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Snow cover-related camouflage mismatch increases detection by predators

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Abstract

Camouflage expressed by animals is an adaptation to local environments that certain animals express to maximize survival and fitness. Animals at higher latitudes change their coat color according to a seasonally changing environment, expressing a white coat in winter and a darker coat in summer. The timing of molting is tightly linked to the appearance and disappearance of snow and is mainly regulated by photoperiod. However, due to climate change, an increasing mismatch is observed between the coat color of these species and their environment. Here, we conducted an experiment in northern Sweden, with white and brown decoys to study how camouflage (mis)-match influenced (1) predator attraction to decoys, and (2) predation events. Using camera trap data, we showed that mismatching decoys attracted more predators and experienced a higher likelihood of predation events in comparison to matching decoys, suggesting that camouflage mismatched animals experience increased detection by predators. These results provide insight into the function of a seasonal color coat and the need for this adaptation to maximize fitness in an environment that is exposed to high seasonality. Thus, our results suggest that, with increasing climate change and reduced snow cover, animals expressing a seasonal color coat will experience a decrease in survival.

KEYWORDS

adaptation, climate change, coat color, predation, survival

1 | INTRODUCTION

Animal species have adapted to their environment to increase survival and consequential fitness. One main adaptation, camouflage, is considered to be one of the most important evolutionary forces in the colouration of animals (Caro, 2005). Various types of concealment have been observed across animal species, varying from pattern blending to background matching (Caro, 2005; Stevens & Merilaita, 2009). The latter is a mechanism where animals express a cryptic colouration to mimic the colouration of one or more environments and thus lower the detection probability by either prey or predator (Caro, 2005; Cuthill, 2019; Merilaita et al., 2017; Murali et al., 2021). A problem that occurs with background matching is that the environment of an animal can vary in space (e.g., when foraging in different environments) and time (e.g., seasonal changes in landscape colouration) (Matchette et al., 2020; Merilaita et al., 1999; Murali et al., 2021). Thus, animals are required to match their color to various backgrounds and specializing colouration to one background might not be sufficient (Murali et al., 2021).

From temperate to polar zones, animals express specific seasonal and circannual traits, such as hibernation, seasonal migration, and color coat molting, to increase fitness in periods of low productivity and survival (Varpe, 2017; Williams et al., 2015; Zimova et al., 2018). Seasonal color coat (SCC) molting is a key trait used by at least 21 bird and mammal species in the Northern Hemisphere to adapt to harsh winter conditions (Mills et al., 2013, 2018). During SCC molting, animals change their fur or plumage color to white in autumn and brown or gray in spring (Mills et al., 2018; Zimova et al., 2018). The shifting from a white color in autumn to a darker color in spring ensures that the match between animal coat color and their background continues throughout the year (Caro, 2005; Caro & Koneru, 2021; Di Bernardi et al., 2021; Murali et al., 2021). Camouflage is not the only function of SCC; it also provides thermoregulatory advantages in winter fur and plumage in some species through increased radiation penetration (Stuart-Fox et al., 2017; Zimodva et al., 2018). However, crypsis is recognized as the main driver of winter colouration, as it provides a lower predation risk for prey and predation advantage for predators expressing SCC (Caro, 2005; Di Bernardi et al., 2021; Galeotti et al., 2003; Zimova et al., 2018).

Due to climate change, environmental conditions are changing rapidly. At high latitudes, where the increase in temperature has been greatest, climate change already results in an earlier onset of spring and late end of autumn (IPCC, 2021; Parmesan, 2006; Trenberth, 2011). Reduced number of snow days as a result of climate change impose a mismatch between animals expressing SCC and their environment (Kunkel et al., 2016; Mills et al., 2013; Zhu et al., 2019; Zimova, Giery, et al., 2020; Zimova, Sirén, et al., 2020). This mismatch between SCC molting and the corresponding environment should result in fitness costs for prey through a reduction in survival through increased detection by predators. Previous research on snowshoe hares *Lepus americanus*, for example, predicted that a temporal mismatch between white hares and brown backgrounds in either spring or autumn will increase rapidly in this century (Mills et al., 2013). If animals do not adjust their seasonal molt to reduce this mismatch, the expected decrease in snow cover duration will result in increased predation pressure on a variety of species expressing SCC, lowering fitness (Atmeh et al., 2018; Mills et al., 2013; Pedersen et al., 2017). Like other life events, molting of fur and plumage is coordinated by internal circannual rhythms in combination with external cues, the most important one being photoperiod (Helm et al., 2013; Melin et al., 2020; Zimova et al., 2018). While other external cues such as rainfall and temperature can adjust the phenology of molting locally, previous studies show that plasticity in SCC molting is limited and not able to adjust to the rapidly proceeding climate change (Mills et al., 2013; Quintero & Wiens, 2013; Zimova et al., 2018; Zimova, Sirén, et al., 2020).

