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Title: Local climate determines vulnerability to camouflage mismatch in snowshoe hares

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Biosketch: Marketa Zimova is a postdoctoral researcher interested in the effects of global environmental change on wild populations. The majority of her work aims to understand species adaptive potential to climate change and to yield useful information that can guide conservation and management decisions necessary for maintaining biodiversity. The research team includes scientists from the United States and Canada who study climate change and the ecology and evolutionary biology of wild organisms.

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8 **Title**: Local climate determines vulnerability to camouflage mismatch in snowshoe hares

9 **Running title**: Local climate determines mismatch

10

11 **ABSTRACT:**

12 **Aim**: Phenological mismatches, when life-events become mistimed with optimal environmental

13 conditions, have become increasingly common under climate change. Population-level

14 susceptibility to mismatches depends on how phenology and phenotypic plasticity vary across a

15 species distributional range. Here, we quantify the environmental drivers of color molt

16 phenology, phenotypic plasticity, and the extent of phenological mismatch in seasonal

17 camouflage to assess vulnerability to mismatch in a common North American mammal.

18 **Location**: North America.

19 **Time period**: 2010-2017.

20 **Major taxa studied**: Snowshoe hare (Lepus americanus).

21 **Methods**: We used >5,500 by-catch photographs of snowshoe hares from 448 remote camera

22 trap sites at three independent study areas. To quantify molt phenology and phenotypic plasticity,

23 we used multinomial logistic regression models that incorporated geospatial and high-resolution

24 climate data. We estimated occurrence of camouflage mismatch between hares' coat color and

25 the presence and absence of snow over seven years of monitoring.

26 **Results**: Spatial and temporal variation in molt phenology depended on local climate conditions

27 more so than on latitude. First, hares in colder, snowier areas molted earlier in the fall and later

28 in the spring. Next, hares exhibited phenotypic plasticity in molt phenology in response to annual

29 variation in temperature and snow duration, especially in the spring. Finally, the occurrence of

30 camouflage mismatch varied in space and time; white hares on dark, snowless background

31 occurred primarily during low-snow years in regions characterized by shallow, short-lasting

32 snowpack.

33 **Main Conclusions**: Long-term climate and annual variation in snow and temperature determine

34 coat color molt phenology in snowshoe hares. In most areas, climate change leads to shorter

35 snow seasons, but the occurrence of camouflage mismatch varies across the species range. Our

36 results underscore the population-specific susceptibility to climate change-induced stressors and

37 the necessity to understand this variation to prioritize the populations most vulnerable under

38 global environmental change.

39 **Keywords**: adaptation, camouflage mismatch, climate change, latitudinal gradient, phenological

40 mismatch, phenotypic plasticity, range edge, snow, snowshoe hares.

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42 **Main text**:

43 INTRODUCTION

44 As a result of anthropogenic climate change, plant and animal populations are increasingly

45 confronting environmental conditions different from the ones to which they are adapted.

46 Organisms occupying seasonal environments have evolved mechanisms for the timing of their

47 life cycles (i.e., phenology) to match with optimal environmental conditions and resources at

48 their location (Bradshaw & Holzapfel, 2007; Williams et al., 2015). When phenology and

49 favorable environmental conditions become asynchronized, organisms can suffer negative fitness

50 costs (Both et al., 2006; Post & Forchhammer, 2008; Lane et al., 2012; Zimova et al., 2016;

51 Senner et al., 2017). Such phenological mismatches are becoming increasingly common under

52 climate change (Parmesan & Yohe, 2003; Thackeray et al., 2010; Cohen et al., 2018), which in

53 the absence of adaptive responses could lead to population declines and local extinctions (Visser

54 & Gienapp, 2019). Thus, there is a pressing need to understand the degree to which climate

55 change leads to phenological mismatches and the capacity of wild populations to withstand

56 attendant fitness costs.

57 Understanding the variation in phenology and its environmental drivers is fundamental

58 for assessing current and future species' vulnerability to phenological mismatches. For the

59 majority of traits in plants and animals in temperate regions, photoperiod serves as the principal

60 cue for phenology, with temperature and other environmental factors exerting lesser influence

61 (Hofman, 2004; Bradshaw & Holzapfel, 2007). Because photoperiod, latitude, and climate

62 covary across most species' ranges, variation in phenology is often distributed along latitudinal

63 gradients. Northern populations typically experience harsher and colder climates that correspond

64 with later initiation of spring and earlier initiation of fall events compared to southern

65 populations (Bradshaw & Holzapfel, 2007; Hut et al., 2013). However, latitude may not be a

66 reliable predictor of phenology for two reasons. First, the covariance between latitude and

67 climate is imperfect when other geographic factors such as elevation also affect climatic

68 conditions (Chuine, 2010; Visser et al., 2010). Secondly, species show year-to-year in situ

69 variation in phenological traits in response to annual variation in climate. This temporal

70 phenological variation is referred to as "population-level" phenotypic plasticity, and is different

71 from between-individual level phenotypic plasticity (Phillimore et al., 2010; Gienapp &

72 Brommer, 2014). Overall, both spatial and temporal variation in phenology may have

73 consequences for susceptibility to phenological mismatch on both the local population and

74 broader species levels.

75   Seasonal coat color molt, a key phenological trait, has received increased attention as a

76 trait shaped by climate. Across the Northern Hemisphere, 21 species of mammals and birds

77 change coat or plumage color from brown in the summer to white in the winter to match snow-

78 covered landscapes (Mills et al., 2018; Zimova et al., 2018). As with other phenological traits,

79 photoperiod serves as the principal cue for molt phenology, with some evidence that year-to-year

80 variation in winter weather modulates the progression of molt (Hofman, 2004; Zimova et al.,

81 2018). However, decreasing duration of snow cover due to climate change (Choi et al., 2010;

82 Vaughan et al., 2013; Kunkel et al., 2016) may result in phenological mismatch, whereby winter

83 white animals become color mismatched against dark, snowless backgrounds (Mills et al., 2013).

