The number of deployed remote cameras ranged from 23 in fall 2016 to 57 in spring 2018. To reduce pseudo-replicating estimates of the same individuals' coat color phenology, we used a 350 meter spacing of cameras derived from home range estimates for long-tailed and short-tailed weasels (King and Powell 2007). At a camera location, we

opportunistically placed cameras in areas with coarse woody debris, a habitat feature favored by a primary prey species, red-backed voles (*Myodes gapperi*) (Ucitel 2002).

Weasels are active predators with erratic movement patterns, making them difficult to photograph. Therefore, at each remote camera site, we placed a scent lure (i.e. Cavens Gusto scent lure) and bait (i.e. beef liver) in a 4” corrugated irrigation tube to attract and keep weasels in the remote cameras detection zone (i.e. the area in front of the remote camera that detects movement to trigger photo burst). Because the scent lure also attracted snowshoe hares we could record phenology of both species at the same cameras.

Cameras were mounted on trees at knee height, perpendicular to and aimed downward toward the bait tube. Over the duration of our four field seasons, we deployed a variety of camera models including: Reconyx PC900 Hyperfire Professional infrared camera, Reconyx PC850 Hyperfire Pro White Flash camera, Reconyx Ultrafire XR6, and the Browning Dark OPS 940. All camera settings were set to the fastest trigger speed possible per model (e.g. 5 picture rapid fire, 5 second delay between pictures).

iii. COAT COLOR PHENOLOGY

We adapted protocols used for snowshoe hare coat color phenology (Mills et al. 2013, Kumar 2015, Zimova et al. 2016) for weasels. The pattern of the weasel coat color molt (i.e. beginning on the belly and ending on the back in the fall and reversed in the spring) is similar for both long-tailed and short-tailed weasels (van Soest and van Bree 1969, King 1979, King and Moody 1982, Zimova et al. 2018). Both long-tailed and short-tailed weasels have a black tip at the end of their tail that remains black year round (King and Powell 2007), which we omitted from measurements of coat color phenology.

Photos of both species were uploaded into Microsoft PowerPoint, with date information deleted to remove any expectancy bias (Mills and Knowlton 1989) from estimating coat color with knowledge of the expected coat color based on date. A single observer (BD) quantified coat color of each photographed animal. Every animal received a score of proportion white (i.e. 0, 0.05, 0.2, 0.4, 0.6, 0.8, 0.95, 1 white). Next, in Program R (version 3.5.3, R Development Core Team 2019) we binned all animals into three categories of proportion white (i.e. 0 – 0.05 = brown, 0.06 – 0.94 = molting, and 0.95 – 1 = white).

iv. STATISTICAL ANALYSIS

Snowshoe hares and weasels were not individually identifiable and often remained near the bait tube for hundreds of consecutive images. Therefore, to reduce pseudo-replicating the same individual's coat color phenology, we treated as a single independent detection all consecutive photos of an individual until it left the camera's frame for at least one intervening picture.

We investigated the effect of two covariates (i.e. snow and temperature) on coat color phenology. We used temperature data (i.e. daily average temperature) and daily snow data (i.e. snow water equivalent) from a SNOTEL site (Kraft Creek, Lat. = 47.42750°, Long. = -113.77527°) approximately 21 kilometers away. The data from all cameras that detected weasels and snowshoe hares was strongly correlated with the SNOTEL site for both snow presence (phi coefficient = 0.85) and temperature data (phi coefficient = 0.83).

Because we could not distinguish individual animals and animals were not detected every day, we used a generalized linear model in a Bayesian framework to determine probability of being white for each species (using an R package we developed; [CamoMismatch]). We used a multinomial model to predict the population level average daily coat color phenology for each

species. Next, we used daily predictions of percent white to build a time series of the coat color molt for each species over four seasons. The model was fit with Markov Chain Monte Carlo (MCMC) in R2Jags using three chains of 200,000 iterations with the first 100,000 being discarded as burn-ins. The Gelman-Rubin statistic was used to indicate chain convergence ($\hat{R} \leq 1.1$).

RESULTS

i. COAT COLOR PHENOLOGY

Snowshoe hares and short-tailed weasels showed differences in coat color phenology (Figure 1). For all seasons, short-tailed weasels molted faster and completed the molt earlier than snowshoe hares (Table 2; results from fall 2017 are uncertain and are further being analyzed). In addition, short-tailed weasels molted faster in the fall than in the spring. Long-tailed weasel coat color phenology could not be estimated due to low sample size.

ii. TEMPERATURE AND SNOW

Both snow and temperature affected snowshoe hare and short-tailed weasel coat color phenology (Table 3). Over all seasons, colder temperature and greater snowfall increase the probability that both snowshoe hares and short-tailed weasels were white (Table 3).

DISCUSSION

Most coat color research has focused on the phenology of a single species, such as snowshoe hares (Mills et al. 2013, Zimova et al. 2014, Kumar 2015), least weasels (Atmeh et al. 2018), Arctic fox (Moberg 2017), and ptarmigan (Montgomerie et al. 2001). Hewson (1958)

compared coat color phenology of sympatric rock ptarmigan and mountain hares in Scotland and determined that the timing and duration of the coat color molt was similar.