Under the current projections of climate change, temperature rise is expected to increase the mismatch between animals expressing SCC and their environment, causing a decline in survival (Zimova et al., 2016). By becoming more conspicuous animals expressing SCC will become more susceptible to predation. Some subspecies of animals expressing SCC have already lost their ability to become white in winter, such as *Mustela nivalis vulgaris* in NE Poland (Atmeh et al., 2018), and Mountain hare in the Faroe Islands (Giska et al., 2019). The loss of animals expressing SCC could have cascading effects on their prey, predators, and other interconnected species, leading to potential disruptions in food chains and altering ecosystem dynamics (Wilson et al., 2022). Previous studies on SSC-environment mismatches focused heavily on North American snowshoe hares, whereas other species, and species in other parts of the northern hemisphere, are heavily understudied (Wilson et al., 2019; Zimova et al., 2014; Zimova, Sirén, et al., 2020).

Here, we used an experimental set-up in northern Fennoscandia to test how a camouflage mismatch: (a) influences detection by predators, and (b) how differences in detectability might influence predator events over time. We used decoys resembling the average size of animals expressing SCC in Fennoscandia, with the aim of getting information for a broader range of small animals expressing SCC in Fennoscandia, including mountain hare or willow ptarmigan *Lagopus lagopus* (Hofmeester et al., 2020; Melin et al., 2020). Decoys were placed in front of camera traps to measure predator detection in both periods of snow cover and after snow cover as well as in open and in closed habitats. Camera traps are widely used in ecological studies, including phenological mismatch studies, and can monitor a broad range of predators (Hofmeester et al., 2020; Meek et al., 2016; Zimova, Sirén, et al., 2020). First, we expected that a mismatch between the color of the environment and the coat of the decoy would result in higher detection probability by predators in comparison to a situation where camouflage matched the background environment (Zimova et al., 2016, 2018). Second, we hypothesized that mismatched decoys were detected faster by predators compared to matched decoys. In this study we use predator events such as attraction and interaction of a predator with a decoy as a measure for predation of hypothetical prey, the decoys. Thus, we expect mismatched decoys to experience increased predator events in comparison to matched decoys, resulting in a decrease in survival over time. Third, we expected that detectability is higher, and therefore survival lower, in open meadow habitats in comparison to closed forest habitats as detection probability by predators is lower when more obstacles, such as vegetation and woody debris, are present within a habitat or when the background is more complex (Murali et al., 2021; Rowe et al., 2021; Wheatley et al., 2020). The negative effect of being mismatched has been found to be reduced by increasing vegetation density (Wilson et al., 2019). Furthermore, we expected that mammalian predator species that are predominantly olfactory hunters, such as red fox *Vulpes vulpes* and pine marten *Martes martes*, would be less attracted to decoys (Díaz-Ruiz et al., 2016; Ruzicka & Conover, 2011; Willebrand et al., 2017). Mammalian predators are expected to be most prevalent in closed habitat as our study area is close to human settlement, resulting in an expected preference of mammalian predators for habitats with dense vegetation (Díaz-Ruiz et al., 2016; Van Etten et al., 2007; Willebrand et al., 2017) In contrast, we expected avian predators such as short-eared owls *Asio flammeus*, which rely on visual cues (Heninger et al., 2020; Potier et al., 2018), to forage more in the open habitat. Hence, as camouflage mismatching is a visual que for predators, we expect a larger negative effect of being mismatched in open habitat where the predator community is expected to be composed of mainly avian predators.

2 | METHODS

2.1 | Study area

We conducted the study in the area surrounding the Röbäcksdalen field station of the Swedish University of Agricultural Sciences, southwest of Umeå, Sweden (63.811° N/20.242° E). The area is dominated by agricultural fields with some patches of boreal forest on the northeastern sides of the field station (Figure 1). Agricultural fields in the study area consisted of pastures and arable land with a variety of crops, from here on regarded as "open habitats," while we refer to the patches of boreal forests as "closed habitats." For open habitat, we selected pastures managed for livestock grazing (Figure 1). Potential predator species in the area consisted of several mammalian species, such as red fox, pine marten, European badger *Meles meles*, domestic dogs *Canis lupus familiaris*, and domestic cat *Felis domesticus*, and several avian species such as common raven *Corvus corax* and several raptor and owl species such as short-eared owl.

2.2 | Camera trapping design

We used 18 camera traps (RECONYX® HyperFire 2™) to monitor the attraction and detection of the decoys by predators. Camera trapping is an ideal method to determine how SCC mismatch affects detectability by predators as multiple species as well as interactions among species, specifically predator–prey interactions, can be investigated (Caravaggi et al., 2017; Smith et al., 2020). We deployed clusters consisting of three cameras (Figure 2). Within each cluster, we placed cameras 20 m apart: one control with no decoy, one with a white decoy, and one with a brown decoy in random order. We attached cameras to trees in the closed habitat and poles on pedestals in open habitat. Each camera was placed at knee height (roughly 50 cm) above the surface, aimed in northern direction and angled to be parallel with the slope of the ground (Apps & McNutt,

FIGURE 1 Study area map showing the location of the open and closed habitats and camera trap locations at the Röbäcksdalen field station of the Swedish University of Agricultural Sciences, southwest of Umeå, Sweden. The map was constructed in QGIS 3.10 (QGIS.org 2021) and used as a background map © OpenStreetMap and © Google Satellite.