84 Field studies indicate that mismatch in seasonal coat color and snow presence or absence leads to

85 high fitness costs due to increased predator-induced mortality (Zimova et al., 2016; Atmeh et al.,

86 2018) and may have already contributed to range contractions for several species including

87 Lagopus and Lepus spp. (Imperio et al., 2013; Diefenbach et al., 2016; Sultaire et al., 2016;

88 Pedersen et al., 2017).

89   The snowshoe hare (Lepus americanus), a key prey species of the boreal forest of North

90 America (Krebs et al., 2001), exhibits seasonal color molts in the majority of its range

91 (Nagorsen, 1983; Gigliotti et al., 2017; Mills et al., 2018). Because of their broad distribution

92   (Fig. 1a), hares inhabit a large range of environmental conditions, making them an ideal species

93   for investigating variation in molt phenology and camouflage mismatch. In the only two areas

94   where molts have been recently investigated in relation to climate change (i.e., Montana and

95   Wisconsin, USA), phenotypic plasticity is not sufficient to prevent camouflage mismatch (e.g.,

96   Mills et al., 2013; Wilson et al., 2018). For example, hares in Montana experience about a week

97   of mismatch annually whereby hares are in the wrong coat color in relation to their background

98   (i.e., white hares on snowless background or brown hares on snow; Mills et al., 2013; Zimova et

99   al., 2014, 2016). Because hares rely heavily on their camouflage for survival, mismatch has

100   strong negative fitness costs (i.e., 7-12% reduced weekly survival) that in the absence of

101   evolutionary shifts and under projected snow declines would be sufficient to cause steep

102   population declines and local extinction (Zimova et al. 2016, Wilson et al. 2018). To date, no

103   study has evaluated the phenological drivers and camouflage mismatch across the heterogeneous

104   snowshoe hare range in a unified analytical framework.

105   To understand snowshoe hare vulnerability to camouflage mismatch, we quantified the

106   spatial and temporal variation in color molt phenology, phenotypic plasticity, and the occurrence

107   of camouflage mismatch across three disjunct, climatically and geographically distinct

108   populations. First, we hypothesized that the spatial variation in molt phenology would be

109   determined by latitude and local climate. We tested two predictions: i) populations in more

110   northern sites molt earlier in the fall and later in the spring, ii) populations in colder and snowier

111   sites molt earlier in the fall and later in the spring. Second, we hypothesized that hares exhibit

112   temperature- and snow-mediated phenotypic plasticity in molt phenology and we predicted that

113   molts occur earlier in fall and later in spring during colder and or snowier years. Third, we

114   quantified the occurrence of camouflage mismatch for each population in spring and fall and

115   assessed which snowshoe hare populations may be the most vulnerable to camouflage mismatch

116   now and under future climate change.

117   MATERIALS AND METHODS

118   **Study Areas**

119   Our analysis integrated three regional monitoring studies in North America: the Canadian

120   Rockies, the San Juan Mountains in Colorado, and northern New England (Fig. 1a). Together,

121   these areas encompass wide latitudinal, altitudinal and habitat variation across the distributional

122　range of snowshoe hares (Table 1). Our northernmost study area in the Canadian Rockies

123　included three national parks (Banff, Yoho, and Kootenay National Parks) and was characterized

124　by rugged, forested mountainous regions with a long snow season. This area is located within a

125　homogeneous boreal habitat at the core of the snowshoe hare distribution range (Cheng et al.,

126　2014). The southernmost study area was located in the San Juan Mountains of southwest

127　Colorado; an isolated patch of high-elevation southern boreal forest near hares' southern range

128　boundary. The northern New England study area, also near the southern edge of hare

129　distribution, encompassed portions of the Green Mountains in Vermont and the White Mountains

130　in New Hampshire. This area stretched across a transition zone between the northern hardwood

131　and boreal forests and had, on average, the mildest climate of the three areas. Major hare

132　predators at all areas included coyotes (Canis latrans), red fox (Vulpes vulpes), Canada lynx

133　(Lynx canadensis), bobcats (L. rufus), martens (Martes spp.), weasels (Mustela spp.), northern

134　goshawks (Accipter gentilis), and great-horned owls (Bubo virginianus). The study area in

135　Canada also had wolves (C. lupus) and grizzly bears (Ursus arctos).

136　**Camera trapping design**

137　We obtained our snowshoe hare phenology data as by-catch photos from three long-term

138　independent studies of forest carnivores. A combination of motion-triggered camera models was

139　used across the sites, but all produced comparable high-quality images during the day and night.

140　The camera spacing differed between regions, but at any given time the minimum distance

141　between cameras was >1 km; grid sizes varied by study area (10×10 km in Canada, 4×4 km in

142　Colorado, and 2×2 km in New England). Each camera site was stationary and remained within

143　a grid cell for a minimum duration of one year. We combined all observations for the cameras

144　that were moved between years within <1 km distance and assigned them an average latitude,

145　longitude and elevation. The 1-km threshold was chosen because it far exceeds average

146　individual hare seasonal movement and home range size at all three areas (Hodges, 1999; Mills

147　et al., 2005; Ivan, 2011).

148　**Coat color monitoring**

149　Coat color was visually estimated from the by-catch hare photographs by one observer,

150　following a standardized protocol for color classification and image quality filtering. Briefly,

151　hares were classified as 1) white when >90% of the body (excluding belly and feet) was white, 2)

152   brown when <10% of the body was white, and 3) molting for all other instances. As per

153   previously developed classification methods (Zimova et al., 2014), we excluded the feet and

154   belly color as these stay white all year in all three areas (Grange, 1932). Because hares cannot be

155   individually identified from photos, we considered photos spaced by >24 hours as independent

156   events, unless different individuals were distinguishable (e.g., two hares in one photo, a hare in a

157   different molt stage recorded within 24 hrs).

158   In Canada, 121 cameras operated continuously from September 2011 to November 2016,

159   yielding 1,888 independent coat color observations. In Colorado, 206 cameras operated from

160   September 2010 to June 2011 and continuously from January 2014 to August 2017, yielding

161   2,027 independent observations. In New England, 121 cameras operated continuously from

162   January 2014 to January 2018, yielding 1,608 independent observations.

163   **Statistical analysis**

164   We used R (version 3.4.3) (R Core Team, 2016) for all statistical analyses.

165   Climate variables

166   To characterize annual and long-term climate conditions at each camera site, we prepared a set of

167   temperature and snow cover variables relevant to molt phenology (Mills et al., 2018; Zimova et

168   al., 2018). Annual minimum (tmin) and maximum (tmax) temperature during spring and fall

169   were calculated for each year of monitoring (2010-2017) at each camera site using daily gridded

170   1 x 1 km resolution data (Daymet; Thornton et al., 2018). We used the same dataset to calculate

171   mean seasonal tmin and tmax during the 30-year period 1980-2009 to describe long-term climate

172   at each camera site. The seasons were defined as spring (March 1- May 31) and fall (September

173   1- November 30), because at all areas the majority of molting occurs during those months.

