

1 Title: Coat color mismatch improves survival of a keystone boreal herbivore: energetic
2 advantages exceed lost camouflage

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27 Open Research Statement:

28 Data will be permanently archived following acceptance in the digital repository Figshare and
29 code will be available in the code repository Github.

30 Running head: Coat color mismatch in snowshoe hares

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33 **Abstract**

34 Climate warming is causing asynchronies between animal phenology and environments.

35 Mismatched traits, like coat color change mismatched with snow, can decrease survival.

36 However, coat change does not serve a singular adaptive benefit of camouflage, and alternate

37 coat change functions may confer advantages that supersede mismatch costs. We found that

38 mismatch reduced rather than increased, autumn mortality risk of snowshoe hares in Yukon by

39 86.5 %. We suggest that the increased coat insulation and lower metabolic rates of winter

40 acclimatized hares confer energetic advantages to white mismatched hares that reduce their

41 mortality risk. We found that white mismatched hares forage 17-77 minutes less per day than

42 matched brown hares between 0 and -10 °C, thus lowering their predation risk and increasing

43 survival. We found no effect of mismatch on spring mortality risk, where mismatch occurred at

44 warmer temperatures, suggesting a potential temperature limit where the costs of

45 conspicuousness outweigh energetic benefits.

46

47 Keywords: camouflage, thermoregulation, phenological mismatch, coat color, snowshoe hare,

48 foraging, energetic expenditure, survival, accelerometer, *Lepus americanus*

49

50 **Introduction**

51 Phenological mismatch is one of the most documented pathways by which climate change
52 negatively impacts species (Radchuk et al. 2019, Visser and Gienapp 2019). Earlier onset of
53 spring and delayed onset of winter have the potential to cause incongruous timing of seasonal
54 phenotypes (Møller et al. 2008, Lehikoinen 2011, Kudo and Ida 2013). Mismatch occurs in the
55 timing of numerous seasonal traits such as calving date with plant growth onset, and laying date
56 with peak of key food sources, and has resulted in reduced reproductive success and recruitment
57 (Post and Forchhammer 2008, Reed et al. 2013). However, the costs associated with
58 phenological mismatches vary within species across populations (Heard et al. 2012, Doi et al.
59 2017). Species are often adapted to broad ranges of ecological conditions, particularly those with
60 large geographic distributions (Valladares et al. 2014). Local adaptations and variable selection
61 pressures across environmental gradients alter the magnitude of phenological mismatch across
62 populations (Phillimore et al. 2010, Gordo and Doi 2012, Porkert et al. 2014). Such spatial
63 variability in phenology across ecological conditions may also involve differences in the
64 mechanistic pathways governing the demographic costs and benefits associated with
65 phenological mismatch across species ranges.

66 An example of phenological mismatch that occurs in species across multiple taxa is coat and
67 plumage color change mismatched with snow onset and melt (Zimova et al. 2016, Pedersen et al.
68 2017, Atmeh et al. 2018, Melin et al. 2020). At least 21 bird and mammal species in the Northern
69 Hemisphere change color biannually and improved camouflage is considered the primary
70 function of this change (Mills et al. 2018, Zimova et al. 2018) As snow cover duration is
71 forecasted to decrease across the Northern Hemisphere (Danco et al. 2016), coat and plumage
72 color mismatch is likely to increase. Mismatch may reduce survival due to decreased camouflage

73 (Atmeh et al., 2018; Zimova et al., 2016; Melin et al., 2020). However, aside from color change,
74 high-latitude species benefit from other winter acclimatization strategies meant to increase cold
75 tolerance and endure periods of food shortage, including increasing insulation, decreasing lower
76 critical temperature, altering activity patterns, and, ultimately reducing daily energy requirements
77 (Humphries et al. 2005, Fuglestad et al. 2006, Sheriff et al. 2009b). Accordingly, coat color
78 transitions coincide with multi-trait change that differentiates long photoperiod, i.e., summer,
79 from short photoperiod, i.e., winter, phenotypes (Lovegrove 2005, Boratyński et al. 2016). As
80 such, the thermal and energetic benefits provided by a more insulative, white coat and associated
81 metabolic and thermoregulatory adaptations may outweigh the negative costs of color mismatch
82 in colder conditions.

83 The snowshoe hare (*Lepus americanus*) is a keystone species distributed across the boreal
84 forests of North America (Krebs et al. 1995) that undergoes seasonal coat color change to match
85 the presence of snow (Ferreira et al. 2017). The initiation of coat color change in snowshoe hares
86 is likely affected by photoperiod (Nagorsen 1983) and in the absence of evolutionary change, is
87 predicted to become increasingly mismatched with anticipated reductions in snow cover duration
88 (Brown and Mote 2009, Mills et al. 2013). Coat color mismatch may impact snowshoe hare
89 demography, as recent studies have reported high mortality rates in mismatched snowshoe hares
90 at multiple locations in the southern extent of their range, presumably due to increased
91 conspicuousness to predators (Zimova et al., 2014; Wilson et al., 2018). However, the thermal
92 benefits of winter acclimatization in hares, including reduced metabolic rate (Sheriff et al.
93 2009a), may also affect susceptibility to predation and ultimately survival.

94 White winter-acclimatized snowshoe hares benefit from lower energetic demands compared
95 to brown summer-acclimatized hares. Indeed, while temperatures below 0 °C increase energetic

96 requirements for summer hares, white winter hares remain in their thermoneutral zone until
97 temperatures below -10 °C (Sheriff et al. 2009a). As such, lower energetic demands reduce
98 foraging requirements for winter-acclimatized hares (Balluffi-Fry *et al.*, In Review). Balancing
99 the trade-off between obtaining sufficient food to meet energetic requirements and avoiding
100 predators is a central assumption of prey behavior theory (McNamara and Houston 1987, Lima
101 and Dill 1990). Therefore, white mismatched hares may benefit from lower energetic
102 requirements, reduced foraging time, and thus reduced predator exposure. These benefits could
103 compensate for the adverse effects of conspicuousness, particularly when seasonal temperatures
104 remain low and the energetic demands for brown summer acclimatized hares are elevated
105 (Balluffi-Fry *et al.*, In Review). Geographic variation in winter adaptations and acclimatization
106 exists across the broad geographic range of the snowshoe hare (Sheriff et al. 2009b, Gigliotti et
107 al. 2017). As such, the effects of coat color mismatch may vary across populations according to
108 the relative importance of the reduced camouflage cost relative to energy conservation benefits
109 in different ecological contexts.