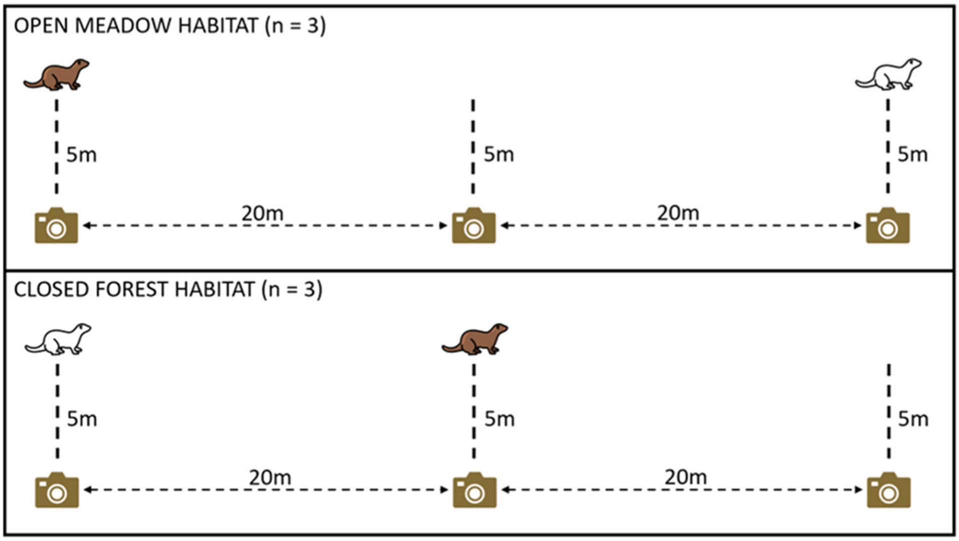


FIGURE 2 Experimental set-up as used during the study with a mustelid depicting a decoy. Each cluster of three cameras and two models was repeated three times per habitat. Decoy order was randomized.

2018; Meek et al., 2014). When triggered, cameras took 10 consecutive pictures with no delay. No quiet period was scheduled to fully monitor behavior of the animal triggering a camera. Furthermore, cameras were set to take a daily time-lapse image at 12:00 to check camera functioning and to monitor snow cover (Hofmeester et al., 2020).

We made a total of 12 decoys, 6 brown and 6 white, using rough "hairy" fabric of white and brown color (Supporting Information: Figure S1). The decoys resemble "Primos Sit n spin – crazy critter" which are used as attractants by hunters to lure predator species. The fabric was cut into pieces of 50 by 20 cm, and one end on the long side was filled with pillow stuffing to mimic a head. The size of the decoys resembled a variety of species expressing SCC in Scandinavia and fit somewhere between a mountain hare and stoat *Mustela erminea*. We attached decoys to aluminum sticks of 50 cm with iron wire to assure the decoys would stand upright when placed in the snow or ground in front of a camera trap (Supporting Information: Figure S2). Decoys were placed 5 m in front of the camera without any obstacles in between (Figure 2). The use of decoys has proven useful in a similar study executed by Atmeh et al. (2018).

We placed cameras in three clusters per habitat type, open and closed, during each recording round. Clusters were ideally placed at least 70 m apart during a recording round to secure independent observations between sites (Meek et al., 2014). Each recording round lasted for roughly 2 weeks, starting on the 2nd of March, and lasting for five rounds, until the 16th of May. During recording rounds, cameras were regularly visited to ensure that decoys were not removed, still visible and that cameras were properly functioning to minimize downtime of the cameras. After each recording round, the memory cards of the cameras were replaced, and clusters were moved at least 30 m to a new location to assure no overlap between clusters. Due to a lack of space in the closed forest habitat, we minimized the distance between clusters in the closed habitat to 15 m during the last experimental round. When relocating a cluster, treatment order (i.e., control, white decoy, and brown decoy) was changed so no decoy stood in the same location as the previous round to control for an effect of placement within clusters. We argue that the limited space between clusters in the same rounds or between rounds should not be problematic as spatial autocorrelation between camera trapping deployments is minimal even at distances as low as 10 m between cameras (Kays et al., 2021; Kolowski et al., 2021). Based on these studies, we assume our experimental set up will limit spatial autocorrelation as clusters are placed at a minimum of 70 m from each other during each round of sampling, while the minimum distance between clusters among different rounds of sampling was 15 m.

2.3 | Image processing

To analyze and process camera trapping data, we used the open-source application Trapper (Bubnicki et al., 2016). Pictures of the same deployment taken within 15 min of the previous picture were grouped into one single sequence or event (Hofmeester et al., 2020; Meek et al., 2014, 2016). For each sequence containing animals, we determined the following attributes: species, number of animals, interaction with decoy (True/False), camouflage mismatch of decoy (match/mismatch), and snow cover (%). We classified a predator as interacting with the decoy if it showed one of the following behaviors: observing the decoy, attacking the decoy, grabbing the decoy, sniffing the decoy, or urinating on the decoy, the latter two were mainly expected to be observed in mammalian predators (Atmeh et al., 2018). These interactions were considered as a potential "predation event." Camouflage mismatch of the decoy depended on the amount of snow or bare ground surrounding the decoy during each deployment. If a white decoy was standing in a snow-covered area with a radius of roughly 2 m, we classified the decoy as matching camouflage, otherwise, camouflage was set as a mismatch (Supporting Information: Figure S3). We applied the same principle for brown decoys but with bare ground instead of snow cover resulting in a match. We estimated snow cover for each picture in classes of 10%. We classified a decoy with no animal visits as mismatching with its environment when the decoy was mismatched with its environment for the majority the deployment (>50%), and vice versa for matched decoys based on time-lapse images.