174   We used modeled snow water equivalent (SWE) to quantify the duration of the

175   continuous snow season and the total number of snow days for the spring and fall. For the years

176   of monitoring (2010-2017), we used daily gridded 1 x 1 km resolution data by Snow Data

177   Assimilation (hereafter SNODAS: Barrett, 2003). Because SNODAS is unavailable prior to

178   2000, we used daily gridded 6 x 6 km resolution data (Livneh et al., 2015) to describe the mean

179   long-term snow conditions during the 30-year period (1980-2009). The duration of spring snow

180   season each year was calculated as the number of days between January 1st and snowmelt date,

181   i.e. the first day when snow is absent (SWE= 0) at a camera site for a minimum of 7 days. Fall

182 snow season was estimated as the number of days following the summer (i.e., the longest

183 snowless period at each camera site each year), between snow onset date (i.e., first day when

184 SWE >0 for a minimum of 7 days) and December 31st. We used the 7-day buffers to discard

185 spurious early spring snowmelts followed by further extended snow season and to account for

186 spurious snow flurries in the fall. The total number of snow days was calculated as the sum of

187 days with SWE >0 from January 1st to August 31st for the spring and from September 1st to

188 December 31st for the fall.

189 **Molt phenology**

190 We used a hierarchical multinomial logistic regression analysis within a Bayesian framework to

191 describe molt phenology and its phenotypic plasticity. For all models, we estimated the

192 probability of a hare being in color category i at a camera site j on a Julian day d as:

193
$$\Pr(y = i) = \frac{e^{\alpha_i + \beta 1_i * d + s_{i,j}}}{1 + \sum_{k=1}^{i-1} e^{\alpha_i + \beta 1_i * d + s_{i,j}}}$$

194 Coat color was treated as a categorical variable, such that a hare on day d was either brown

195 (p_{brown}), white (p_{white}), or molting (p_{molt}) and $\Sigma(p_{1:3, j,d}) = 1$. Camera site was coded as a random

196 covariate $s_{i,j}$ to reflect the hierarchical structure of the dataset and allow for repeated

197 measurements. α_i was the intercept and $\beta 1_i$ was the effect of Julian day on the probability of

198 being either brown, white, or molting. Fall and spring molts were modeled separately.

199 Spatial variation in molt phenology

200 First, to quantify average molt phenology of each population (Canada, Colorado, New England),

201 we combined color observations from all years at that area and ran the model separately for each.

202 We used the estimated probabilities to derive approximate dates when hares initiated and

203 completed their molts as 'initiation' and 'completion' dates at each area. Fall start was specified

204 as the first Julian day when mean $p_{brown}<0.9$ and end date when mean $p_{white}>0.9$; the opposite

205 condition was used to estimate the spring dates (i.e., start when $p_{white}<0.9$ and end when

206 $p_{brown}>0.9$).

207 Next, to test the effect of local environmental covariates on phenology, we combined

208 color observations from all years and populations in one dataset and constructed a set of

209 univariate models. Each model included a single fixed effect of an environmental covariate $\beta 2_i$

210 on the probability of being brown, white, or molting. The environmental covariates were latitude,

211 elevation, and the 30-year long-term temperature and snow conditions (i.e., tmin and tmax,

212 duration of snow season) in spring and fall during each season at each camera site. We used

213 univariate models to avoid problems associated with multicollinearity as most environmental

214 covariates were highly correlated (Pearson correlation coefficients > |0.60|; Table S1). To

215 facilitate comparisons between models, all covariates were standardized to a mean of 0 and SD

216 of 1.

217   The resulting β coefficients represented the increase in the probability of being in a

218 certain color category on the multinomial-logit scale for every one-unit (SD) change in the

219 covariate. We considered a covariate to have a significant effect on molt phenology when the

220 resulting β coefficients' 95% credible intervals (CRIs) did not overlap zero. Because we were not

221 interested in quantification of the effect size per se, but rather on the direction and the relative

222 sizes of the different covariates, we did not convert the coefficients to normal scale. We

223 primarily focused on the covariate effects on probability of the season's final color (i.e., $\beta2_{white}$ in

224 the fall, $\beta2_{brown}$ in the spring) not the initial color or molting color category, in part to simplify

225 the reporting of results. Furthermore, because photoperiod is known to strongly control the

226 hormonal cascade that triggers the molt, we expected the effects of climate to be more apparent

227 in the final rather than the initial stage of the molt (i.e., follicle stimulation and hair growth

228 initiation versus the appearance of the newly grown hairs and shedding of the old hairs; Zimova

229 et al., 2018). Finally, in most cases, the significance or absolute effect size of initial and final

230 color probabilities were similar (all β coefficients shown in Tables S2 and S3).

231 Temporal variation in molt phenology

232 Next, to test the effect of annual variation in temperature and snow season duration, we

233 constructed an alternative set of univariate models. Each model included a single fixed effect of

234 climate covariate $\beta2_i$ on the probability of being in a certain color category to avoid

235 multicollinearity issues (Table S1). The covariates included mean annual tmin, tmax, and

236 duration of snow season in spring and fall at each camera site. The resulting $\beta2_i$ coefficients were

237 the slopes of reaction norms of the climate covariates on probabilities of being brown ($\beta2_{brown}$) or

238 white ($\beta2_{white}$).

239   For all models, we obtained posterior distributions of all parameters along with their 95%

240 CRIs using Markov chain Monte Carlo (MCMC) implemented in JAGS (version 4.0.1), which

241   we called using the R2jags package (Su & Yajima, 2012). Model convergence was assessed

242   using the Gelman–Rubin statistic, where values <1.1 indicated convergence (Gelman & Rubin,

243   1992). We generated three chains of 300,000 iterations after a burn-in of 150,000 iterations and

244   thinned by three. Parameters α_i, $\beta1_i$, and $\beta2_i$ received a vague prior of N(0, 0.001), and the

245   standard deviation of random effect $s_{i,j}$ received uniform prior of U(0, 100).