Likewise, studies of mechanisms driving plasticity in molt phenology (such as snow and temperature) have also been species-specific [mountain hare (Watson 1963, Flux 1970, Jackes and Watson 1975, Clinging 1982), snowshoe hare (Zimova et al. 2014, Kumar 2015), short-tailed weasel (Rothschild 1942, Rust 1962), Siberian hamster (*Phodopus sungorus*)(Larkin et al. 2001), collared lemming (*Dicrostonyx groenlandicus*) (Degerbøl and Møhl-Hansen, 1943)], and birds [rock ptarmigan (Salomonsen 1939, Watson 1973)]. Our study is the first to consider under a unified framework the effects of both snow and temperature for two sympatric color changing species.

We document coat color phenology of both weasels and snowshoe hares. We found that snowshoe hares and short-tailed weasels had similar dates of initiation of seasonal color molts, but species specific differences in the rate of the molt. Furthermore, we found seasonal differences in the rate of the coat color molt for short-tailed weasels, with faster molts in the fall compared to spring. We also found that colder temperature and more snow increase probability that snowshoe hares and short-tailed weasels are white, whereas warmer temperature and less snow increase probability that each species is brown.

Our investigation of convergence in coat color phenology rests on a strong understanding of how related traits evolve through different lineages (Zimmer and Emlen 2012). Understanding how traits converge in different lineages can reveal how each lineage reached a common phenotype, and can uncover various solutions to different stressors within the constraints of phylogeny. Apes and corvids, for instance, have repeatedly evolved the cognitive ability to solve problems, leading to convergent evolution of intelligence (Emery and Clayton. 2004). Similar

auditory biochemical mechanisms evolved in two phylogenetically remote organisms, katydids and mammals, despite different physiologies (Montealegre-Z et al. 2012). At the molecular level, different light sensitive opsin proteins arose in bacteria even though they are nonhomologous (Larusso et al. 2008). As a final example, serine protease venoms converged on nearly identical protein structures in spite of evolving independently in mammals and lizards (Brodie 2010).

Seasonal coat color is a convergent trait providing camouflage for species across taxa from the Siberian hamster to the Arctic fox (Zimova et al. 2018). The coat color trait has evolved to match a seasonally transient snowy background (Mills et al. 2018).

Despite general convergence of the trait, we have shown that details of the coat color phenology can differ across sympatric species. The differences in the rate of the molt between short-tailed weasels and snowshoe hares could be due to species-specific energetic constraints. For instance, short-tailed weasels are long and thin, a morphology well-suited to hunt and move in small spaces. Although both species endure a metabolic cost of living in a cold environment (Brown and Lasiewksi 1972, Sheriff et al. 2009), the metabolic cost on short-tailed weasels may be more severe than snowshoe hares (Brown and Lasiewksi 1972). For example, the metabolism of cold stressed weasels is 50 – 100% greater than that of similar sized mammals (Brown and Lasiewksi 1972). Least weasels (*Mustela nivalis*) account for changes in temperature by adjusting their activity patterns (Zub et al. 2009). Maintaining a relatively constant energy output across varying temperatures exemplifies a metabolic niche of a small mammal having extremely high energy expenditures primarily driven by ambient temperature (Zub et al. 2009). Maintaining the metabolic niche while balancing activity patterns, temperature, and possibly the coat color molt may require weasels to molt faster than snowshoe hares.

Our result that the rate of the short-tailed weasel molt occurs faster in fall than spring aligns with previous findings (Rothschild 1942). The seasonal differences in the rate of the short-tailed weasel molt may be due to reproduction. Short-tailed weasels breed in the summer, however, implantation is delayed until the following spring. In spring, once photoperiod changes, the hormone prolactin triggers both implantation and initiation of the coat color molt (Rust 1965, Zimova et al. 2018).

The connection between reproduction and the coat color molt may reduce potential for phenotypic plasticity in the spring, with greater potential for phenotypic plasticity in the fall. However, snowshoe hares show the opposite, with phenotypic plasticity in the rate of the spring but not the fall coat color molt (Zimova et al. 2014).

Climate models predict drastic changes in temperature and snow regimes over the next century, with special emphasis on decreasing winter snow duration (Thomas et al. 2004, Urban 2015, Mills et al. 2018). Studying how plastic a trait is in response to a changing climate is one of the biggest challenges we face. Our results highlight phenotypic plasticity in the rate of the coat color molt between sympatric short-tailed weasels and snowshoe hares. As climate-induced mismatch increases, persistence of coat color changing species depends on adaptation via natural selection on molt phenology.

