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Ignite

Scottish mountain hares do not respond behaviorally to camouflage mismatch

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Climate change has resulted in a myriad of stressors to wild organisms. Phenotypic plasticity, including behavioral plasticity, is hypothesized to play a key role in allowing animals to cope with rapid climate change and mitigate its negative fitness consequences. Camouflage mismatch resulting from decreasing duration of snow cover presents a stressor to species that undergo coat color molts to maintain camouflage against seasonally changing backgrounds. Winter white animals appear highly conspicuous against dark, snowless background and experience increased predation-induced mortality. Here, we evaluate the potential of behavioral plasticity to buffer against camouflage mismatch in mountain hares *Lepus timidus* in Scotland. We carried out field surveys in three populations over two years and found no evidence that hares modify their behaviors in response to increasing camouflage mismatch. Hares did not prefer to rest closer to light-colored rocks or farther from conspecifics with increasing color contrast. Furthermore, whiter hares did not seek to rest closer to snowy backgrounds; rather, hares preferred to sit farther from snow. These results suggest that behavioral plasticity might not be a universal, rapid mechanism facilitating adaptation to climate change.

Keywords: behavioral plasticity, camouflage, climate change, mountain hares, phenological mismatch

Introduction

Climate change is a significant threat to the persistence of many wild species (Urban 2015, Scheffers et al. 2016, IPBES 2019). Understanding how species respond to climate change is a key question in ecological research. Phenotypic plasticity, the ability of a genotype to vary its phenotype across environments, can facilitate rapid phenotypic change in response to environmental change (West-Eberhard 2003, Chevin et al. 2010). Phenotypic plasticity in behavior can mount particularly fast responses and is often expected to help species mitigate negative consequences associated with some aspects



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of global climate change (Tuomainen and Candolin 2011). However, the scope for behavioral plasticity to facilitate adaptation to climate change is not well understood (Beever et al. 2017, Snell-Rood et al. 2018, Buchholz et al. 2019).

At least 21 species of mammals and birds undergo seasonal coat color molts from brown in the summer to white coats in the winter to maintain camouflage against snow (Mills et al. 2018, Zimova et al. 2018). As snow cover duration declines under climate change, color molting species experience phenological mismatch (Fig. 1) when winter white animals appear highly conspicuous against dark, snowless background and potentially experience increased predation-induced mortality (Zimova et al. 2016, Wilson et al. 2018). Some populations have responded to camouflage mismatch by shifting molt phenology either via phenotypic plasticity (Mills et al. 2013, Kumar et al. 2020, Laporte-Devlyder et al. 2022, Zimova et al. 2022) or potentially evolution (Zimova et al. 2020b, Oli et al. 2023, Peltier et al. 2023). However, accumulating evidence suggests that these documented shifts are insufficient to prevent camouflage mismatch in years with least snow cover (Mills et al. 2013, Zimova et al. 2014, 2020a, Atmeh et al. 2018, Kumar et al. 2020).

Behavioral plasticity remains a little explored mechanism for adaptation to camouflage mismatch in color molting species (Zimova et al. 2018). Species across the animal kingdom use a variety of behavioral strategies to improve camouflage (Stevens and Ruxton 2019). For example, prey species often select backgrounds that match their color (Endler 1984, Isaac and Gregory 2013, Marshall et al. 2016) or position themselves near uninteresting, inedible objects to reduce recognition by predators (masquerade; Cooper and Sherbrooke 2012, Nafus et al. 2015). However, the few studies that investigated whether winter white animals adjust their behaviors in response to mismatch provide mixed evidence. For example, color molting ptarmigan (*Lagopus* spp.) preferentially rest and forage in areas that match their coloration (Steen et al. 1992) or smear their feathers with soil when mismatched (Montgomerie et al. 2001). On the other hand, mismatched snowshoe hares *Lepus americanus* do not select microsites that



Figure 1. White mountain hare experiencing camouflage mismatch at one of the study sites in the northeast and central highlands of Scotland, UK. The hare is resting near a light-colored rock.

would improve their camouflage, nor show any detectable preference for environments (e.g. denser stands) that would increase concealment (Litvaitis 1991, Zimova et al. 2014, Kumar et al. 2020).