246   Camouflage mismatch

247   Camouflage mismatch was calculated based on the daily presence or absence of snow and the

248   modeled coat color at each camera site. Snow was present at a camera site when SWE>0, and

249   absent when SWE=0, based on daily gridded 1 x 1 km resolution data (SNODAS, for validation

250   of dataset see Sirén et al., 2018). Next, we defined white hares as when mean $p_{white} \geq 60\%$ and

251   brown hares as $p_{brown} > 60\%$ as these thresholds included mostly white or brown hares,

252   respectively, when compared to observations. The camera days with brown and white hares were

253   calculated using color probabilities from the models that included the best annual climate

254   predictor (effect sizes in Table 3) in order to account for inter-annual variation in phenology.

255   To quantify the annual frequency of camouflage mismatch within each population, we

256   calculated the number of days at all camera sites (camera days) when the color of hares would

257   either match or mismatch against the background color. 'White mismatch' occurred on days

258   when hares were white and snow was absent at the site. 'Brown mismatch' occurred on days

259   when hares were brown and snow was present (Mills et al., 2013). 'Match' occurred on days

260   when hares were white (brown) and snow was present (absent). The proportion of white

261   mismatch occurrence, for example, was calculated as the count of all camera days when hares

262   would experience white mismatch, divided by the total number of camera days (i.e., number of

263   camera sites at each area multiplied by the total number of days in a season). We calculated the

264   mismatch occurrence for two four-month periods when mismatch might occur at all three study

265   areas; February 1- May 31 (spring) and September 1- December 31 (fall). All proportions were

266   multiplied by 100 for interpretation in %.

267   RESULTS

268   Spatial variation in molt phenology

269   Snowshoe hare molt phenology varied across the three study areas (Fig. 1). In the fall,

270   populations in Colorado and Canada initiated fall molts in early October, with some evidence

271   that hares in Canada molted faster (32 days total) than hares in Colorado (42 days; Fig. 1b). The

272   hare population in New England initiated fall molts almost three weeks later and took the longest

273   to complete the molts (46 days). In the spring, hares in New England initiated the white-to-

274   brown molts first, in late March, followed almost two weeks later by populations in Canada and

275   four weeks later by the southernmost population in Colorado. The Colorado population took the

276   shortest to complete the transitions (44 days vs. 48 and 51 days in Canada and New England,

277   respectively) and became brown only 2 and 3 weeks later than the populations in Canada and

278   New England, respectively (Fig. 1b).

279   Variation in molt phenology between populations did not follow the north-south

280   latitudinal gradient as predicted. Among populations, latitude had a significant effect on the

281   spring molt phenology, but the effect was negative; hares at higher (i.e., northern) latitudes

282   became brown earlier than hares in lower latitudes (Table 2). In the fall, latitude had no effect on

283   molt phenology (Table 2). Local climate and elevation were strong predictors of molt phenology

284   and always in the predicted direction in both seasons; earlier fall and later spring molts were

285   associated with sites that are generally colder, snowier and located in higher elevation. Elevation

286   and long-term minimum temperature had the strongest effect on molt phenology in both seasons

287   (Table 2).

288   Temporal variation in molt phenology

289   We found evidence of population-level temperature- and snow-mediated plasticity in molt

290   phenology. All annual temperature and snow covariates affected molt phenology in the predicted

291   direction; molts occurred later in the spring and potentially earlier in the fall during colder and or

292   snowier years (Table 3). In the spring, this annual variation in temperature and snow duration

293   resulted in two- to three-week differences in mean population initiation and completion dates

294   between some years in Canada and New England (Fig. 2). In contrast, we found no significant

295   differences between spring initiation and completion dates in the Colorado population.

296   Furthermore, we did not detect any differences in the fall molt phenology start or end dates in
297   any population (Fig. S3).

298   Camouflage mismatch
299   The occurrence of camouflage mismatch varied between study areas and years (Fig. 3, Table 4,
300   Fig. S1). White mismatch (white hare against snowless background) was relatively infrequent at
301   all sites and occurred only during low snow years in New England and Colorado. Hares in New
302   England experienced the highest frequency of white mismatch during both seasons (Table 4),
303   with the highest proportions of camera days with white mismatch in fall 2015 (15%) and in
304   spring 2016 (9%); seasons with 37-40 fewer snow days than observed during 1980-2009 (Fig. 3).
305   Brown mismatch was rare in the New England population, with the exception of fall 2016, with
306   6% brown mismatch (Fig. S1). Snowshoe hares in Colorado had lower proportions of white
307   mismatch days than in New England but reached 7% in the fall of 2016 with very short snow
308   season (Fig. 3). In the springs, brown mismatch was more common than white mismatch in
309   Colorado (Table 4). In Canada, white mismatch was very rare, exceeding 1% in only 3 out of the
310   9 seasons of monitoring (Fig. 3), but brown mismatch was frequent (Table 4, Fig. S1).

311   DISCUSSION
312   Using by-catch photographs from remote camera traps, we quantified the spatial and temporal
313   variation in snowshoe hare molt phenology and camouflage mismatch across nearly the full
314   range of environmental conditions experienced by the species. To our knowledge, this was the
315   first study to evaluate these processes at such resolution in any seasonally molting species. First,
316   local climate conditions were the main drivers of spatial and temporal variation in molt
317   phenology; hares in colder and snowier sites and in higher elevations molt later in the spring and
318   earlier in the fall. Second, hare populations exhibited temperature- and snow-mediated plasticity
319   in molt phenology; we found strong evidence of later spring- and suggestive evidence of earlier
320   fall-molts during colder and or snowier years. Third, the occurrence of camouflage mismatch
321   varied in space and time, but white mismatch was more common in areas characterized by
322   shallow, short-lasting snowpack. Finally, because areas with shallow snowpack are expected to
323   face the steepest declines in snow cover duration (Lute et al., 2015; Ning & Bradley, 2015), we
324   conclude that hares occupying those southern edge portions of their range are the most
325   vulnerable to camouflage mismatch under current and future climate change.