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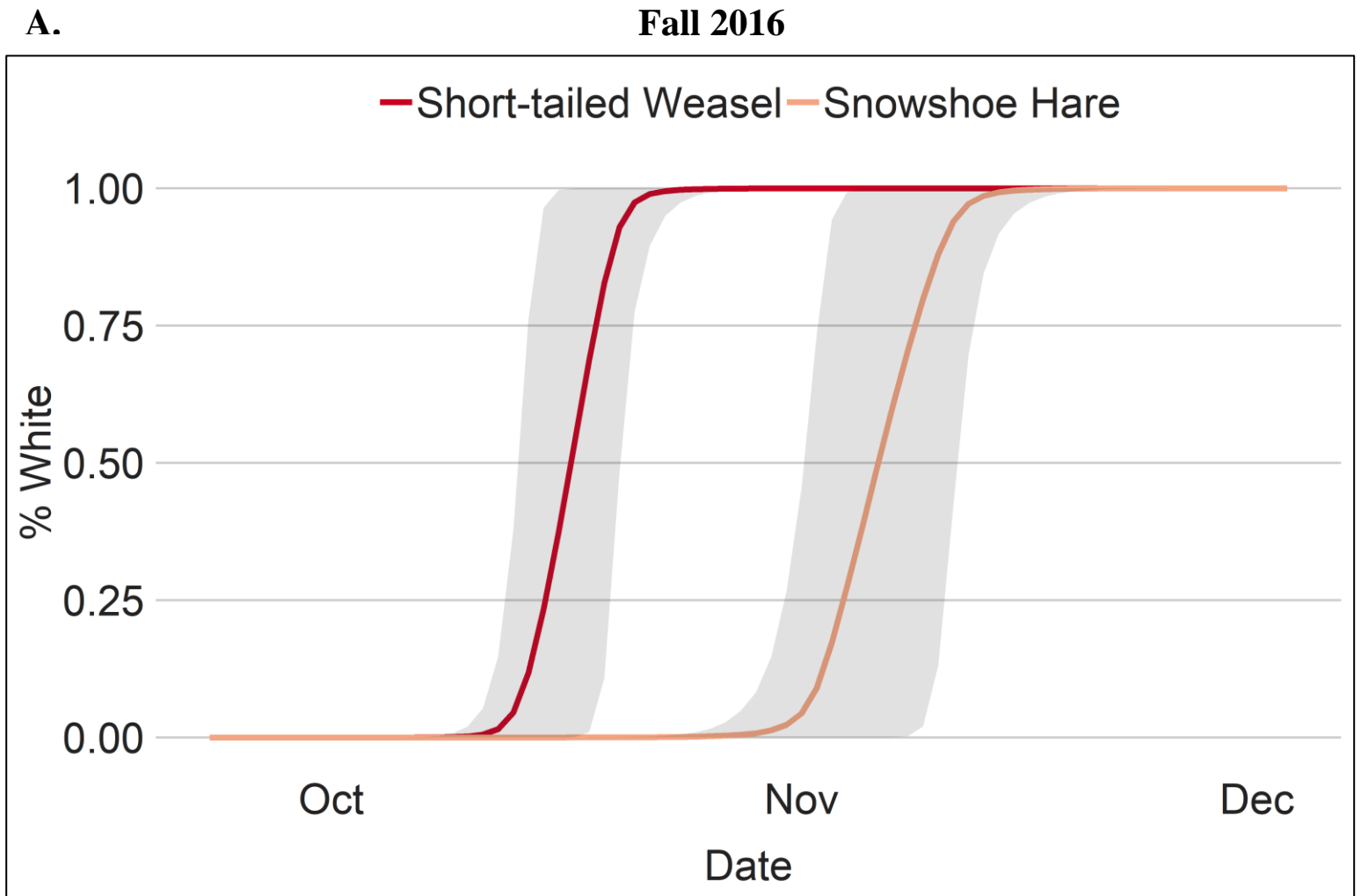
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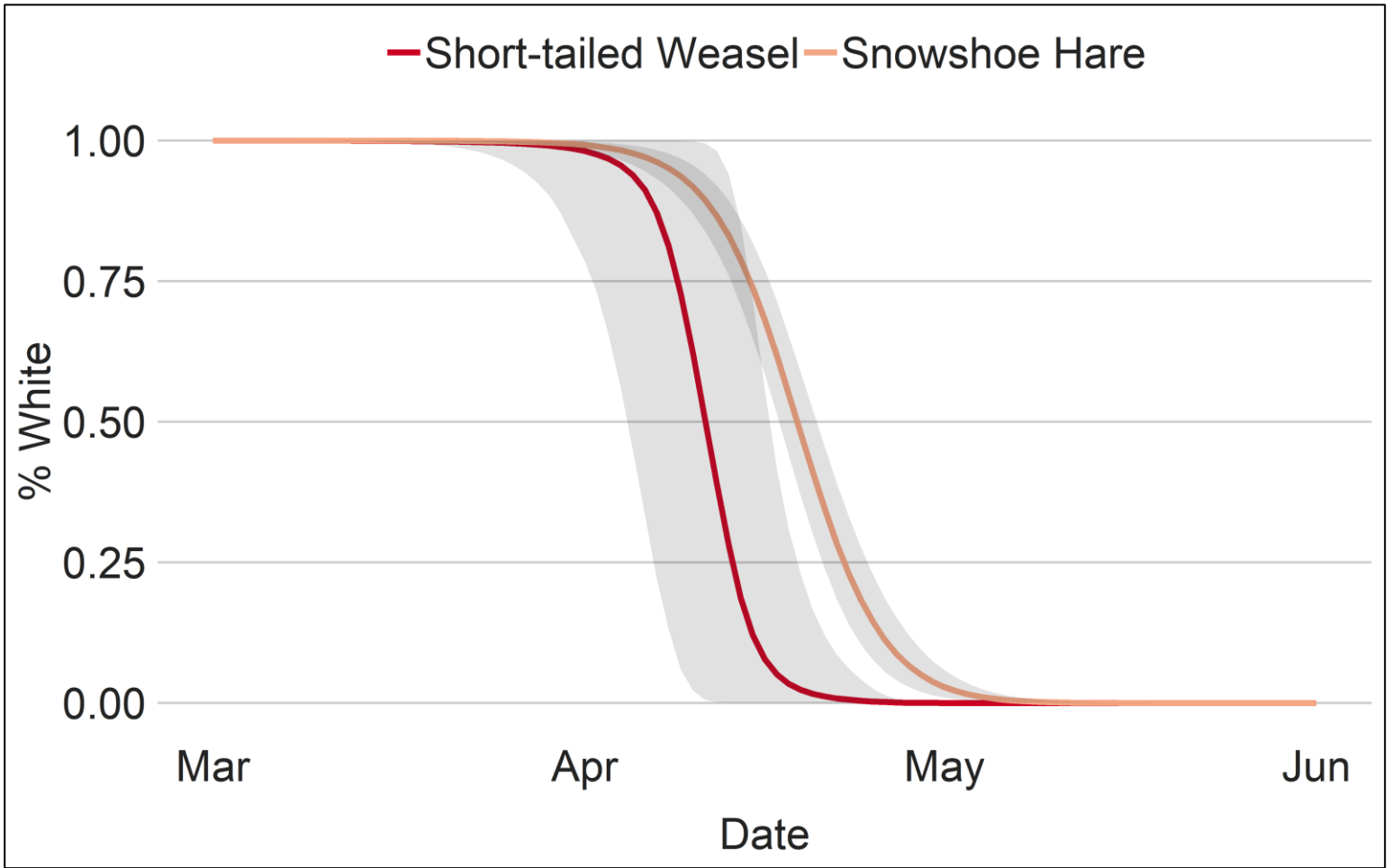
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Figure 1. Snowshoe hare and short-tailed weasel coat color phenology from fall 2016 – spring 2018. Each line is the daily probability of how white the population of each species is through time. A.) The fall 2016 coat color molt progresses from brown to white. B.) The spring 2017 coat color molt progresses from white to brown. C.) The fall 2017 coat color molt progresses from brown to white. D.) The spring 2018 coat color molt progresses from white to brown.