110 Here, we test the hypothesis that reduced foraging requirements with winter acclimatization
111 reduces the costs of coat color mismatch in snowshoe hares. To examine this, we monitored the
112 survival, coat color, and foraging time of individuals over the autumn and spring in southwest
113 Yukon, Canada. First, we predict that mismatched white hares will spend less time foraging than
114 matched brown individuals, particularly below the thermoneutral zone of summer brown hares
115 (i.e. 0 °C; Sheriff *et al.* 2009a). If this foraging difference and thus reduced time spent vulnerable
116 to predation outweighs the costs of conspicuousness, we further predict no difference in survival
117 between matched and mismatched individuals. However, if camouflage loss is the primary driver
118 of predation risk during coat color change, regardless of foraging differences, we expect that

119 mismatched hares are more likely to be predated than camouflaged individuals, echoing results
120 from previous studies in the southern extent of their range (Zimova et al. 2016, Wilson et al.
121 2018). We found that white mismatched snowshoe hares experiencing cold temperatures in
122 snowless environments benefitted from reduced foraging time and thus increased survival
123 relative to brown matched hares.

124 **Methods**

125 Study area

126 We studied snowshoe hares for three autumns (September 1st to December 1st of 2015, 2016, and
127 2017) and four springs (March 1st to May 31st of 2015, 2016, 2017, and 2018) in southwestern
128 Yukon, Canada (Lat: 60.9 N, Long: -138.0 W). Snowshoe hares have been monitored for over 40
129 years in this region (Krebs et al., 2018). Our study area consists predominantly of white spruce
130 (*Picea glauca*), trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus*
131 *balsamifera*). Gray willow (*Salix glauca*) and dwarf birch (*Betula glandulosa*) dominate the
132 understory. The main predators of snowshoe hares in this region include Canada lynx (*Lynx*
133 *canadensis*), coyotes (*Canis latrans*), goshawks (*Accipiter gentilis*), and great horned owls (*Bubo*
134 *virginianus*) (Peers et al. 2020). Snowshoe hares went through the increase, peak, and early
135 decline phase of their population cycle during our study period (Krebs et al. 2018).

136 Field methods

137 The study area was divided into three 35-ha snowshoe hare trapping areas, located within ~ 8 km
138 of each other (Peers et al. 2020). We captured snowshoe hares using Tomahawk live-traps
139 (Tomahawk Live Trap Co. Tomahawk, WI, USA) baited with alfalfa and rabbit chow. Traps
140 were set 30 minutes before sunset and checked either three hours after sunset or at sunrise. We

141 attached a numbered ear tag to each hare to identify individuals on subsequent recaptures, and
142 we assessed coat-color during each capture. To evaluate coat color, we examined hares from the
143 front and sides and visually estimated their percentage white coat to the nearest 5%. We later
144 binned coat color in 10% white categories for analyses to account for inter- and intra- observer
145 ranking variability. We consider 10% bins as reasonably precise given that intra- and inter-
146 observer intraclass correlation coefficients (ICC) for coat color assessment were high (ICC>0.9
147 in all cases, See Appendix S1: Table S1). To monitor survival, we fit hares weighing > 1100g
148 (n=347) with very high frequency (VHF) collars that were each equipped with a mortality sensor
149 (Model SOM2380, Wildlife Materials Inc., USA, or Model MI-2M, Holohil, Canada, both < 27
150 ± 1 g). We performed mortality checks of VHF collared hares almost daily, i.e., 96.3% of checks
151 occurred within 1 to 3 days. To monitor behavior, we also fit a subset (n =102) of VHF collared
152 hares with an accelerometer (model Axy3, 4 g, Technosmart, Rome, Italy). Accelerometers
153 measure force variation on three different axes and are increasingly being used to infer behavior
154 in free-ranging animals (Mikkelsen et al. 2019, Studd et al. 2019). Fully equipped collars with
155 both VHF and accelerometers had a total weight below 2.5% of each individual's body mass.
156 Handling and collaring procedures were approved by the University of Alberta Animal Care and
157 Use Committee (Protocol: AUP00001973).

158 We measured snow depth, snow cover, and temperature throughout our study period. We
159 measured snow depth on >60% of days at three locations per trapping area, in relatively open
160 forest, to the nearest 0.5 cm. Days with missing snow depth records were linearly interpolated
161 using the “zoo” function in the zoo package in R (Zeileis et al. 2021). We measured snow cover
162 by visually assessing daily landscape photographs from three camera traps installed on each
163 trapping area. We calculated a combined average daily snow cover value to the nearest 10% in

164 our study region. We converted % snow cover to a binary type variable above or below 60%
165 snow cover (presence/absence) for the autumn seasons, as there were very few instances when
166 snow cover estimates were between 0% and 100%. We measured temperature at least six times a
167 day on each trapping area using a minimum of 2 temperature loggers (ibutton, DS1922L, Maxim
168 Integrated, Whitewater, USA) to obtain a single average daily temperature value for each
169 trapping area.

170 Measuring coat color mismatch

171 Coat color mismatch was defined as the difference between hare percent white (10% bins) and
172 the daily percent snow cover (10% bins for both autumn and spring). For all analyses, we treated
173 mismatch as a binary variable, defining mismatch as greater than 50% difference between hare
174 % white and snow cover (%). As such, mismatched hares were white (> 50 % white) individuals
175 in a snowless (< 50% snow cover) environment. Considering that brown mismatched hares in a
176 snowy environment were rare (1% of trapping records), we did not consider this type of
177 mismatch in analyses. Although the threshold for mismatch used in some previous studies is
178 60% contrast (Mills et al. 2013, Wilson et al. 2018), mismatch at this contrast threshold was rare
179 in our study region, i.e., in 11% of trapping records, so we used 50% as our mismatch threshold
180 to increase our sample size. That being said, analyses using 40% or 60% thresholds for mismatch
181 revealed similar results (Appendix S1: Tables S5, S6, S9, S10).