2.4 | Statistical analyses

2.4.1 | Differences between deployment treatments

We used a generalized linear mixed model (GLMM) with Poisson error distribution and log link function to test for a difference in the number of predator visits per deployment between mismatched decoys, matched decoys, and control deployments within clusters and differences between habitats. The models were built using the R packages *lme4* and *lmerTest* (Bates et al., 2015; Kuznetsova et al., 2017, 2020). The model contained the number of visits as response variable and decoy treatment (control/match/mismatch) and habitat (closed/open) as fixed effects. We included the natural logarithm of camera effort (measured in days) as offset to correct for cameras that did not function properly for the whole deployment (e.g., due to cameras on poles falling over during snowmelt). Furthermore, we included cluster ID as a random intercept to correct for our clustered experimental design. We did not conduct model selection as we had clear hypotheses that we tested using single models. Thus, we used the slope estimates and *p*-values for each of the covariates in our models as a test of our hypotheses, precluding the need for model selection. We visualized the model outcomes as effect plots where the difference in the number of visits between treatments using the R add-on packages *jtools* and *interactions* to control for the variance created by habitat and random variables (Long, 2021a, 2021b). To test for differences in predator visits between control, mismatched, and matched deployments, we used Tukey's post hoc test using the *multcomp* package (Hothorn et al., 2008). We also assessed potential variation in the attraction of different predator types (mammalian vs. avian) using the previously mentioned model. In addition, we tested for an effect of decoy color (brown/white) and snow cover (0/1) on predator visits. Snow cover (0/1) was determined by estimating if a decoy was, within a diameter of 2 m around the decoy, mainly (>50%) surrounded by snow (1) or not (0). The model again contained number of visits as response variable and decoy color, snow cover and the interaction between decoy color and snow cover as fixed effects. Cluster-ID was set as a random intercept and the log of camera effort as an offset. In addition, we tested for a difference in predator occurrence between open and closed habitat by only using the data from the control cameras (cameras without decoys) and fitting a GLM with Poisson error distribution and log link function to the number of predator passages with habitat as covariate and the natural logarithm of camera effort as offset. To test if predators were more likely to interact with mismatched decoys, we constructed a GLMM with the interaction between a predator and decoy (0 = no interaction, 1 = interaction) per observation as response variable, camouflage (match/mismatch) as fixed effect, and cluster ID as random intercept. Lastly, we tested if a there was a difference in interaction likelihood between mammalian and avian predators, as these groups might react differently to decoys based on foraging strategies (olfactory vs. visual). For this, we ran the same model for mammalian and avian predators separately.

2.4.2 | Time-to-event analysis

To assess for differences in predation events between decoys that matched and mismatched with their environment, we used time-to-event or survival analysis. Time-to-event analysis is a statistical analysis using the time until an event occurs as an outcome variable (Bischof et al., 2012, 2014; Kleinbaum & Klein, 2012). Time-to-event analysis uses "events" to analyze survival over time and, in this study, we interpret a predator interacting with the decoy as a proxy for predation and thus for survival, survival and fitness are commonly used terms in camouflage studies (Cuthill et al., 2005; Heninger et al., 2020). We used right-censoring for deployments with decoys which had no interaction with predators, even if a predator was captured on camera. Right-censoring allows to include data where no interaction between a predator and a decoys has been observed by including the full deployment time (Bischof et al., 2014; Kleinbaum & Klein, 2012). If a decoy had multiple predator interactions, we reset the time of the event after each interaction creating a theoretical new decoy. Time to event for these decoys is set to be the time from one interaction to the next interaction. In addition, we performed the analysis without repeated interactions to test if including repeated measurements from one deployment as independent observations influenced our results. Next, we conducted a survival analysis where any predator visit, so not only interactions, were considered as predation events to test if a similar pattern is found compared to the survival analysis with only interactions. We did this to test whether results were not dependent on how we defined a "predation event." In this analysis, deployments with no predator visits were right censored.

For the time-to-event analysis, we used the R add-on package *survival* (Therneau & Grambsch, 2000). To visualize survival over time, using Kaplan–Meier curves and summarizing survival analysis results, we used the R add-on packages *survminer* and *ggplot2* (Kassambara et al., 2021; Wickham et al., 2021). Kaplan–Meier curves show survival probabilities based on cumulative events. We conducted two versions of the time-to-event analyses. First, we tested the difference between matched and mismatched decoys independent of habitat. Second, we tested the difference between matched and mismatched decoys in both open and closed habitats. Differences between survival curves of different variables (camouflage: match/mismatch and habitat: open/closed) were calculated using a non-parametric log-rank test. In addition to survival curves, we calculated hazard ratios (HRs) for camouflage and habitat to assess the difference in risk between habitats and matched and mismatched decoys. We used R version 4.1.2 in R Studio 2021.09.1 (R Core Team, 2023; RStudio Team, 2023) for all analyses.