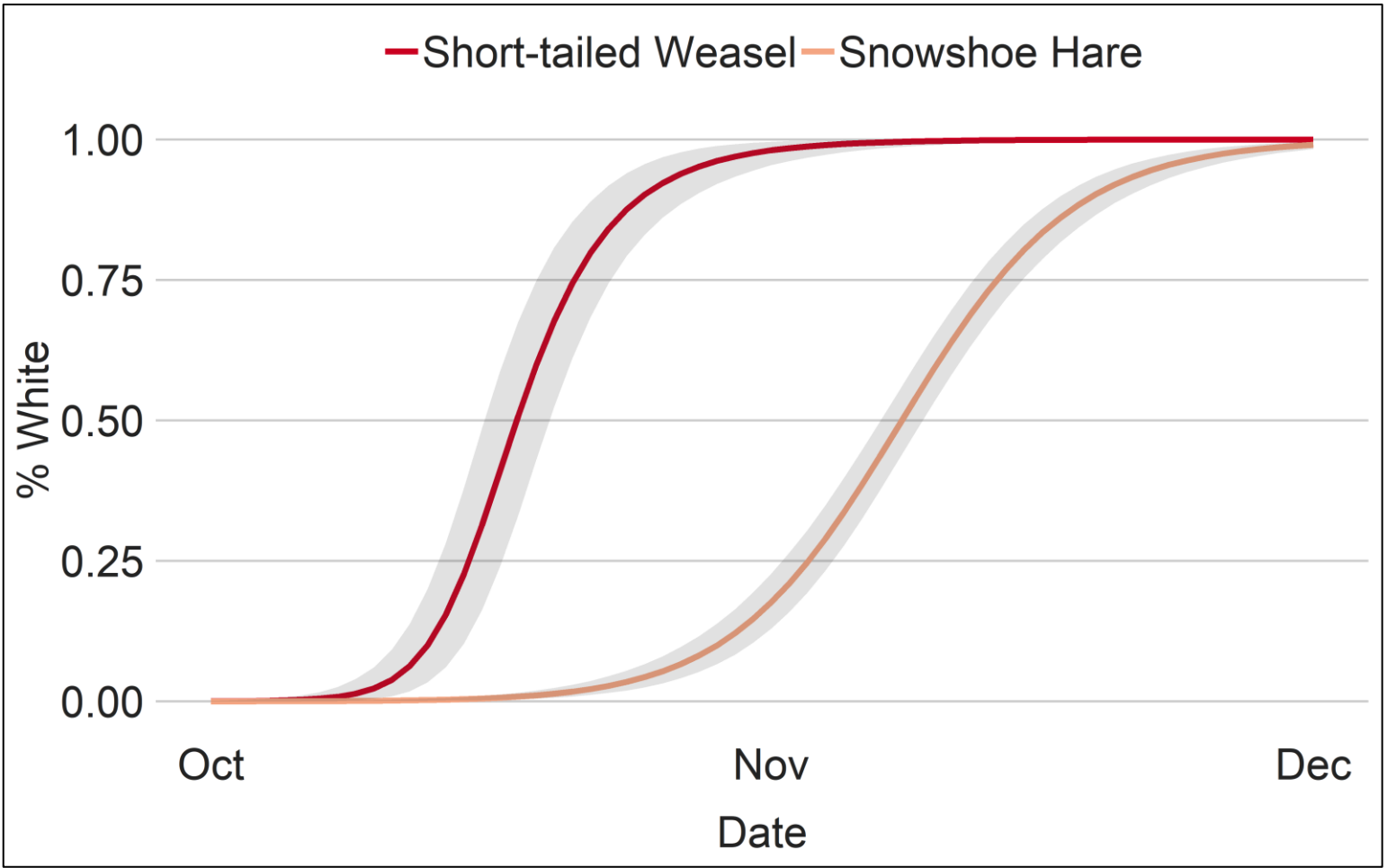
B.