326 Local climate drives variation in molt phenology

327 Our analysis based on 448 camera sites and spanning over 15 degrees of latitude showed that

328 local climate influenced molt phenology in snowshoe hares (Fig. 1). Mean phenology in both

329 seasons structured strongly along elevational, temperature, and snow cover gradients. Similar

330 findings were described for other phenological traits across taxa (e.g., migration, reproduction,

331 and hibernation) where phenology correlated with local variation in climate (e.g., Fielding et al.,

332 1999; Sheriff et al., 2011; While & Uller, 2014; Duursma et al., 2018). As for seasonal color

333 molt phenology, local climatic factors have been previously described to determine phenology in

334 color molting species including snowshoe hares (Grange, 1932; Zimova et al., 2014), mountain

335 hare (Watson, 1963), stoats (Feder, 1990), and rock ptarmigan (Salomonsen, 1939), although all

336 were examined over relatively small spatial scales or conclusions were based on opportunistic

337 observations and low sample sizes. Likewise, for multiple color molting species, the global

338 distribution of genetically determined winter brown and winter white coat color morphs is driven

339 by variation in snow cover duration (Mills et al., 2018).

340 　　　We found no evidence that molt phenology variation was distributed along a latitudinal

341 (i.e., north-south) gradient. While the effects of climate and elevation were strong in both

342 seasons, the effects of latitude were not detected in the fall and in the opposite direction than

343 expected in the spring (i.e., during the spring molt, the probability of being brown increased with

344 latitude, Table 2). We think that the positive effect of latitude in the spring was driven by spatial

345 variation in climate; the southernmost study area, Colorado, was as cold as the northernmost

346 area. Although our study lacked the spatial coverage to give a definite conclusion on the role of

347 latitude on molt phenology, we showed that latitude alone cannot predict molt phenology across

348 a species range. Future studies that include more replicates across the latitudinal gradient will

349 help elucidate the interacting effects of latitude and local environmental conditions on seasonal

350 molt phenology.

351 Phenotypic plasticity in response to temperature and snow

352 We found that annual temperature and snow affect the molt phenology of snowshoe hares.

353 However, this variation resulted in differences in population molt initiation and completion dates

354 between years only in the spring (Fig. 2). For example, hares in Canada became brown 21 days

355 earlier in spring 2016 which was on average 2.9°C warmer (tmin) with a snow season 22 days

356 shorter than spring 2014 (Fig. 2, Fig. S2). Similar difference was observed between the same two
357 years in New England, where the 2.4°C higher tmin and 21-day shorter snow season in spring
358 2016 than in 2014 corresponded with an 11- and 14-day advances in molt initiation and
359 completion dates, respectively (Fig. 2, Fig. S2). In contrast, we did not detect any differences
360 between the spring molt phenologies in the Colorado population during all years of monitoring
361 (Fig. 2). However, annual temperature and snow season length were less variable in Colorado
362 than in the other two study areas (Fig. S2). For example, the 11-day difference in snow duration
363 and 1.3°C difference in tmin between the two most extreme springs (2011 and 2015) might not
364 have been sufficient to observe significant differences between phenology dates (Fig. 2). To
365 determine whether hares in Colorado have lower phenotypic plasticity or whether this finding
366 was caused by lower inter-annual variation will require analyses of additional years across a
367 wider range of climatic conditions.

368 We found some evidence for population-level phenotypic plasticity in the fall molt
369 phenology (Table 3), but we did not detect significant differences between initiation or
370 completion dates in any study area (Fig. S3). Lower phenological plasticity in the fall than in the
371 spring was previously described in least weasels and connected to lower variation in the fall than
372 in the spring temperatures (Atmeh et al., 2018). In this study, the lower inter-annual variation in
373 climatic conditions might have similarly contributed to the seasonal variation in plasticity in
374 some cases (e.g., low variation in tmax in fall in Canada; Fig S2). However, in most cases, the
375 inter-annual variation in temperature and snow at our study areas was comparable between
376 spring and fall seasons (Fig. S2). For example, snow season duration differed by up to 44 days
377 and tmax by 2.3°C between the most extreme falls in New England (2015 and 2016; Fig. S2), yet
378 we observed no differences between molt phenology dates (Fig. S3). Furthermore, low plasticity
379 in the fall and similar level of phenotypic plasticity in the spring as observed here were
380 previously described for individual snowshoe hares in the Rocky Mountains in Montana (i.e., 2-3
381 weeks in the spring) (Mills et al., 2013; Zimova et al., 2014). However, in this study, the number
382 of independent snowshoe hare color observations was lower during the falls than in the spring at
383 most of the sites (Table 1), which may have resulted in reduced statistical power to detect
384 differences during this season.

385 Finally, we note that the methodology prevented phenology monitoring of the same
386 individuals - and their fates - over multiple years. Therefore, we were unable to investigate to

387 what extent natural selection against camouflage mismatch might have contributed to the
388 observed differences in temporal variation molt phenology. Specifically, during the few very
389 short snow duration years, natural selection might have removed highly mismatched individuals
390 from the population and contributed to the observed shift in the phenological distribution.
391 Quantifying the relative importance of natural selection and individual plasticity on population-
392 level responses in phenology will require intensive field studies with tagged individuals over
393 multiple years.

394 Spatial variation in camouflage mismatch
395 We observed high variation in the number of snow days each year but, overall, snow cover
396 duration has decreased over the last 30 years in all three areas (Fig S4, Harpold et al., 2012; Ning
397 & Bradley, 2015; Kunkel et al., 2016; Fassnacht et al., 2018; Mote et al., 2018). The declines in
398 snow cover manifested differently in each population, however. In the Canadian population,
399 white mismatch was very low each year, while the number of snow days ranged from 1 to 28
400 fewer days than observed on average during 1980-2009 (Fig. 3). This is likely due to the very
401 deep, long-lasting snowpack in the study area (Table 1, Fig. 4). For example, during the years of
402 monitoring, spring snow season ended on average on June 9 (Fig. 4), more than two weeks after
403 hares finished their white-to-brown molts (i.e., molts initiated on April 5 and completed on May
404 23; Fig. 1b). Yet, annual snow season duration in the Canadian Rockies is predicted to decrease
405 by about one month by the end of the century (Pomeroy et al., 2015). Those predictions would
406 advance average snowmelt to about two weeks prior to when hares become fully brown.
407 Although increase in white camouflage mismatch will likely occur in very short snow years,
408 based on our results a mean decrease of snow season by one month will unlikely lead to dramatic
409 increases in the frequency of white hares on snowless background (see Fig. 3).
410   In contrast, hares in Colorado and New England are much more vulnerable to white
411 camouflage mismatch. For both populations, the proportion of white mismatch increased rapidly
412 with fewer snow days, especially once the snow days anomaly exceeded 21 days (Fig. 3).
413 Beyond this three-week threshold, hares began to experience elevated white mismatch (i.e., 15%
414 in fall and 9% in spring in New England; 7% in fall in Colorado). This suggests that phenotypic
415 plasticity in molt phenology is insufficient to buffer against the snow declines in those marginal
416 areas where snow season is already short (Table 1, Fig. 4). To contrast the New England study

417 area with the previous example from Canada, the continuous snow season ended on average on

418 April 18 (Fig. 4) but hares underwent spring molts from March 23 to May 13 (Fig. 1b).

419 Therefore, with mean snowmelt occurring before hares are halfway through the molt, early snow

420 melt years (e.g., 2016 seasonal snow melted on April 1; Fig. S2) result in steep increases in white

421 mismatch.