182 Effect of coat color mismatch on survival

183 To evaluate the effect of coat color mismatch on snowshoe hare survival, we generated Cox's
184 proportional hazards (CPH) models (Cox and Oakes 1984) with the "coxph" function in the
185 survival package in R (Therneau et al. 2021). The CPH model is a semi-parametric approach

186 used to analyze binary response data, in our case: alive or dead (Sievert and Keith 1985). We
187 monitored 347 hares and recorded 41 deaths over four springs and 34 deaths over three autumns.
188 We excluded mortality checks that exceeded seven days to limit the uncertainty in the timing of
189 death events (Murray and Bastille-Rousseau 2020). We censored 15 individuals whose collars
190 were removed before the end of the study period and six individuals with permanently missing
191 VHF signals. We pooled data from different years, trapping areas, and sex, as exploratory
192 analysis indicated that none of those variables had a significant effect on autumn or spring
193 mortality risk (Appendix S1: Table S2). Considering that coat color was assessed only during
194 capture opportunities (on average every $13.1 \pm \text{SD: } 10.8$ days per individual), we assigned coat
195 color for each record in our survival analysis as the nearest coat color assessment completed in
196 the field (average difference of $4.95 \pm \text{SD: } 3.70$ days between telemetry check and coat-color
197 assessment). We removed telemetry records where a coat color assessment within 14 days did
198 not exist to ensure that coat color and derived mismatch values were an accurate representation
199 of each individual at the time of the telemetry check. Results from models using survival records
200 within 8 days of a coat-color assessment were qualitatively similar to those we obtained with our
201 chosen 14-day threshold (Appendix S1: Table S3).

202 We generated three competing CPH models for both autumn and spring. The first model
203 included snow cover and snow depth, based on prior evidence of snow effects on hare survival
204 (Meslow and Keith 1971, Peers et al. 2020). Our second model included those same snow
205 variables in addition to coat color mismatch, our variable of interest. The third model was the
206 null (intercept-only) model. We used Akaike Information Criterion for our model selection
207 (Akaike 1974) and identified our top model based on AIC_c (Burnham and Anderson 2002) with
208 the package `AICcmodavg` (Mazerolle 2019). We assessed multicollinearity in our top model

209 using the variance inflation factor (VIF) and ensured no variables had VIF's greater than 2. The
210 proportionality assumption of CPH models, which implies that the hazard ratio (HR; i.e., risk of
211 death) is assumed to be constant over time (Joshua Chen and Liu 2006), was met for our top
212 spring and autumn CPH model. Our results were not affected by informative censoring, as we
213 found qualitatively similar results for both spring and autumn model coefficients when we
214 treated censored individuals as deaths (Murray and Bastille-Rousseau 2020) (Appendix S1:
215 Table S4).

216 Effect of coat color mismatch on time spent foraging

217 To test our proposed mechanistic pathway, whereby white mismatched hares experience
218 reduced energetic requirements leading to reduced foraging time (Balluffi-Fry *et al.* In Review;
219 Sheriff *et al.* 2009a), we used linear mixed-effects models using the “lmer” function in the
220 package lme4 (Bates et al. 2015). Daily time spent foraging (minutes) was derived from tri-axial
221 accelerometer data using behavioral classifications previously developed in this hare population
222 (see Studd et al., 2019 for more information on classification methods). Daily time spent
223 foraging was classified over 4 second intervals at a 96% accuracy (Studd et al. 2019). We
224 recorded 1505 daily foraging records from 66 hares over the three autumns and 838 daily
225 foraging records from 44 hares over the four springs. Similar to our survival analysis, we only
226 kept foraging records that were within 14 days of a coat-color assessment (average difference of
227 4.48 ± 3.51 (SD) days). We reran our top foraging time models with data restricted to daily
228 foraging records that were within 8 days of a coat-color assessments instead to ensure that our
229 results were not affected by this 14-day threshold, and obtained qualitatively similar results
230 (Appendix S1: Table S8). To eliminate the potential of seasonal changes in foraging impacting
231 our results (Griffin et al. 2005), we restricted our data to only the autumn and spring periods

232 when snow cover was $\leq 50\%$, i.e., mismatch was possible given our chosen threshold and
233 therefore both matched and mismatched individuals occurred simultaneously.

234 We generated four linear mixed-effects models per season to test for differences in daily
235 minutes spent foraging (our response for all models) between matched brown hares and
236 mismatched white hares and their responses to changes in temperature. We included a random
237 effect for individual ID in all models to control for non-independence of data. We included sex
238 as a fixed factor in all spring models only, as exploratory data analysis indicated that sex had a
239 significant effect on time spent foraging for spring but not autumn (Appendix S1: Table S7).
240 Furthermore, we included year as a fixed effect in each model to account for potential effects of
241 yearly changes in predation risk on hare foraging behavior (Shiratsuru et al. 2021). Our first
242 model included two fixed effects, temperature and year. Our second model included temperature,
243 year, and coat color mismatch, and our third model included the same variables as the second in
244 addition to an interaction between mismatch and temperature. Our fourth model was a null
245 intercept-only model. We checked model fit using marginal and conditional R- squared
246 calculated using the “r.squaredGLMM” function in the package MuMIn (Barton 2020),
247 according to Nakagawa *et al.* 2017. We used Akaike Information Criterion (Akaike 1974) to
248 rank our four competing models and identified our top model in each season based on AIC_c
249 (Burnham and Anderson 2002). We completed all statistical analyses in R version 3.6.2 (2019) (R
250 Core Team, 2019). We considered results where $P \leq 0.05$ as significant and reported all means
251 with ± 1 standard error.

252 **Results**

253 Permanent snow cover date, i.e., 100% snow cover without melting until the spring, was variable
254 across our autumn seasons, occurring almost 3 weeks later in 2015 (November 3rd) than in 2016
255 (October 16th) and 2017 (October 17th). Completion of snowmelt date, i.e., no more snow on
256 ground, was similar across study years (May 6th, 2015, May 1st 2016, May 2nd 2017 and May 1st
257 2018). When considering both seasons and all years together, the prevalence of coat color
258 mismatched hares that contrasted with their snowless environment was low (14% of trapping
259 records) in our population. Mismatch occurred more frequently in the autumn (19% of trapping
260 records) than the spring (8% of trapping records). The autumn with the latest permanent snow
261 cover arrival date, i.e., 2015, had the highest prevalence of mismatch (33% of records).
262 Prevalence of mismatch in the autumns of 2016 and 2017 were 10% and 13% of trapping
263 records, respectively. Spring mismatch was consistent across years around 10% (2015-9% of
264 trapping records, 2016-10%, 2018-12%), with the exception of 2017 when only 1% of trapped
265 hares were mismatched.