Here, we evaluate the potential of behavioral plasticity to buffer against camouflage mismatch in mountain hares *Lepus timidus* in Scotland. We previously showed that Scottish mountain hare populations experience high levels of camouflage mismatch as their molt phenology has failed to shift in response to shorter snow cover duration (Zimova et al. 2020b). In Scotland, mountain hares are primarily found on upland heather moorlands – open landscapes with low structural complexity – where mismatched hares appear highly conspicuous when contrasted with their background (Zimova et al. 2020b, Fig. 1). Here, we hypothesize that in response to camouflage mismatch, mountain hares modify their behaviors to reduce detection or recognition by predators. We predict that mountain hares would prefer to rest 1) closer to light-colored rocks (as these look similar to light and white hares) and 2) farther from conspecifics with increasing color contrast, and 3) on- or closer to snow with increasing body whiteness.

Material and methods

Study sites

Field surveys were carried out at three sites (Lecht [57°11'34.7994"N, -03°14'24"W], Findhorn High [57°14'6"N, -04°08'09.6"W], Findhorn Low [57°12'21.6"N, -04°06'07.2"W]) in the northeast and central highlands of Scotland, UK. All sites were located between 430–730 m a.s.l. and dominated by dwarf heath and subalpine plant communities. The Lecht site included areas of eroded peat, and both sites were scattered with occasional white/pale, sometimes lichen covered, hare-sized rocks.

Field surveys

We surveyed mountain hares twice a month in fall (October–January) and spring (March–June) seasons during 2015 and 2016 for a total of 5–11 surveys per season and 67 surveys total (Zimova et al. 2020b). During each survey, one surveyor walked along a predetermined route (ca 3–6 km long) and observed hares as they were either flushed (moved from their resting site in response to disturbance), or less frequently, detected by the surveyor during the frequent and thorough binoculars scans of the landscape. Hares are largely inactive during the day when they sit at a resting site above ground. We only used observations during which the observer had a clear view that allowed coat color to be assessed and was confident of the hare's original resting location.

For all hares detected within 200 m of the observer, we photographed the hare and recorded coat color following Watson (1963). Coat color was ranked into four categories; 0% (completely dark), 25% (mostly dark), 50% (half-dark and half-white), 75% (mostly white) or 100% white

(completely white) (for detailed description of categories see [Zimova et al. 2020b](#)). For observations accompanied by photographs (> 80% of all observations) field estimates of molt were later verified by one of us (MZ).

We measured color contrast as the difference between hare coat color (percent white) and the percent snow cover at each hare's original resting site following the methods of ([Zimova et al. 2014](#)). The percent snow cover was visually estimated in 25% increments within 5- and 10-m radii circles centered at the resting site. We used the two different radii circles as it is not known at which spatial scale camouflage may be perceived by either hares or predators. We used color contrast values that ranged between 0 and 100 in our main analyses where a positive contrast values indicated hares that were whiter than their backgrounds. Furthermore, there were relatively few negative color contrast values (= brown colored hares on snowy backgrounds; < 9% of all observations) and so excluding these values did not have a major impact on our sample size.

Finally, for each hare's original resting site, we visually estimated the minimum distance a hare was to 1) any light-colored rocks of equal or larger size than the size of a resting hare, 2) another hare, and 3) snow. All distances between 0 and 20 m were estimated in 1 m increments; all other distances were recorded as '> 20 m' as we were not able to accurately estimate distances beyond 20 m.

Statistical analysis

Proximity to rocks and other hares

We used a two-step approach to test whether hares rested closer to light-colored rocks or other hares with increasing value of color contrast to accommodate two different spatial scales. First, to accommodate a larger spatial scale, we tested whether hares are more likely to rest in closer proximity of a rock (or another hare) with increasing color contrast. Using separate models, we modeled the probability that a hare is found within 20 m of a rock or another hare as a function of color contrast (at either 5- or 10-m scale) using generalized linear mixed effects models in the 'lme4' package ([Bates et al. 2015](#)) with a binomial distribution and a logit link function (i.e. 1 = distance \leq 20 m, 0 = distance > 20 m). We also included study area as a random effect to control for variation between areas, and season (= spring, fall) as a fixed effect to control for potential seasonal differences.