422   Based on our results, in the absence of evolutionary shift in phenology, snowshoe hares

423 in New England and Colorado will suffer drastic increases in white mismatch over the next

424 century. In the Colorado study area, the frequency of low snow years is expected to increase and

425 the annual snow season to decrease by 20-50 days (for comparison see mismatch in fall 2016,

426 Fig. 3) by mid-century (Lute et al., 2015). Similarly, in many parts of New England, snow cover

427 duration is predicted to shorten from the current five months to three months by 2100 (Ning &

428 Bradley, 2015). Under such projections, hare in both study areas will by the end of the century

429 routinely experience the same amount of mismatch as they experienced during the very low

430 snow years of fall 2016 in Colorado and 2015 in New England.

431   The pattern observed with white mismatch was somewhat mirrored by that of brown

432 mismatch. In both seasons in New England and during the fall in Colorado, white mismatch was

433 more frequent than brown mismatch as snow cover was more likely to be absent when hares

434 were white than vice versa (Fig. 4). In contrast, during springs in Canada and Colorado, hares

435 experienced long periods when they had already molted to summer brown pelage, but snow was

436 still present on the ground (Fig. 4). Furthermore, the onset of snow during fall often occurred

437 prior to hares completing their brown-to-white molts in Canada. Overall, the relatively high

438 occurrence of brown camouflage mismatch, despite the recorded snow declines, was unexpected.

439 Eventually, however, as climate change will continue to lead to shorter snow duration across

440 most of the snowshoe hare range (Danco et al., 2016; Easterling et al., 2017; Fyfe et al., 2017),

441 the occurrence of brown mismatch will decrease.

442   The relative fitness costs of white versus brown mismatch are unknown, but we suspect

443 that white mismatch has a higher survival cost than brown mismatch based on our experience in

444 the field while locating radio-collared hares. First, brown animals and objects (e.g., branches,

445 tree trunks, brown animals) are relatively common year-round, but white animals and objects are

446 rare outside of winter. Perhaps due in part to this frequency difference in the two mismatch

447 types, a white hare against a snowless background appears far more conspicuous than a brown

448   hare resting on snow. Previous quantifications of survival costs were carried out for 'absolute

449   mismatch', that is both white and brown mismatch combined (Zimova et al., 2016; Wilson et al.,

450   2018). Nonetheless, as documented here and elsewhere (Zimova et al., 2016; Wilson et al.,

451   2018), white mismatch is already high in some populations and will increase under climate

452   change (Mills et al., 2013). Therefore, fitness costs of white and brown mismatch should be

453   quantified to inform conservation efforts, notably in situ management actions that foster

454   evolutionary rescue, or genetic rescue by assisted gene flow of individuals with preadapted molt

455   phenologies or winter coat color (Mills et al. 2018).

456   Understanding the spatial and temporal variation in phenological traits is critical for

457   understanding the impact of climate change and species' adaptive potential to environmental

458   stressors. Here, we showed that snowshoe hare molt phenology is determined by local climate,

459   but populations vary in their susceptibility to camouflage mismatch. Snowshoe hares responded

460   to annual variation in temperature and snow via some adjustments in molt phenology, but the

461   buffering effects of phenotypic plasticity were diminished in populations distributed along the

462   southern edge of their range. In those areas, characterized by mild climate and shallow, short-

463   lived snowpack, climate change mediated snow declines led to higher phenological mismatch.

464   Therefore, hares occupying southern, marginal areas will in the absence of rapid evolution

465   experience steep increases in camouflage mismatch, as those areas are expected to experience the

466   largest declines in snow cover duration (Ning & Bradley, 2015; Fyfe et al., 2017), consistent

467   with theoretical expectations of range contraction (Sirén & Morelli, 2019). More generally, our

468   results underscore that populations vary in their susceptibility to environmental stressors and

469   management efforts should consider this intra-specific variation to identify populations most

470   vulnerable under global environmental change (Hampe & Petit, 2005; Nadeau et al., 2017).

471

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642   DATA ACCESSIBILITY STATEMENT
643   The data used in this study are available from the corresponding author upon request.
644

645   SUPPORTING INFORMATION
646   Additional supporting information may be found online in the Supporting Information section at
647   the end of the article.

648 TABLES

649 **Table 1.** Geospatial and long-term climate details regarding the camera trap networks in the study areas. Number of camera sites and

650 independent coat color observations are given for each season and area. Other metrics include mean values across all camera sites

651 within a study area with standard deviation in parentheses. Long-term mean minimum (tmin) and maximum (tmax) temperature and

652 snow season duration are based on 1980-2009 period.

Study Area	Latitude (degrees)	Elevation (m)	Fall					Spring				
			Camera sites (n)	Obs. (n)	tmin (°C)	tmax (°C)	Snow season (days)	Camera sites (n)	Obs. (n)	tmin (°C)	tmax (°C)	Snow season (days)
Canada	51.38 (0.33)	1850.98 (266.20)	98	967	-5.41 (1.33)	5.22 (1.86)	93.08 (10.93)	91	921	-6.62 (1.68)	5.17 (2.33)	168.69 (18.18)
Colorado	37.63 (0.30)	3200.79 (215.46)	110	322	-4.68 (1.09)	9.70 (1.78)	72.83 (6.91)	183	1,705	-7.24 (1.28)	8.03 (1.71)	155.70 (11.07)
New England	44.54 (0.51)	627.18 (284.59)	65	486	0.25 (0.89)	10.61 (1.63)	52.07 (7.30)	105	1,122	-3.44 (0.93)	8.35 (1.84)	125.01 (12.49)

653

654 **Table 2.** Effect of latitude, elevation and long-term climate covariates on snowshoe hare molt

655 phenology. Mean effect sizes and 95% credible interval (CRI) estimates for slopes for univariate

656 models including data from all years and populations combined. Betas indicate effects of

657 covariates on the probability of the molt's final color category ($\beta2_{brown}$ in the spring, $\beta2_{white}$ in the

658 fall). Snow is the duration of continuous snow season (days), tmax and tmin are the mean

659 minimum and maximum temperature (°C) in springs and falls during 1980-2009. Asterisks

660 indicate CRIs not overlapping 0. Values reflect standardized data.