266 Effect of coat color mismatch on mortality

267 The CPH model with the strongest support in both seasons included snow depth, snow cover and
268 mismatch (Appendix S1: Table S11, S12 & S13). However, the second highest ranking CPH
269 model for spring, i.e., the model including only snow variables, was within 2 Δ AICc (AICc =
270 0.09) from our top spring CPH model (Appendix S1: Table S11). Mortality risk for mismatched
271 hares in autumn was significantly reduced ($z = -2.43$; $P = 0.02$) relative to matched hares (Hazard
272 Ratio (HR) = 0.135; 95% Confidence Intervals (CI): 0.027, 0.679; Fig. 1a). In contrast, coat color
273 mismatch was positively correlated with mortality risk for hares in the spring (Fig. 1b), but this
274 effect was non-significant ($z = 1.60$; $P = 0.11$). Models were qualitatively similar regardless of our
275 classification of mismatch, except when considering mismatch as a minimum 40% contrast

276 between coat color and snow cover; in this case mismatch significantly increased mortality risk
277 in the spring (HR= 6.780; 95% CI: 2.390, 19.240; $z= 3.60$; $P<0.001$). Snow depth ($z= -2.29$; $P=$
278 0.02) and snow cover ($z= 2.98$; $P=0.003$) significantly affected mortality risk in the top spring
279 model, but not in the top autumn model. In spring, the risk of dying decreased as snow depth
280 increased (HR=0.95; 95% CI: 0.92, 0.993; Appendix S1: Fig S1a) and mortality risk increased as
281 snow cover increased (HR=1.046; 95% CI: 1.01, 1.08; Appendix S1: Fig S1b).

282 Effect of coat color mismatch on foraging time

283 Across our study years, hares foraged on average 706 ± 2.29 minutes per day in the spring and
284 751 ± 1.65 minutes per day in the autumn. Coat color mismatch was an important predictor of
285 daily foraging time in the autumn, but not the spring (Appendix S1: Table S14 and S15). The top
286 model for autumn foraging time included coat color mismatch, temperature, year, and the
287 interaction between temperature and mismatch (Table 1). As autumn temperature decreased,
288 mismatched hares decreased daily foraging time, whereas matched hares increased foraging time
289 (Fig. 2a; Table 1). For instance, when the temperature was $-8\text{ }^{\circ}\text{C}$, brown-matched hares foraged
290 65 minutes more per day than white-mismatched hares (Fig. 2a). The top model for spring
291 included temperature, year, and sex (Table 1). When coat color mismatch was included in our
292 spring foraging models, its effect on daily foraging time was non-significant ($t = -0.759$, $P > 0.05$).

293 Discussion

294 Phenotypes and climate change can vary widely within a species' distribution, as can
295 phenological mismatch and its consequences on survival. Elucidating potential unifying
296 mechanisms is crucial to reconcile varied responses to phenological mismatch. We evaluated the
297 effect of coat color mismatch on snowshoe hare survival in a northern population and further

298 tested a potential mechanism that may influence this effect. We hypothesized that the thermal
299 and energetic benefits of winter acclimatization in white hares, i.e., increased coat insulation and
300 reduced metabolic rate (Sheriff et al. 2009a, Gigliotti et al. 2017), ultimately reduce their
301 foraging requirements (Balluffi-Fry *et al.* In Review) and thus predation risk, which may
302 influence the costs of coat color mismatch. Surprisingly, we found that mismatched hares had a
303 higher survival than matched hares in the autumn (Fig. 1a) but that survival did not differ
304 between matched and mismatched hares in the spring (Fig. 1b). Although this result contradicts
305 previous studies that link coat color mismatch in snowshoe hares to reduced survival (Zimova et
306 al. 2016, Wilson et al. 2018), our proposed mechanism for why this might be the case is
307 supported. Mismatched white hares spent significantly less time foraging than matched
308 individuals in the autumn (Fig. 2a), presumably due to the thermal and energetic benefits of
309 winter acclimatization. Indeed, reduced foraging time likely decreases exposure to predators and
310 subsequently improves survival (Fig 1a). We reconcile our findings with those of previous
311 studies with a unifying factor: temperature.

312 Matched hares foraged longer than mismatched white individuals in the autumn, and this
313 difference was pronounced at lower ($< -3^{\circ}\text{C}$) temperatures (Fig. 1a). Given the wide range of
314 ecological contexts, selection pressures, and local adaptations that exist across the distribution of
315 snowshoe hares (Gigliotti et al. 2017), the cost-benefit ratio of lost camouflage versus energy
316 conservation may vary across populations experiencing different temperatures. For example,
317 northern populations experiencing cold temperatures benefit from the energetic advantages of
318 winter coats despite mismatch during snow-free periods, whereas southerly populations
319 experiencing warmer temperatures may not. Indeed, adverse survival effects associated with
320 mismatch in southern snowshoe hare populations in Montana (Zimova et al. 2016) and

321 Wisconsin (Wilson et al. 2018) occur in regions that experience warmer temperatures than those
322 in southwestern Yukon (Fig. 2). During the period when mismatch is possible in Montana,
323 autumn temperatures can range from $\sim 3^{\circ}\text{C}$ to 17°C and spring temperatures can range from \sim
324 4°C to 20°C .

325 The seasonal differences in mismatch effects on survival and foraging time that we found
326 within our study population highlight temperature as a unifying factor affecting the survival costs
327 of coat color mismatch. In spring, mismatch did not influence mortality risk (Fig. 1b) and
328 matched and mismatched hares spent similar amounts of time foraging (Fig. 2b). Mismatched
329 hares in the spring occurred at temperatures (-0.5°C to 11°C , Fig. 2b) that were approximately
330 within the thermoneutral zone of both summer and winter-acclimatized hares (Sheriff et al.
331 2009a). In contrast, mismatched hares in the autumn experienced temperatures between -7°C and
332 4°C (Fig. 2a) which fall below the lower critical temperature for summer-acclimatized brown
333 hares, but not winter-acclimatized white hares (Sheriff et al. 2009a). Animals must increase their
334 energetic expenditure when they are exposed to temperatures outside of their thermoneutral zone
335 (Kingma et al. 2012), which may represent a likely mechanism explaining the longer foraging
336 time in matched brown hares in the autumn relative to mismatched white hares (Fig. 2a). These
337 results further support that the thermal and energetic benefits of winter acclimatization may
338 outweigh the costs of coat color mismatch at cold temperatures.