Spring 2017



C.

Fall 2017



D.

Spring 2018

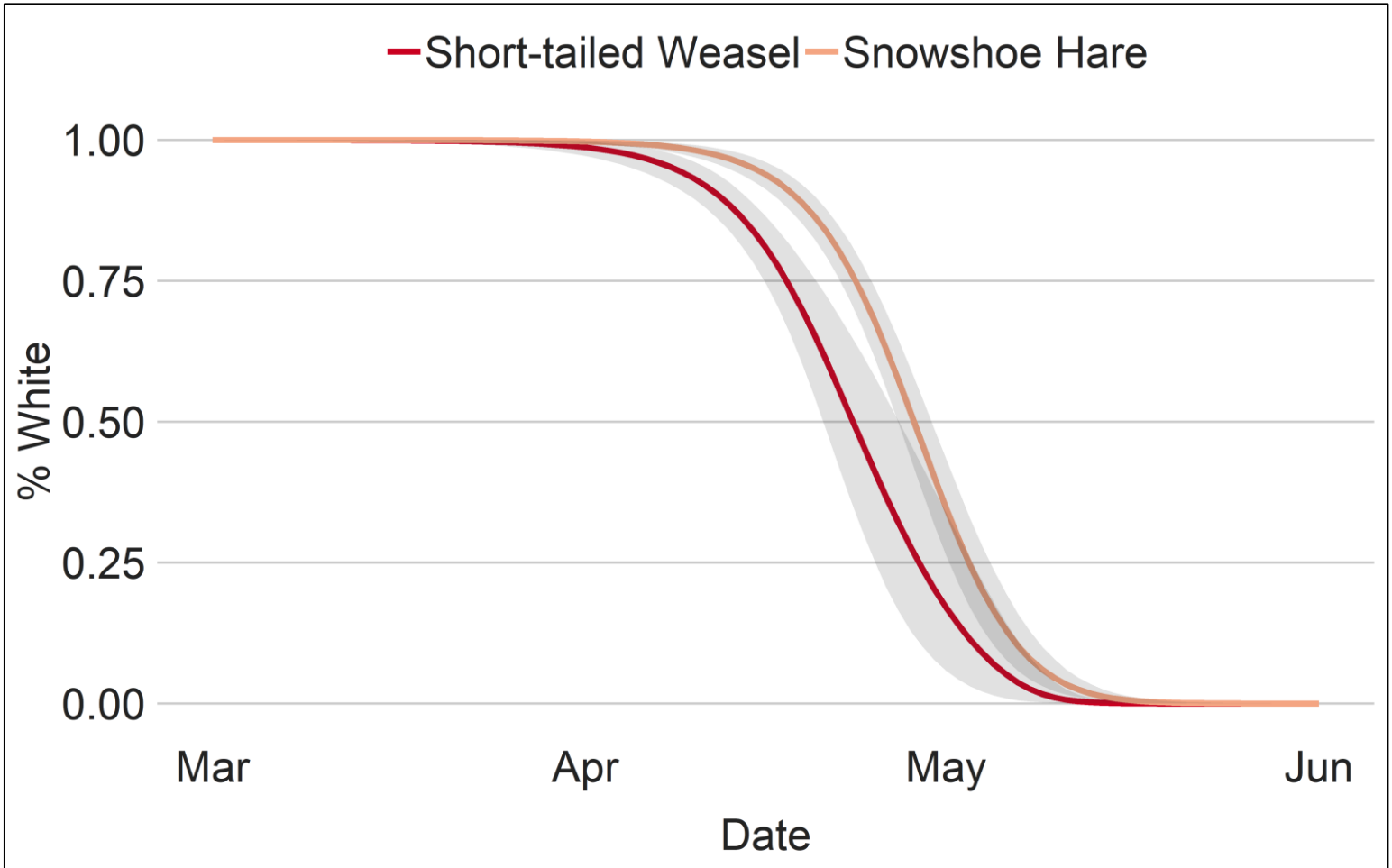


Table 1. Number of independent detections of each species per season.

	<i>Fall 2016</i>	<i>Spring 2017</i>	<i>Fall 2017</i>	<i>Spring 2018</i>
<i>Snowshoe Hare</i>	33	699	915	1586
<i>Short-tailed Weasel</i>	36	15	405	646
<i>Long-tailed Weasel</i>	0	3	36	2

Table 2. The initiation, rate, and completion date of the seasonal coat color molt for each species each season. * indicates low sample size.

	LTW	SSH	STW
<i>Fall 16</i> Initiation	*	Oct 8	Oct 2
<i>Fall 16</i> Rate	*	34 days	19 days
<i>Fall 16</i> Completion	*	Nov 11	Oct 21
<i>Spring 17</i> Initiation	*	Apr 8	Apr 4
<i>Spring 17</i> Rate	*	45 days	28 days
<i>Spring 17</i> Completion	*	May 23	May 2
<i>Fall 17</i> Initiation	Oct 25	Sep 24	Oct 8
<i>Fall 17</i> Rate	18 days	60 days	20 days
<i>Fall 17</i> Completion	Nov 12	Nov 23	Oct 28
<i>Spring 18</i> Initiation	*	Apr 15	Apr 8
<i>Spring 18</i> Rate	*	41 days	37 days
<i>Spring 18</i> Completion	*	May 26	May 15

Table 3. The effect of snow and temperature on short-tailed weasel and snowshoe hare coat color molt. Colder temperature and more snow increase probability that snowshoe hares and short-tailed weasels are white, whereas warmer temperature and less snow increase probability that each species is brown.

<i>Species</i>	<i>Season</i>	<i>Beta Coefficient</i>	<i>95% CI</i>	<i>Interpretation</i>
<i>Short-tailed Weasel</i>	Fall 2016	β_{Temp} (5.172)	1.660 – 10.113	Probability of being in brown category increases as temp increases
	Fall 2016	β_{Snow} (9.245)	0.637 – 23.456	Probability of being in white category increases as snow increases
	Spring 2017	β_{Snow} (-15.526)	-29.655 – -4.465	Probability of being brown category decreases as snow increases
	Spring 2017	β_{Snow} (14.105)	3.981 – 27.825	Probability of being in white category increases as snow increases
	Fall 2017	β_{Snow} (5.262)	1.652 – 11.567	Probability of being in white category increases as snow increases
	Fall 2017	β_{Temp} (-1.745)	-2.584 – -0.942	Probability of being in white category decreases as temp increases
	Spring 2018	β_{Snow} (-8.386)	-13.449 – -4.728	Probability of being in brown category decreases as snow increases
	Spring 2018	β_{Snow} (-1.526)	-2.808 – -0.354	Probability of being in white category decreases as snow increases

<i>Snowshoe Hare</i>	Spring 2018	β_{Temp} (-3.142)	-4.224 – -2.141	Probability of being in white category decreases as temp increases
	Fall 2016	β_{Temp} (2.254)	0.799 – 4.235	Probability of being in brown category increases as temp increases
	Fall 2016	β_{Snow} (9.829)	1.525 – 23.786	Probability of being in white category increases as snow increases
	Spring 2017	β_{Snow} (-8.996)	-15.343 – -4.250	Probability of being in brown category decreases as snow increases.
	Spring 2017	β_{Snow} (4.213)	3.430 – 5.118	Probability of being in white category increases as snow increases.
	Fall 2017	β_{Snow} (-2.181)	-3.042 – -1.456	Probability of being in brown category decreases as snow increases
	Fall 2017	β_{Snow} (2.396)	2.078 – 2.736	Probability of being in white category increases as snow increases
	Fall 2017	β_{Temp} (0.367)	0.157 – 0.587	Probability of being in brown category increases as temp increases
	Spring 2018	β_{Snow} (-2.297)	-2.889 – -1.755	Probability of being brown decreases as snow increases
	Spring 2018	β_{Snow} (1.547)	1.031 – 2.103	Probability of being white

Spring 2018	$\beta_{\text{Temp}} (-2.521)$	-3.070 – -2.001	increases as snow increases Probability of being in white category decreases as temp increases
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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