Covariate	Fall $\beta2_{white}$	Spring $\beta2_{brown}$
Latitude	0.566 (-0.136, 1.293)	0.689* (0.376, 1.012)
Elevation	2.165* (1.450, 3.033)	-1.325* (-1.631, -1.039)
Snow	0.446 (-0.214, 1.123)	-0.809* (-1.143, -0.492)
tmax	-1.855* (-2.479, -1.288)	0.776* (0.440, 1.123)
tmin	-2.370* (-2.894, -1.909)	1.280* (0.998, 1.579)

661

662

663 **Table 3**: Effect of annual temperature and snow season duration on molt phenology in snowshoe

664 hares. Betas are the slopes of reaction norms β2 (=mean effect size of annual climate covariate)

665 and their 95% credible intervals (CRI) on the probability of the molt's final color category.

666 Asterisks indicate CRIs not overlapping zero. Values reflect standardized data.

Covariate	Fall $\beta 2_{white}$	Spring $\beta 2_{brown}$
Snow annual	1.466*	-1.627*
	(1.009, 1.929)	(-1.969, -1.303)
tmax annual	-2.070*	1.587*
	(-2.850, -1.432)	(1.208, 2.003)
tmin annual	-2.344*	1.273*
	(-2.943 -1.845)	(0.921, 1.655)

667

668 **Table 4.** Modeled mean percent of camera days with white and brown mismatch at each study

669 area. Mean percent were calculated based on annual estimates (Canada: 6 falls and 5 springs,

670 Colorado and New England: 4 springs and 4 falls). Standard deviations are given in parentheses.

	Canada		Colorado		New England	
	white	brown	white	brown	white	brown
spring	0.56 (0.55)	11.96 (4.31)	1.74 (1.34)	6.39 (0.68)	2.41 (4.36)	0.98 (0.73)
fall	0.55 (0.47)	9.54 (3.60)	2.69 (2.80)	1.11 (0.66)	4.72 (7.00)	2.42 (2.68)