339 Although camouflage is thought to be the primary adaptive benefit of coat color
340 polymorphism, like most traits, alternate benefits, e.g., thermal and physiological, exist (Caro
341 2005, Duarte et al. 2017, Zimova et al. 2018). We found that these alternate benefits offset the
342 costs of camouflage loss at cold temperatures. Our proposed hypothesis, whereby the thermal
343 and energetic benefits of winter acclimatization may influence coat color mismatch effects

344 through reduced time spent foraging, has the potential to reconcile intraspecific variation among
345 other snowshoe hare populations and merits testing in other color changing species, i.e. arctic
346 hares (*Lepus arcticus*), mountain hares (*Lepus timidus*). Climate change-induced variation in
347 temperature and precipitation regimes are likely to vary across species ranges (Loarie et al.
348 2009). Such variation in climate change effects will be particularly large for species with broad
349 distributions, i.e., circumboreal color-changing species. Ultimately, as temperatures in the
350 Northern Hemisphere are projected to warm (Danco et al. 2016), northern snowshoe hare
351 populations are likely to reach the threshold ($> -3^{\circ}\text{C}$) at which the energetic benefits of white
352 coats are lost, and survival costs driven by coat color mismatch could occur (Zimova et al. 2016,
353 Wilson et al. 2018). However, elucidating the mechanisms through which phenological
354 mismatches may be operating is essential to enable predictions on broad-scale changes in species
355 distributions.

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367 **Literature cited**

- 368 Akaike, H. 1974. A New Look at the Statistical Model Identification. *IEEE Transactions on*
369 *Automatic Control* 19:716–723.
- 370 Atmeh, K., A. Andruszkiewicz, and K. Zub. 2018. Climate change is affecting mortality of
371 weasels due to camouflage mismatch. *Scientific Reports* 8:1–7.
- 372 Balluffi-Fry, J., S. J. Leroux, Y. F. Wiersma, I. C. Richmond, T. R. Heckford, M. Rizzuto, J. L.
373 Kennah, and E. Vander Wal. (n.d.). (In Review at *Oecologia*). Integrating plant
374 stoichiometry and feeding experiments: state-dependent forage choice and its implications
375 on body mass.:bioRxiv [Preprint: doi: 10.1101/2021.02.16.431523].
- 376 Barton, K. 2020. Multi-Model Inference. R package version 1.43.17.
- 377 Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. Fitting linear mixed-effects
378 models using lme4. *Journal of Statistical Software* 67:1–51.
- 379 Boratyński, J. S., M. Jefimow, and M. S. Wojciechowski. 2016. Phenotypic flexibility of
380 energetics in acclimated Siberian hamsters has a narrower scope in winter than in summer.
381 *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental*
382 *Physiology* 186:387–402.
- 383 Brown, R. D., and P. W. Mote. 2009. The response of Northern Hemisphere snow cover to a
384 changing climate. *Journal of Climate* 22:2124–2145.
- 385 Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference*.
386 Springer, New York, New York USA.
- 387 Caro, T. 2005. The adaptive significance of coloration in mammals. *BioScience* 55:125–136.
- 388 Cox, D. R., and D. Oakes. 1984. *Analysis of survival data*. Chapman and Hall, New York, New
389 York USA.

- 390 Danco, J. F., A. M. Deangelis, B. K. Raney, and A. J. Broccoli. 2016. Effects of a warming
391 climate on daily snowfall events in the Northern Hemisphere. *Journal of Climate* 29:6295–
392 6318.
- 393 Doi, H., O. Gordo, T. Mori, and M. T. Kubo. 2017. A macroecological perspective for
394 phenological research under climate change. *Ecological Research* 32:633–641.
- 395 Duarte, R. C., A. A. V. Flores, and M. Stevens. 2017. Camouflage through colour change:
396 Mechanisms, adaptive value and ecological significance. *Phil. Trans. R. Soc. B* 372:1–8.
- 397 Ferreira, M. S., P. C. Alves, C. M. Callahan, J. P. Marques, L. S. Mills, J. M. Good, and J. Melo-
398 Ferreira. 2017. The transcriptional landscape of seasonal coat colour moult in the snowshoe
399 hare. *Molecular Ecology* 26:4173–4185.
- 400 Fuglestad, B. N., Ø. E. Haga, L. P. Folkow, E. Fuglei, and A. S. Blix. 2006. Seasonal variations
401 in basal metabolic rate, lower critical temperature and responses to temporary starvation in
402 the arctic fox (*Alopex lagopus*) from Svalbard. *Polar Biology* 29:308–319.
- 403 Gigliotti, L. C., D. R. Diefenbach, and M. J. Sheriff. 2017. Geographic variation in winter
404 adaptations of snowshoe hares (*Lepus americanus*). *Canadian Journal of Zoology* 95:539–
405 545.
- 406 Gordo, O., and H. Doi. 2012. Drivers of population variability in phenological responses to
407 climate change in Japanese birds. *Climate Research* 54:95–112.
- 408 Griffin, P. C., S. C. Griffin, C. Waroquiers, and L. S. Mills. 2005. Mortality by moonlight:
409 Predation risk and the snowshoe hare. *Behavioral Ecology* 16:938–944.
- 410 Heard, M. J., S. H. Riskin, and P. A. Flight. 2012. Identifying potential evolutionary
411 consequences of climate-driven phenological shifts. *Evolutionary Ecology* 26:465–473.
- 412 Humphries, M. M., S. Boutin, D. W. Thomas, J. D. Ryan, C. Selman, A. G. McAdam, D.