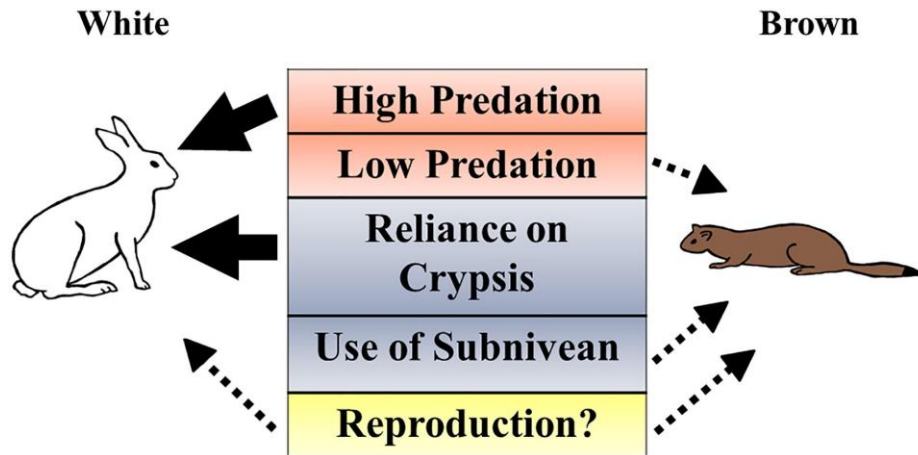


Fig. 3. Potential forces that drive maintenance of year-round brown coloration or selection for winter white coloration. Because snow is present, white would seem to be the preferred winter wardrobe as seen in snowshoe hares. Despite seasonal snow cover, however, weasels maintain brown coloration in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

Quantifying Coat Color with Cameras

I am involved in a collaboration within our lab to quantify the accuracy of coat color scoring from remote camera photos. In addition, we will identify factors affecting accuracy and provide general recommendations on how to setup and monitor coat color phenology using remote cameras. This study will determine the limitations and applications of remote cameras to quantify coat color phenology, mismatch, and potential adaptation across species globally. Experiments take place at an outdoor enclosure at the University of Montana Field Research Center in Missoula, Montana. We photograph captive snowshoe hares with remote cameras, quantify coat color using these photos, and compare estimates to those obtained by visual observation. We will finish experiments this summer and plan to submit our manuscript for publication in fall 2019.

APPENDIX B

The Waltzing Weasel

As noted in chapter 1, we wanted to quantify mortality cost of camouflage mismatch in weasels. Weasels, however, are elusive predators that are difficult to study in the field and we were unable to identify individual weasels or record predation events from remote camera photos. Therefore, Eben Sargent, an engineer, and I developed the *Waltzing Weasel* (Figure 1), a cost efficient device (Table 1) that mimics weasels' rapid movement using brown and white short-tailed weasel pelts. The *Waltzing Weasel* uses two servo motors to move mounted white and brown short-tailed weasel (*Mustela erminea*) pelts in a motion to mimic weasel movement. While one weasel pelt is in motion the other pelt is hidden below a platform. We mounted remote cameras next to the *Waltzing Weasel* to capture predation events. When set in the field year-round, the *Waltzing Weasel* presents both weasel color morphs on snow and snow free backgrounds, allowing us to quantify predation risk of camouflaged and camouflage mismatched weasels (i.e. brown animal on snow, white animal on non-snowy background).

After six months of field testing we finalized adjustments to the *Waltzing Weasel*, and even photographed a predation event (Figure 2). This project will continue as a senior thesis of an undergraduate student in the wildlife program.

Figure 1. The *Waltzing Weasel*, a device that mimics weasels' rapid movement using brown and white short-tailed weasel pelts. A.) Inverted *Waltzing Weasel*. Brown and white weasel pelts are mounted to piano wire that attach to servo motors. B.) Three RC car batteries power the *Waltzing Weasel*. RC batteries and circuit board are stored in dry box.

A.



B.