3 | RESULTS

3.1 | Camera trap data

Camera traps recorded a total of 102,390 pictures of which blank, animal, human, and vehicle pictures contributed 76.9%, 12.4%, 4.2%, and 6.5%, respectively. Of the 12,696 animal pictures, 86.8% and 13.2% were nonpredator and predator pictures, respectively, resulting in 1680 predator pictures. Due to snowmelt causing our cameras in the open habitat to continuously fall over during the fifth round of data collection, we decided to omit this last round of data and keep the fifth round in closed habitat as we have limited observations in the absence of snow. We thus used four rounds of data in the analysis of the open habitat and five rounds in the closed habitat.

In terms of events, or sequences, mismatched decoys, matched decoys, and control deployments had 64, 47, and 46 predator visits, respectively. In closed habitat, 119 predator visits were recorded and in open habitat 38 predator visits were recorded. When only looking at the control cameras without decoys, predators occurred more often in closed habitat in comparison to open (GLM, $\beta = -1.7384$, $p < 0.001$). Various avian and mammalian predators were recorded vising the decoys both in open as closed habitat (Supporting Information: Table S1).

Snow cover remained relatively high in both closed and open habitats until the middle of April (Supporting Information: Figure S4). Hereafter, the snow quickly started to melt creating more bare ground. Closed habitat showed higher variation in periods of snow cover and bare ground in comparison to open habitat.

3.2 | Decoy attraction

Mismatched decoys attracted more predators compared to both decoys that matched their environment (Tukey HSD, $\beta = 0.7351$, $p < 0.001$) and the controls with no decoy (Tukey HSD, $\beta = 0.5624$, $p = 0.0074$), while matched decoys did not differ from the control (Tukey HSD, $\beta = -0.1728$, $p = 0.6928$; Figure 3a). Deployments in open habitats attracted fewer predators in comparison to closed habitats (GLMM, $\beta = -0.0112$, $p = 0.0499$). We observed more mammalian predator visits at the deployments compared to avian when including predator type (mammalian vs. avian) in the analysis (GLMM, $\beta = 0.3655$, $p = 0.0205$).

We found strong evidence that the interaction between decoy color and snow cover affected predator visits, meaning that snow