- 413 Berteaux, and J. R. Speakman. 2005. Expenditure freeze: The metabolic response of small
414 mammals to cold environments. *Ecology Letters* 8:1326–1333.
- 415 Joshua Chen, Y. H., and G. H. F. Liu. 2006. A note on the estimate of treatment effect from a
416 cox regression model when the proportionality assumption is violated. *Communications in*
417 *Statistics - Theory and Methods* 35:521–526.
- 418 Kingma, B., A. Frijns, and W. V. M. Lichtenbelt. 2012. The thermoneutral zone: Implications for
419 metabolic studies. *Frontiers in Bioscience - Elite* 4 E:1975–1985.
- 420 Krebs, C. J., R. Boonstra, and S. Boutin. 2018. Using experimentation to understand the 10-year
421 snowshoe hare cycle in the boreal forest of North America. *Journal of Animal Ecology*
422 87:87–100.
- 423 Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Martin,
424 and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. *Science*
425 269:1112–1115.
- 426 Kudo, G., and T. Y. Ida. 2013. Early onset of spring increases the phenological mismatch
427 between plants and pollinators. *Ecology* 94:2311–2320.
- 428 Lehikoinen, A. 2011. Advanced autumn migration of sparrowhawk has increased the predation
429 risk of long-distance migrants in Finland. *PLoS ONE* 6:1–4.
- 430 Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a
431 review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- 432 Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. The
433 velocity of climate change. *Nature* 462:1052–1055.
- 434 Lovegrove, B. G. 2005. Seasonal thermoregulatory responses in mammals. *Journal of*
435 *Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*

- 436 175:231–247.
- 437 Mazerolle, M. 2019. Model Selection and Multimodel Inference Based on (Q)AIC(c) Version
438 2.2-2.
- 439 McNamara, J. M., and A. I. Houston. 1987. Starvation and Predation as Factors Limiting
440 Population Size. *Ecology* 68:1515–1519.
- 441 Melin, M., L. Mehtätalo, P. Helle, K. Ikonen, and T. Packalen. 2020. Decline of the boreal
442 willow grouse (*Lagopus lagopus*) has been accelerated by more frequent snow-free springs.
443 *Scientific Reports* 10:1–10.
- 444 Meslow, E. C., and L. B. Keith. 1971. A correlation analysis of weather versus snowshoe hare
445 population parameters. *The Journal of Wildlife Management* 35:1–15.
- 446 Mikkelsen, L., M. Johnson, D. M. Wisniewska, A. van Neer, U. Siebert, P. T. Madsen, and J.
447 Teilmann. 2019. Long-term sound and movement recording tags to study natural behavior
448 and reaction to ship noise of seals. *Ecology and Evolution* 9:2588–2601.
- 449 Mills, L. S., E. V. Bragina, A. V. Kumar, M. Zimova, D. J. R. Lafferty, J. Feltner, B. M. Davis,
450 K. Hackländer, P. C. Alves, J. M. Good, J. Melo-Ferreira, A. Dietz, A. V. Abramov, N.
451 Lopatina, and K. Fay. 2018. Winter color polymorphisms identify global hot spots for
452 evolutionary rescue from climate change. *Science* 359:1033–1036.
- 453 Mills, L. S., M. Zimova, J. Oyler, S. Running, J. T. Abatzoglou, and P. M. Lukacs. 2013.
454 Camouflage mismatch in seasonal coat color due to decreased snow duration. *Proceedings*
455 *of the National Academy of Sciences of the United States of America* 110:7360–7365.
- 456 Møller, A. P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species that
457 did not show a phenological response to climate change are declining. *Proceedings of the*
458 *National Academy of Sciences of the United States of America* 105:16195–16200.

- 459 Murray, D. L., and G. Bastille-Rousseau. 2020. Estimating survival and cause-specific mortality
460 from continuous time observations. Page 448 *in* D. L. Murray and B. Sandercock, editors.
461 Population ecology in practice. Wiley-Blackwell, Hoboken, New Jersey, USA.
- 462 Nagorsen, D. W. 1983. Winter pelage colour in snowshoe hares (*Lepus americanus*) from the
463 Pacific Northwest. *Canadian Journal of Zoology* 61:2313–2318.
- 464 Nakagawa, S., P. C. D. Johnson, and H. Schielzeth. 2017. The coefficient of determination R^2
465 and intra-class correlation coefficient from generalized linear mixed-effects models
466 revisited and expanded. *Journal of the Royal Society Interface* 14:1–11.
- 467 Pedersen, S., M. Odden, and H. C. Pedersen. 2017. Climate change induced molting mismatch?
468 Mountain hare abundance reduced by duration of snow cover and predator abundance.
469 *Ecosphere* 8:1–8.
- 470 Peers, M. J. L., Y. N. Majchrzak, A. K. Menzies, E. K. Studd, G. Bastille-Rousseau, R. Boonstra,
471 M. Humphries, T. S. Jung, A. J. Kenney, C. J. Krebs, D. L. Murray, and S. Boutin. 2020.
472 Climate change increases predation risk for a keystone species of the boreal forest. *Nature*
473 *Climate Change* 10:1149–1153.
- 474 Phillimore, A. B., J. D. Hadfield, O. R. Jones, and R. J. Smithers. 2010. Differences in spawning
475 date between populations of common frog reveal local adaptation. *Proceedings of the*
476 *National Academy of Sciences of the United States of America* 107:8292–8297.
- 477 Porkert, J., S. Gashkov, J. Haikola, E. Huhta, M.-L. Kaisanlahti-Jokimäki, B. Kuranov, R. Latja,
478 R. Mertens, A. Numerov, J. Rutila, A. Sombrutzki, J. Zajíc, E. Belskii, J. Jokimäki, and A.
479 Järvinen. 2014. Variation and long-term trends in the timing of breeding of different
480 Eurasian populations of Common Redstart *Phoenicurus phoenicurus*. *Journal of*
481 *Ornithology* 155:1045–1057.