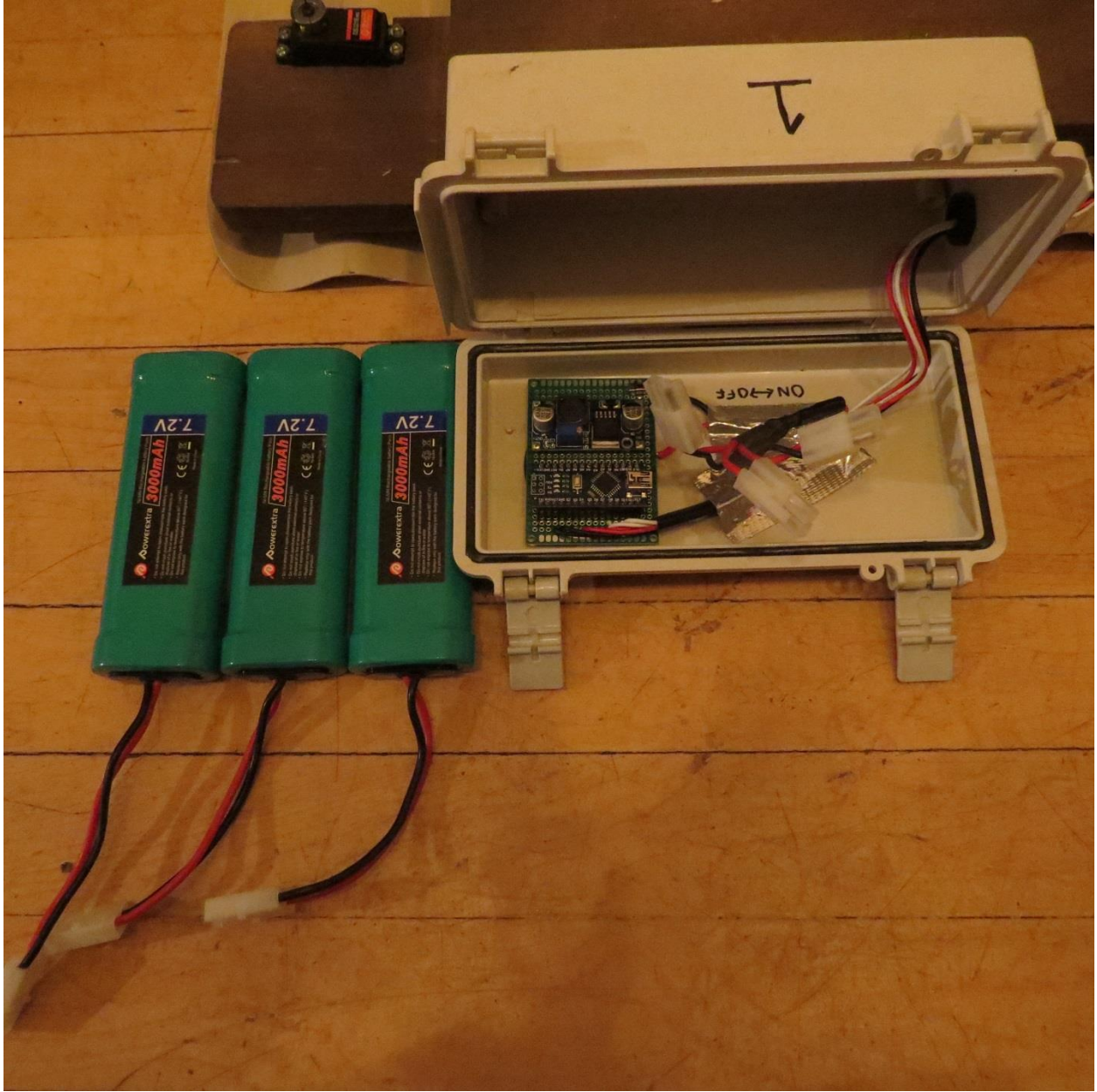


Table 1. Cost of supplies to build *Waltzing Weasel*.

Supplies	Cost
batteries (x3)	36.00
servos (x3)	54.00
arduino	16.00
voltage converters	12.00
battery charger	12.00
servo screws and arms	16.00
servo and battery connectors	19.00
piano wire, misc hardware	10.00
enclosures	24.00
Total	\$199.00

Figure 2. The *Waltzing Weasel* deployed in a snowy field in December. Natural debris camouflages the *Waltzing Weasel* with the background. A photograph of a barred owl (*Strix varia*) attacking the white weasel.



APPENDIX C

Citizen Science Protocol to Detect Weasels

We collaborated with Dr. Roland Kays at North Carolina State University to develop a citizen science protocol to detect weasels throughout the east coast. We plan to write a manuscript describing our method and submit our manuscript to the Wildlife Bulletin.

Materials

1. Game camera
2. 4-in x 12-in black corrugated drain tube (or something similar)
3. Drain pipe cap
4. Caven's Gusto scent lure
<http://www.minntrapprod.com/Cavens-Gusto/productinfo/GUSTO16/>
5. Raw chicken livers (or something similar)

Protocol

1. Find a good place: thick habitat is good, look for tracks in the snow, downed logs, rocky ledges, and hedgerows are also great places.
2. Place the Tube:
 - Wedge the tube into a tight space (under log, between rocks, etc.)
 - Cover remaining tube with debris
 - Put liver in the back
 - Cap one end of the tube
 - 1 tbsp. Scent lure in the front
3. Set Camera, leave for 2-3 weeks
 - Find a tree or stake 8 – 12 feet from the tube's entrance.
 - Set camera ~3ft up and aim down at the front of the tube, knee height will also work.
 - Use walk-test mode to test aim by moving your hand in front of tube
 - Use high sensitivity, no quite period before pictures, take 3-5 pictures for each trigger, with no time between triggers.
 - Be sure the date/time settings are correct.
 - Following the first deployment of the camera you may need to reduce your camera's sensitivity to prevent an overload of mice and voles pictures.



Tube setup