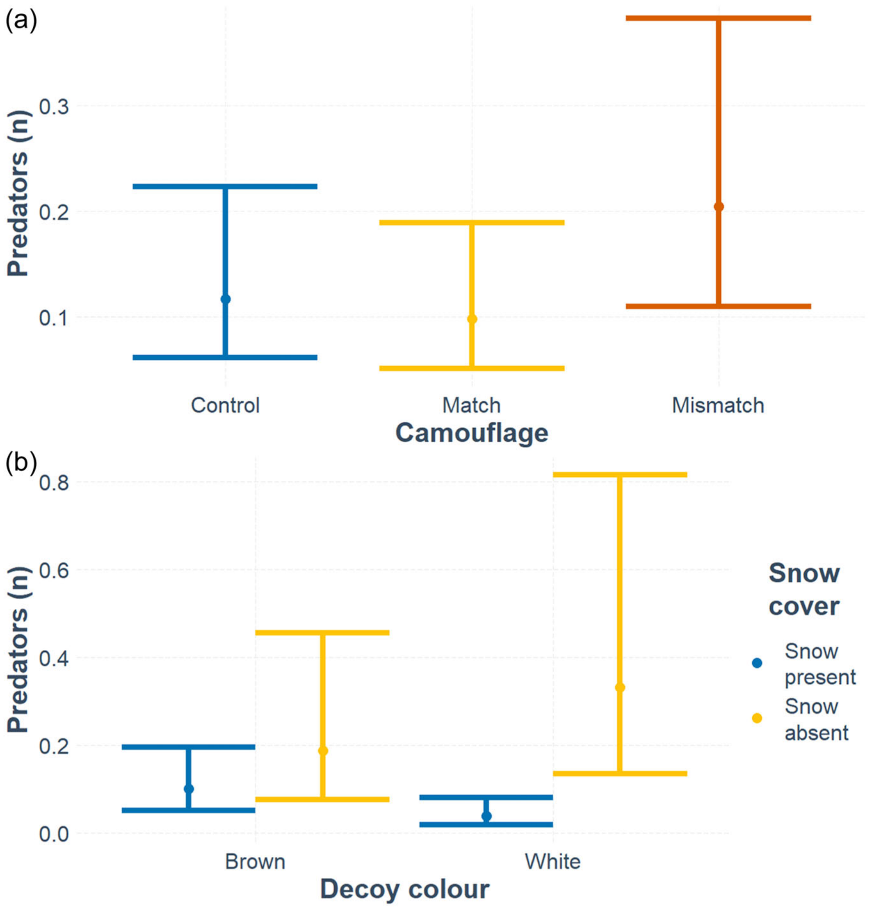


FIGURE 3 (a) Effect plot showing the differences (with 95% confidence intervals) in the number of predator visits for cameras with control, matched, and mismatched treatment based on the generalized linear mixed model (GLMM) predictions. Mismatched decoys attracted more predators in comparison to the control treatment (Tukey HSD, $p = 0.0073$) and matching treatment (Tukey HSD, $p < 0.001$). No difference in attraction was found between control treatment and matching decoys (Tukey HSD, $p = 0.6928$). (b) Effect plot showing the differences (with 95% confidence intervals) in the number of predator visits for cameras with brown and white decoys with snow present and absent. When snow was present white decoys attracted less predators (GLMM, $p < 0.001$). White decoys attracted more predators in periods when snow was absent (GLMM, $p < 0.001$). No evidence was found for a difference in predator visits for brown decoys in the different periods of snow cover (GLMM, $p = 0.2332$).

cover reduced predator visits to white but not to brown decoys (GLMM, $\beta = 2.1306$, $p < 0.001$). (Figure 3b, Supporting Information: Table S2).

When only looking at visits where predators actually interacted with the decoys, we found no evidence that predators were more likely to interact with mismatched decoys ($n = 11$) in comparison to matched decoys ($n = 4$) (GLMM, $z = 0.977$, $p = 0.328$). When separating mammalian and avian predators, we found similar patterns. Interactions with decoys did not differ between matched and mismatched decoys for either mammalian (GLMM, $z = 0.681$, $p = 0.496$) or avian predators (GLMM, $z = 0.312$, $p = 0.755$).

3.3 | Time-to-event analysis

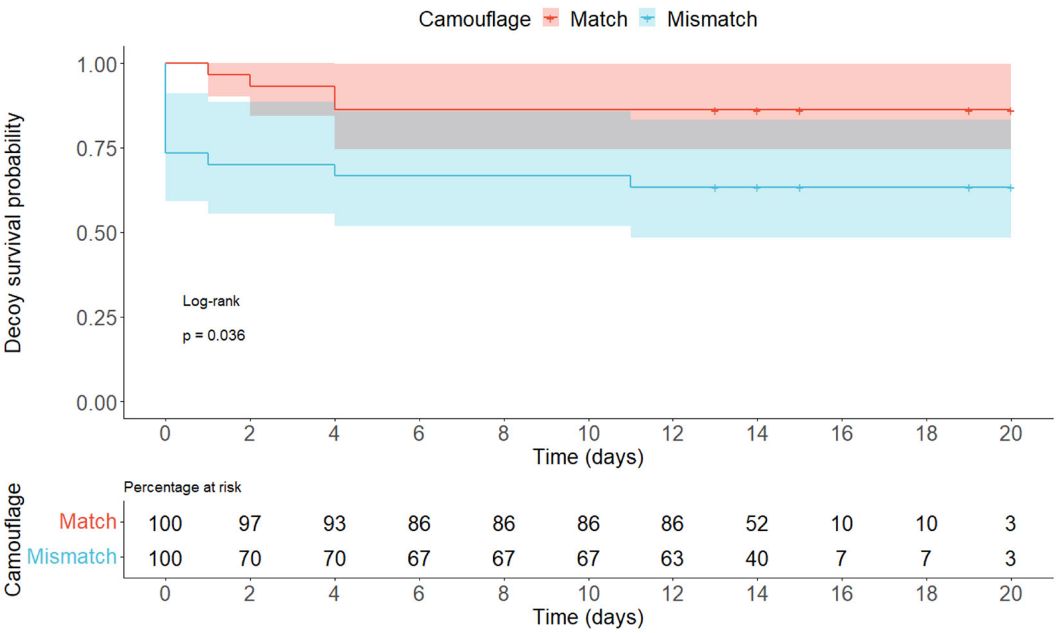
Predation events occurred faster for camouflage-mismatched decoys than for camouflage-matched decoys, thus resulting in a faster decrease in survival (Figure 4, $p = 0.036$). For mismatched decoys survival after 2 days was 0.70 whereas the probability of survival for matched decoys was 0.97 on the second day. The HR for mismatched decoys was 3.50 times (95% confidence interval [CI]: 1.1, 11) higher in comparison to matched individuals ($z = 2.138$, $p = 0.032$). In contrast to our expectations, the HR for decoys was 3.4 (95% CI: 0.08–1.03) times lower for decoys in open meadow habitats in comparison to decoys in closed forest habitats ($z = -1.922$, $p = 0.055$). We found a similar result when eliminating repeated measures (i.e., decoys with multiple events) for camouflage (HR = 4.86, 95% CI = 1.03, 23.0, $p = 0.046$) but no effect of habitat (HR = 0.45, 95% CI = 0.12, 1.76, $p = 0.3$).