- 482 Post, E., and M. C. Forchhammer. 2008. Climate change reduces reproductive success of an
483 Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society*
484 *B: Biological Sciences* 363:2369–2375.
- 485 Radchuk, V., T. Reed, C. Teplitsky, M. van de Pol, A. Charmantier, C. Hassall, P. Adamík, F.
486 Adriaensen, M. P. Ahola, P. Arcese, J. Miguel Avilés, J. Balbontin, K. S. Berg, A. Borrás,
487 S. Burthe, J. Clobert, N. Dehnhard, F. de Lope, A. A. Dhondt, N. J. Dingemanse, H. Doi, T.
488 Eeva, J. Fickel, I. Filella, F. Fossøy, A. E. Goodenough, S. J. G. Hall, B. Hansson, M.
489 Harris, D. Hasselquist, T. Hickler, J. Joshi, H. Kharouba, J. G. Martínez, J. B. Mihoub, J. A.
490 Mills, M. Molina-Morales, A. Moksnes, A. Ozgul, D. Parejo, P. Pilard, M. Poisbleau, F.
491 Rousset, M. O. Rödel, D. Scott, J. C. Senar, C. Stefanescu, B. G. Stokke, T. Kusano, M.
492 Tarka, C. E. Tarwater, K. Thonicke, J. Thorley, A. Wilting, P. Tryjanowski, J. Merilä, B. C.
493 Sheldon, A. Pape Møller, E. Matthysen, F. Janzen, F. S. Dobson, M. E. Visser, S. R.
494 Beissinger, A. Courtiol, and S. Kramer-Schadt. 2019. Adaptive responses of animals to
495 climate change are most likely insufficient. *Nature Communications* 10:1–14.
- 496 Reed, T. E., V. Grtøan, S. Jenouvrier, B. E. Stæher, and M. E. Visser. 2013. Population growth
497 in a wild bird is buffered against phenological mismatch. *Science* 340:488–491.
- 498 Sheriff, M. J., L. Kuchel, S. Boutin, and M. M. Humphries. 2009a. Seasonal Metabolic
499 Acclimatization in a Northern Population of Free-Ranging Snowshoe Hares, *Lepus*
500 *americanus*. *Journal of Mammalogy* 90:761–767.
- 501 Sheriff, M. J., J. R. Speakman, L. Kuchel, S. Boutin, and M. M. Humphries. 2009b. The cold
502 shoulder: Free-ranging snowshoe hares maintain a low cost of living in cold climates.
503 *Canadian Journal of Zoology* 87:956–964.
- 504 Shiratsuru, S., Y. N. Majchrzak, M. J. L. Peers, E. K. Studd, A. K. Menzies, R. Derbyshire, M.

505 M. Humphries, C. J. Krebs, D. L. Murray, and S. Boutin. 2021. Food availability and
506 long-term predation risk interactively affect antipredator response. *Ecology*:e03456.

507 Sievert, P. R., and L. B. Keith. 1985. Survival of Snowshoe Hares at a Geographic Range
508 Boundary. *The Journal of Wildlife Management* 49:854–866.

509 Studd, E. K., M. R. Boudreau, Y. N. Majchrzak, A. K. Menzies, M. J. L. Peers, J. L. Seguin, S.
510 G. Lavergne, R. Boonstra, D. L. Murray, S. Boutin, and M. M. Humphries. 2019. Use of
511 Acceleration and Acoustics to Classify Behavior, Generate Time Budgets, and Evaluate
512 Responses to Moonlight in Free-Ranging Snowshoe Hares. *Frontiers in Ecology and*
513 *Evolution* 7:1–14.

514 Therneau, T. M., T. Lumley, A. Elizabeth, and C. Cynthia. 2021. Survival Analysis. R package
515 version 3.2-10.

516 Valladares, F., S. Matesanz, F. Guilhaumon, M. B. Araújo, L. Balaguer, M. Benito-Garzón, W.
517 Cornwell, E. Gianoli, M. van Kleunen, D. E. Naya, A. B. Nicotra, H. Poorter, and M. A.
518 Zavala. 2014. The effects of phenotypic plasticity and local adaptation on forecasts of
519 species range shifts under climate change. *Ecology Letters* 17:1351–1364.

520 Visser, M. E., and P. Gienapp. 2019. Evolutionary and demographic consequences of
521 phenological mismatches. *Nature Ecology and Evolution* 3:879–885.

522 Wilson, E. C., A. A. Shipley, B. Zuckerberg, M. Z. Peery, and J. N. Pauli. 2018. An
523 experimental translocation identifies habitat features that buffer camouflage mismatch in
524 snowshoe hares. *Conservation Letters* 12:1–8.

525 Zeileis, A., G. Grothendieck, J. A. Ryan, and F. Andrews. 2021. Package “Zoo”. S3
526 infrastructure for regular and irregular time series (Z’s ordered observations). R package
527 version 1.8-9.

- 528 Zimova, M., K. Hackländer, J. M. Good, J. Melo-Ferreira, P. C. Alves, and L. S. Mills. 2018.
529 Function and underlying mechanisms of seasonal colour moulting in mammals and birds:
530 what keeps them changing in a warming world? *Biological Reviews* 93:1478–1498.
- 531 Zimova, M., L. S. Mills, P. M. Lukacs, and M. S. Mitchell. 2014. Snowshoe hares display
532 limited phenotypic plasticity to mismatch in seasonal camouflage. *Proceedings of the Royal
533 Society B: Biological Sciences* 281:1–9.
- 534 Zimova, M., L. S. Mills, and J. J. Nowak. 2016. High fitness costs of climate change-induced
535 camouflage mismatch. *Ecology Letters* 19:299–307.
- 536

537 **Table**

538 Table 1. Summary of variables included in top-ranking linear mixed-effects daily foraging time
 539 models for snow-free autumn and spring periods. Daily foraging time was considered in minutes.
 540 Both autumn and spring models also include individual ID as a random effect and the spring
 541 model includes sex as a random effect.

Response: Daily foraging minutes			
Model	Coefficient (\pm SE)	t	P
Top model autumn from n=1505 daily foraging records from 66 hares			
Intercept	830.909 \pm 9.037	91.942	<0.001
Temperature	-2.306 \pm 0.505	-4.566	<0.001
mismatch	-17.385 \pm 6.170	-2.818	0.005
Year (2016)	-10.364 \pm 8.380	-1.237	0.217
Year (2017)	-101.607 \pm 12.188	-8.336	<0.001
Temperature \times mismatch	5.963 \pm 1.210	4.929	<0.001
Top model spring from n= 838 daily foraging records from 44 hares			
Intercept	858.868 \pm 22.800	37.669	<0.001
Temperature	-1.209 \pm 1.295	-0.933	0.351
Year (2016)	-16.582 \pm 19.380	-0.856	0.396
Year (2017)	-28.914 \pm 19.111	-1.513	0.137
Year (2018)	-93.029 \pm 21.089	-4.411	<0.001
Sex (F)	-34.832 \pm 17.000	-2.049	0.047