Figure 1. Camera site locations and snowshoe hare molt phenologies and molt dates in the Canada, Colorado and New England study areas. (a) snowshoe hare range (IUCN) is colored and shaded by the mean annual number of snow days (Dietz et al. 2015). Colored points represent the 448 remote-camera trap sites. (b) bold lines depict predicted probabilities of being in the final color category (white in the fall, brown in the spring) over time. The dashed lines show 95% credible intervals. The horizontal dashed lines at 0.90 intersect with population means to identify molt completion dates. Population mean molt initiation and completion dates are depicted as a date range in the bottom right corners, with the completion dates in bold. The predicted probabilities and dates were estimated for each season and population based on the model without covariates.
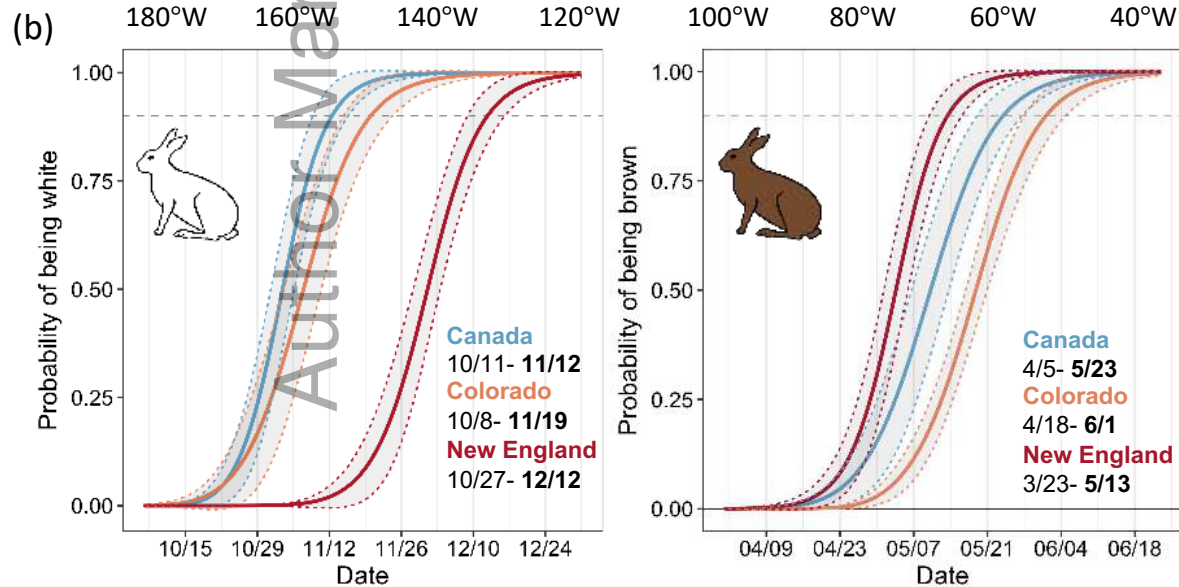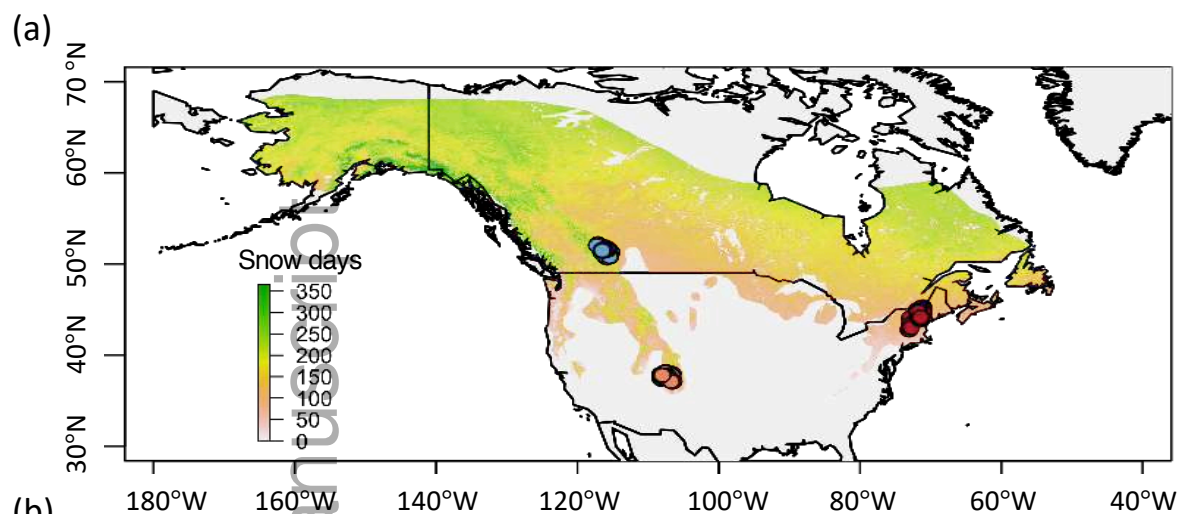
Figure 2. Estimated annual spring molt initiation ('i') and completion ('c') dates in the studied hare populations in Canada, Colorado and New England. Points show mean date estimates and are colored by the annual duration of spring snow season (in days). Horizontal lines show 95% credible intervals (overlapping CRIs identify same dates).
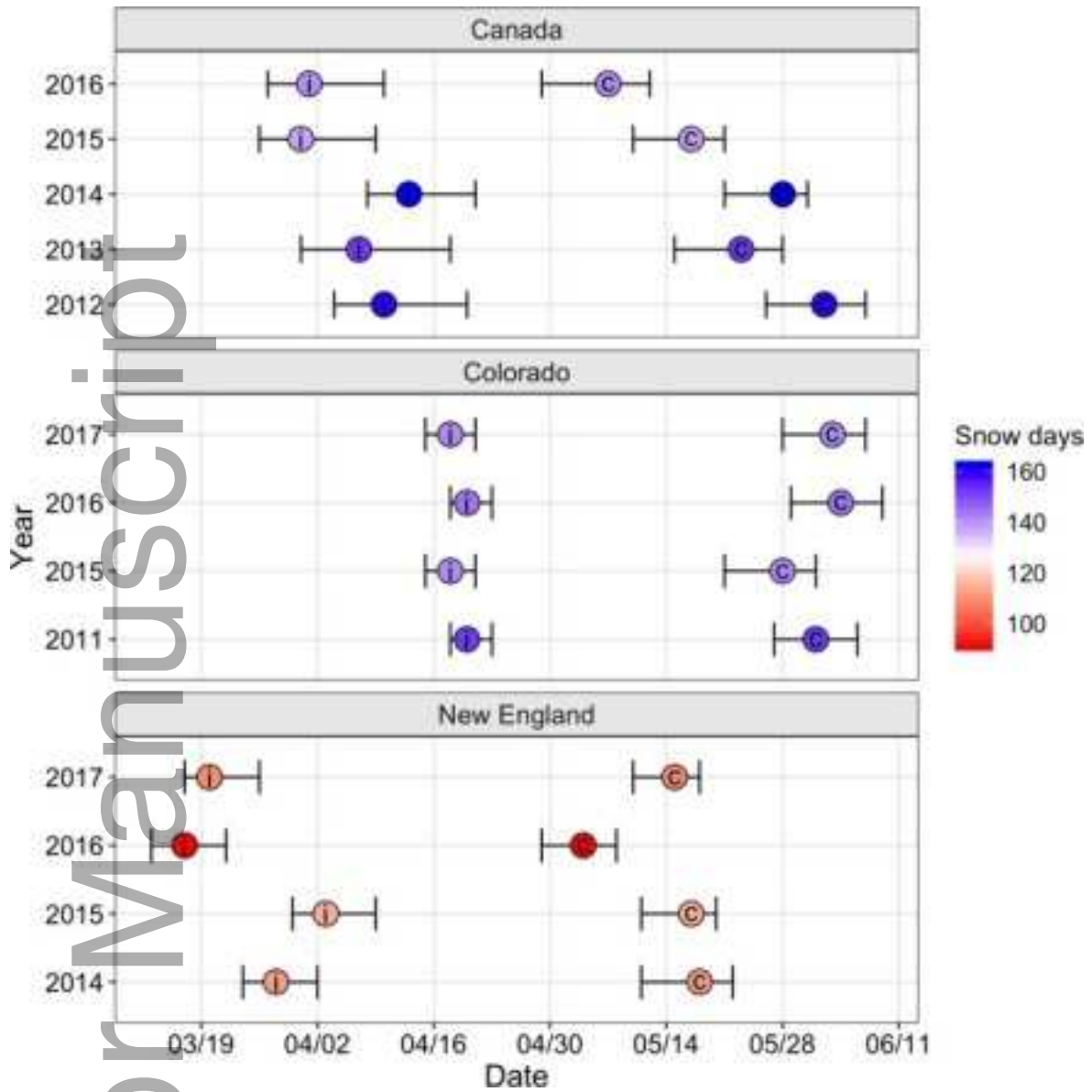
Figure 3. Annual proportions of camera days with white mismatch occurrences plotted against anomalies in the number of snow days each season in Canada, Colorado and New England. Study area-specific anomaly in the number of snow days was calculated for each year as the difference between the mean number of snow days during each season and the mean number of snow days during 1980-2009 at all camera sites. Photo depicts white mismatched hare.

Figure 4. Mean daily snow water equivalent (SWE; mm) at the remote camera sites for the years of molt phenology monitoring. Colored circles along the x axes indicate the population mean molt completion dates for each year, with spring molts on the left and fall molts on the right. Mean number of snow days for years of monitoring is given in facet titles for spring and fall.

(a)

Snow days

350
300
250
200
150
100
50
0

(b)

Probability of being white

Canada
10/11- **11/12**
Colorado
10/8- **11/19**
New England
10/27- **12/12**

Probability of being brown

Canada
4/5- **5/23**
Colorado
4/18- **6/1**
New England
3/23- **5/13**

Date

geb_13049_f2.tiff

Proportion white mismatch (%) vs. Snow days anomaly. Panels: Fall and Spring. Legend: Canada, Colorado, New England. Labels: 2015, 2016. Author Manuscript.