Second, for hares that were in close proximity (i.e. distance \leq 20 m) of a light-colored rock or another hare, we tested whether the distance was dependent on hare's color contrast. Owing to the left-skewed distribution of distances to rocks (0–20 m), we log-transformed the variable to improve normality. We modeled the log-transformed distance to rocks or distance to another hare as a function of color contrast (at either 5- or 10-m scale) with random intercept for study area and fixed effect of season using linear mixed effects models in the lme4 package. We also analyzed the data with a generalized linear mixed effects model with a zero-inflated negative binomial error distribution using the 'glmmTMB' package

([Brooks et al. 2017](#)). The results and model fits were essentially identical and so we only report the results of the linear mixed effects models. Finally, an alternative set of models that included absolute value of color contrast or the interaction term between color contrast and season rendered qualitatively similar results (Supporting information). For all models with distance to rocks as response, we only included observations taken during surveys when the ground was predominantly free of snow because snow cover concealed the rocks and we could not assess distance to rocks.

Proximity to snow

We followed the same two-step approach to test whether hares rest closer to snow cover with increasing body whiteness. First, we tested whether hares are more likely to rest on- or in close proximity of snow with increasing hare's body whiteness using the same generalized linear mixed effects model structure as above but replaced color contrast with body whiteness. Second, for hares that were in close proximity to snow, we tested whether the distance decreased with hare's body whiteness. We used the same linear mixed effects model structure as above but modeled the log-transformed distance to snow as a function of body whiteness. For all models, we excluded observations taken during surveys when snow cover was completely absent or completely continuous across the study area as these conditions did not allow hares to make a behavioral choice.

All data analyses were conducted in RStudio ver.2024.04.2, with R ver. 4.3.2 (www.r-project.org). For all linear mixed models, we assessed significance of parameters using the 'lmerTest' package ([Kuznetsova et al. 2017](#)). Assumptions of all models were checked by visual inspections of the residuals in diagnostic plots using the 'DHARMA' package ([Hartig 2022](#)) with little deviations in terms of normal distribution and equal variances.

Results

Proximity to rocks and other hares

Contrary to our prediction, we found no evidence that hares adjusted their resting site distance to light-colored rocks or one another with increasing degree of color contrast. First, the probability of a hare resting within 20 m of a rock or another hare was not affected by color contrast ([Table 1](#)). Second, for hares that did rest within 20 m of rocks or other hares, the distance to them was independent of color contrast ([Table 2](#)). Seasonal difference in hares' positioning were detected, but only at the larger spatial scale (within 20 m); in the spring, hares were more likely to rest near another hare but less likely near a rock than in the fall ([Table 1](#)).

Proximity to snow

We found no support for our prediction that whiter hares rest on or closer to snow. First, the probability of a hare resting in proximity (within 20 m) of snow was not affected by

Table 1. Color contrast or hare's body whiteness (white) does not affect the probability of mountain hares resting within 20 m of a light-colored rocks, other hares, or snow in Scotland. Results are based on generalized linear mixed effects models with a binomial distribution and a logit-link function. n corresponds to the total number of observations. Color contrast was measured within 5-m radius circle, but models that considered color contrast within 10-m radius circle rendered qualitatively similar results (Supporting information).

	Coefficient	Estimate	SE	z-value	p-value
Rock n=935	Intercept	-0.567	1.410	-0.402	0.688
	Color contrast	-0.003	0.002	-1.368	0.171
	Season (Spring)	-0.593	0.209	-2.832	0.005
Hare n=1116	Intercept	-0.126	0.274	-0.459	0.646
	Color contrast	-0.002	0.002	-1.212	0.225
	Season (Spring)	0.488	0.138	3.534	< 0.001
Snow n=342	Intercept	2.128	0.574	3.706	< 0.001
	White	-0.001	0.007	-0.210	0.833
	Season (Spring)	-1.257	0.287	-4.383	< 0.001

hare's whiteness (Table 1). Second, contrary to our prediction, whiter hares did not prefer to rest near snow; rather, within a 20 m radius circle, whiter hares rested farther away from snow (Table 2). Hares were more likely to sit farther from snow in the spring than in the fall, and this was evident at both spatial scales (Table 1–2).

Discussion

Behavioral plasticity is hypothesized to play a key role in allowing animals to cope with rapid climate change (Beever et al. 2017). Yet, the scope for behavioral plasticity to facilitate adaptation to camouflage mismatch due to decreasing snow cover is not well understood. Here we found no evidence that mountain hares in Scotland modify their preference for daytime resting site in response to increasing camouflage mismatch (i.e. high color contrast). These results suggest that behavioral plasticity in this system might not provide a rapid mechanism facilitating adaptation to climate change.