When separated into four categories based on camouflage and habitat, mismatched decoys in closed habitat presented an 8.64 (95% CI: 1.09, 68.4) higher hazard in comparison to matched decoys in open habitat ($z = 2.044$, $p = 0.041$; Supporting Information: Figure S5). Without repeated measures, HR of mismatched decoys in closed habitats was found to be slightly lower and less evident (HR = 6.12, 95% CI = 0.74, 50.9, $p = 0.094$).

When looking at all predator visits, and not only predators that interacted with the decoys, we found stronger evidence for a lower HR for mismatched decoys (HR = 1.74, 95% CI = 1.21, 2.51, $p = 0.003$) and a less evident effect of open habitat (HR = 0.7, 95% CI = 0.48, 1.02, $p = 0.066$) (Supporting Information: Figure S6).

4 | DISCUSSION

Animals expressing SCC are experiencing an increasing camouflage mismatch between their fur or plumage colouration and their environment, because of shorter periods with snow-cover. As a result, their survival and fitness are expected to decline. Here, we experimentally tested if a camouflage mismatch increases predator attraction and detection, consequently, reducing survival. We found that a mismatch between the color of decoys, resembling animals with seasonal color molts, and their environment increases attraction of potential predator species and subsequently increasing predator events, lowering survival over time. Cameras aimed at mismatched decoys captured more predator visits in comparison to matched decoys. Moreover, we showed that snow cover influenced this pattern, where the presence of snow led to fewer predator visits to



Camouflage	0	2	4	6	8	10	12	14	16	18	20
Match	100	97	93	86	86	86	86	52	10	10	3
Mismatch	100	70	70	67	67	67	63	40	7	7	3

FIGURE 4 Kaplan–Meier curves for the survival of matched and mismatched decoys based on cumulative predator interaction events. Shaded bands depict 95% confidence intervals. The lower survival table shows the percentage of the population at risk over time.

white decoys but not to brown decoys. More predators were observed in the closed forest habitat in comparison to the open meadow habitat, and more mammalian predators were observed at the deployments compared to avian predators. We found no evidence that predators were more likely to interact with mismatched decoys in comparison to matched decoys. Nevertheless, the time-to-event analysis of predators interacting with decoys showed that survival probability decreased faster for mismatched decoys in comparison to matched decoys. Lastly, deployments in the closed forest habitat attracted a higher number of predators in comparison to the deployments in the open meadow landscape, and indeed, we showed that decoys that stood in open habitat experienced higher survival in comparison to decoys in closed habitat. An analysis using only data from the first four rounds, to test for an unbalanced design, showed similar results, however, due to limited numbers of observations, we have decided to only show results including round 5.

As predicted, camouflage-mismatched decoys were detected more often than camouflage-matched decoys (Figure 3a). In addition, we observed evidence of an interaction between decoy color and snow cover, namely white decoys attracted less predators in snow cover in comparison to brown (Figure 3b), supporting the idea that the number of predator visits is not only depending on decoy color but also on the environment. This result is in line with previous research, where mismatched decoys, mimicking moths (Cuthill et al., 2005), mice (Vignieri et al., 2010), and least weasel (Atmeh et al., 2018) were more often visited or detected by predators in comparison to models that matched their environmental background. These findings show that background-matching camouflage plays an important role in the detection of prey species and should be optimized by prey when trying to avoid predators (Caro & Koneru, 2021). Our results are in line with the idea that the main function of camouflage is considered to be an adaptation to decrease detection by predators and therefore decreasing predation risk and increasing potential survival (Stevens & Merilaita, 2009; Stevens & Ruxton, 2019; Zimova et al., 2018).

If the main function of camouflage is indeed to reduce predation, climate change-induced increases in camouflage mismatch could be detrimental to the survival of animals expressing SCC. Indeed, we found moderate evidence for a higher likelihood and faster occurrence of predation events and thus a lower survival for mismatched decoys in comparison to matched decoys (Figure 4). After 2 days, mismatched decoys reached a survival probability of 0.70 whereas matched decoys had a survival probability of 0.97. This finding suggests that animals expressing SCC may indeed experience a lower survival with earlier onset of snowmelt and, therefore, increasing camouflage mismatch. Zimova et al. (2016) previously found that camouflage mismatched snowshoe hares experienced a weekly survival decrease of 7%. The lower effect size found by Zimova et al. (2016), relative to our finding, may be due to their study using live animals, which can express antipredator behavior in contrast to our decoys. When including all predator visits, and not only those directly interacting with the decoys, we found the same, although smaller, effect of mismatch on survival (Supporting Information: Appendix, Figure S5). This shows that the survival decrease of mismatched decoys does not depend on the interpretation of a "predation event" but on a pattern that is observed independently of this interpretation. Importantly, our findings were robust even when excluding repeated interactions of a predator with the same decoy. One could state that a predator would return to a decoy out of interest and including these repeated visits of certain "curious" predator individuals may bias results. Previous studies looking at habituation of predators to unrewarding olfactory cues show that predators are less likely to be attracted to cues which are nonrewarding (Latham et al., 2019; Norbury et al., 2021). Therefore, we do not expect that our, nonrewarding, visual cues resulted in habituation of predators becoming more attracted over time. In conclusion, our experiment with decoys confirm the outcome of previous studies performed on live snowshoe hares showing decreased survival with increasing background mismatch and losing their adaptive advantage (Wilson et al., 2019; Zimova et al., 2016).