542

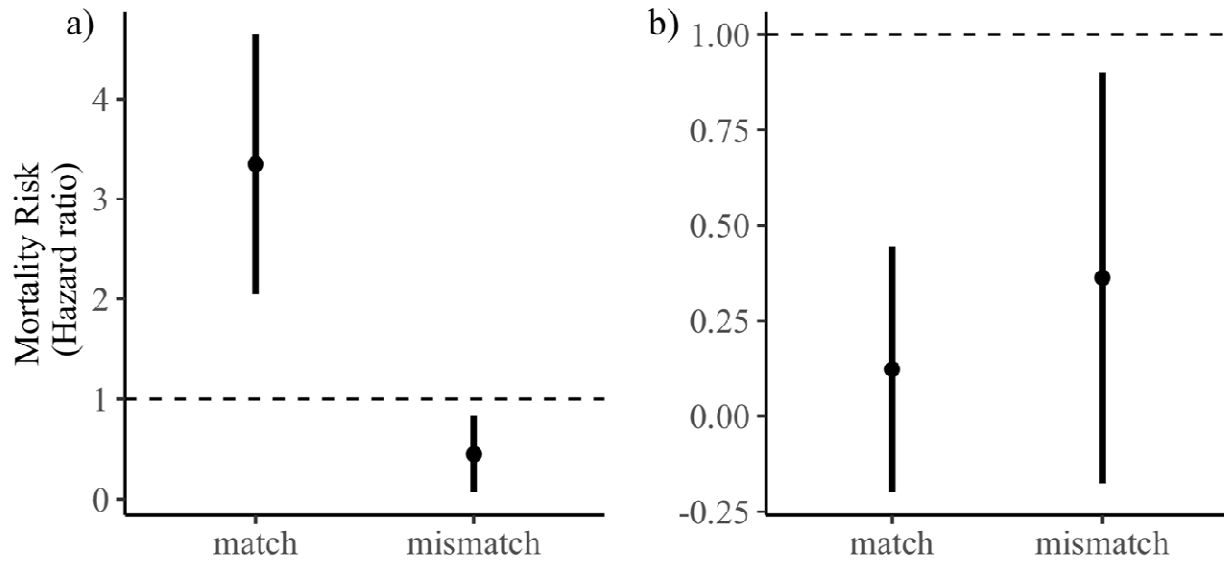
543 **Figure Captions**

544 Fig 1. The modelled effect of coat color mismatch on snowshoe hare mortality risk, generated
545 from our top supported CPH model for a) autumn and b) spring. Points represent predicted
546 hazard ratios (HR) for matched and mismatched hares when snow depth and snow cover are held
547 at zero. Error bars represent predicted standard errors, and the dashed line represents baseline
548 mortality risk (i.e., HR=1).

549 Fig 2. Modelled effect of temperature on daily foraging time (minutes) for matched and
550 mismatched snowshoe hares in the snow-free period of a) autumn (marginal $R^2=0.12$,
551 conditional $R^2=0.32$) and b) spring (marginal $R^2=0.13$, conditional $R^2=0.28$) of 2016 (the year
552 with the most data). Data points show daily foraging records for individuals across all study
553 years and predicted foraging time of mismatched hares is restricted to temperatures where
554 mismatched hares occurred in our study. Predicted values for daily spring foraging time are for
555 males.

556 **Figures**

557 Fig. 1



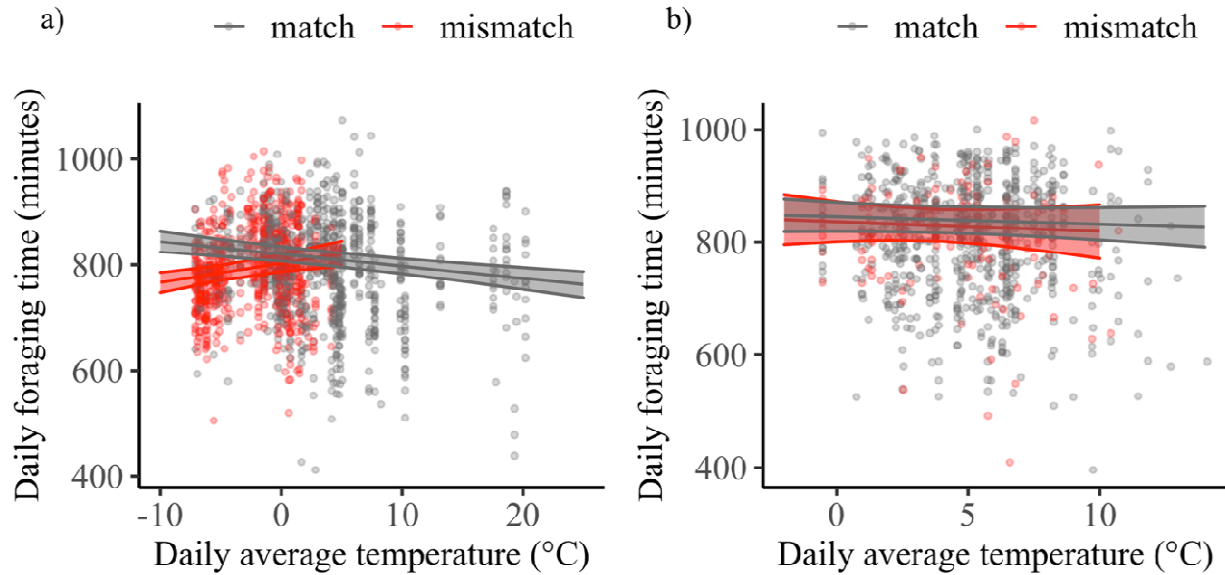
558

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560 from our top supported CPH model for a) autumn and b) spring. Points represent predicted
561 hazard ratios (HR) for matched and mismatched hares when snow depth and snow cover are held
562 at zero. Error bars represent predicted standard errors, and the dashed line represents baseline
563 mortality risk (i.e., HR=1).

564

565

566 Fig. 2



567

568 Fig 2. Modelled effect of temperature on daily foraging time (minutes) for matched and
569 mismatched snowshoe hares in the snow-free period of a) autumn (marginal $R^2=0.12$,
570 conditional $R^2=0.32$) and b) spring (marginal $R^2=0.13$, conditional $R^2=0.28$) of 2016 (the year
571 with the most data). Data points show daily foraging records for individuals across all study
572 years and predicted foraging time of mismatched hares is restricted to temperatures where
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