Contrary to our predictions, mountain hares did not prefer resting sites that might reduce camouflage mismatch. Hares did not prefer to rest among or closer to light-colored rocks to decrease color contrast and did not modify their distance to other resting hares with respect to their color contrast. It is possible that hares adjust other behaviors to reduce camouflage mismatch including positioning to other objects that we did not consider here. However, upland heather moorlands, where hares are commonly found in Scotland, provide little

cover and or structure beyond rocks, seasonal snow fields, and in some areas, patches of eroded peat. Furthermore, mismatched hares might alter their temporal activity patterns to reduce predation exposure as documented in other wildlife in response to the presence of apex predators (Gaynor et al. 2018, Welch et al. 2023). Future research on behavioral plasticity in response to mismatch would benefit from considering landscape structure and additional forms of behavioral plasticity.

Furthermore, our results show that light or white hares did not show a preference to rest on or near snow patches. In fact, the positive relationship between distance to snow and hare's body whiteness suggested that whiter hares preferred to sit farther from snow, although the effect size was low. This is consistent with observations in snowshoe hares, when hares preferred non-snowy sites, resulting in increased color contrast (Zimova et al. 2014, Kumar et al. 2020). We previously speculated that in hares, thermoregulation and locomotion efficiency may play a more important role in resting site choice than does background matching (Zimova et al. 2014, Kumar et al. 2020), but further study is needed.

Speculation

The lack of behavioral plasticity in response to camouflage mismatch was unexpected, especially because behavioral plasticity to increase camouflage is common in nature (Stevens and Ruxton 2019) and has been documented across taxa including color molting birds (MacDonald 1970, Jacobsen et al. 1983, Steen et al. 1992). However, our findings are consistent with

Table 2. Within 20 m, the distance to snow increased with hare's body whiteness (White), but color contrast did not affect the mountain hares' distance to rocks or other hares. Results are based on linear mixed effects models. n corresponds to the total number of observations. Color contrast was measured within 5-m radius circle, but models that considered color contrast within 10-m radius circle rendered qualitatively similar results (Supporting information).

	Coefficient	Estimate	SE	t-value	p-value
Rock n=320	Intercept	1.654	0.309	5.357	0.020
	Color contrast	-0.001	0.001	-1.035	0.301
	Season (Spring)	-0.081	0.110	-0.736	0.462
Hare n=609	Intercept	7.253	1.022	7.099	0.003
	Color contrast	0.011	0.007	1.518	0.130
	Season (Spring)	-0.227	0.591	-0.384	0.701
Snow n=269	Intercept	-0.102	0.449	-0.227	0.836
	White	0.007	0.002	2.987	0.003
	Season (Spring)	0.754	0.118	6.413	< 0.001

behaviors previously described in mismatched snowshoe hares (Zimova et al. 2014, Kumar et al. 2020) and suggest that hares might not have the ability to perceive their coat color or the capacity to behaviorally buffer camouflage mismatch. Our study sites were, or until recently were, actively managed grouse moors where management includes control of a range of generalist predators (Brooker et al. 2018). Therefore, another potential, nonexclusive explanation for our findings could be related to the potentially low density and diversity of predators at our study sites (Brooker et al. 2018, Zimova et al. 2020b). Mountain hares might not behaviorally adjust for camouflage mismatch because natural predation and concomitant costs of being mismatched are likely low in the Scottish Highlands. Additional studies that test antipredatory behavioral responses to mismatch in more natural systems – or in Scottish Highlands if predator numbers increase at our sites in the future – are needed to evaluate this hypothesis.

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Author contributions

Marketa Zimova: Conceptualization (lead); Formal analysis (lead); Funding acquisition (supporting); Investigation (equal); Methodology (lead); Writing – original draft (lead); Writing – review and editing (equal). **Scott Newey:** Conceptualization (supporting); Investigation (equal); Methodology (supporting); Writing – review and editing (equal). **Becks Denny:** Conceptualization (supporting); Investigation (equal); Writing – review and editing (equal). **Simen Pedersen:** Conceptualization (supporting); Writing – review and editing (equal); **L. Scott Mills:** Conceptualization (supporting); Funding acquisition (lead); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.hqbzkh1rc> (Zimova et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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