In contrast to our expectations, we found moderate evidence that decoys in closed habitats attracted more predator visits than open habitat. The HR of decoys placed in the open habitat was almost four times lower in comparison to decoys placed in closed habitats, independent of matching or mismatching camouflage.

We expected the negative effect of mismatching background camouflage to be lower in a structurally more complex habitat such as a forest in comparison to a structurally more simple area such as an open meadow where obstacles are absent, making a mismatched decoy more conspicuous (Merilaita & Merilaita, 2003; Rowe et al., 2021; Stevens & Merilaita, 2009). In a translocation study, conducted by Wilson et al. (2019, 2020), it was found that camouflage mismatch in snowshoe hare was mitigated by vegetation density in early successional habitat. In contrast, we found that both predator attraction and survival decreases were highest in closed habitats. We explain this from a difference in predator composition between both habitats, as our control cameras in closed habitat detected more predators in compared to open habitat. In Northern Sweden, most avian predators are migratory (Calladine et al., 2012; Kjellén & Roos, 2000) and especially avian predators rely on visual cues when hunting and therefore prefer to forage in open landscapes (Heninger et al., 2020; Potier et al., 2018). Therefore, we expected them to have a larger impact in the open habitat. Hence, the low number of predator attractions in the open landscape and the low number of avian predators at the deployments in our study could be explained by the timing of our study with birds of prey not being present in the study area until late April. Furthermore, birds of prey are generally difficult to observe using camera traps and might observe a decoy and respond to it without being captured by the camera trap (Akcali et al., 2019; Blake et al., 2011; Naing et al., 2015). Red foxes show a preference for closed habitat in comparison to open habitat, which could explain the relatively high number of mammalian predator observations in the closed habitat (Díaz-Ruiz et al., 2016; Willebrand et al., 2017).

In our experiment, the period after snowmelt was rather short, which limits our findings for this period and could explain why we did not find an effect of matching brown decoys on survival after snowmelt. The majority of our data was in fact collected during periods of snow cover, during which brown decoys were mismatched and white decoys matched with their environment. This scenario is the opposite of what is expected to increasingly occur, as climate change is expected to increase mismatch between white individuals in periods of little to no snow cover in both autumn and spring (Hofmeester et al., 2020; Mills et al., 2018; Zimova et al., 2018). However, our findings can be seen as evidence for why subspecies of animals expressing SCC that do not turn white in winter, such as *M. n. vulgaris*, do not occur in northern Sweden. As snow cover remains present in northern Scandinavia during almost half of the year, subspecies that do not turn white will have lower survival in comparison to subspecies that do turn white (Irannezhad et al., 2017). Thus, we do not expect local extinction of animals expressing SCC in northern Sweden, at least in the foreseeable future. The future of species expressing SCC might therefore be heavily dependent on their ability to adapt to the changing environment, either behavioral or morphological. When no change is observed, the demographic consequences might be grim (Zimova et al., 2016).

5 | CONCLUSION

To conclude, we present experimental evidence that animals that change to a white coat during winters with snow benefit from reduced detection by predators and reduced predator events, resulting in higher survival. From this, one would expect that such animals will experience reduced fitness with decreasing snow cover due to climate change if they cannot change the timing of their coat color to match the changing snow conditions. The results presented here help us understand why animals have evolved a white winter coat and express SCC at higher latitudes. Camouflage matching with the environment results in a lower detection by predators and consequently higher survival of animals. Negative effects of camouflage mismatch have previously been documented for species such as mountain hares, snowshoe hares, least weasel, willow, and rock ptarmigan (Atmeh et al., 2018; Imperio et al., 2013; Pedersen et al., 2017; Steen et al., 1992; Zimova et al., 2016). However, few studies that we know of have confirmed and quantified this mismatch effect through an experimental set-up. With the predicted climate scenarios, the mismatch between white color morph and background is only expected to increase (Mills et al., 2013). As limited plasticity is observed in the onset of SCC, animals expressing SCC are expected to undergo a decrease in survival, resulting in decreasing populations or even local extinction (Atmeh et al., 2018; Kumar et al., 2020; Zimova et al., 2018).

AUTHOR CONTRIBUTIONS

Pieter J. Otte: Conceptualization (supporting); data curation (lead); formal analysis (lead); investigation (lead); resources (Lead); validation (lead); visualization (lead); writing—original draft (lead); writing—review and editing (supporting). **Joris P. G. M. Cromsigt**: Conceptualization (supporting); methodology (supporting); supervision (supporting); writing—review and editing (supporting). **Christian Smit**: Conceptualization (supporting); methodology (supporting); supervision (supporting); writing—review and editing (supporting). **Tim R. Hofmeester**: Conceptualization (lead); data curation (supporting); formal analysis (supporting); methodology (supporting); resources (supporting); project administration (lead); supervision (lead); visualization (supporting); writing—original draft (supporting); writing—review and editing (lead).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data and scripts used in this manuscript are available from Zenodo: https://zenodo.org/doi/10.5281/zenodo.10478712.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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