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Snow cover related camouflage mismatch decreases survival

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Abstract

Climate change is expected to decrease winter severity at high latitudes, resulting in reduced days of snow cover. Several mammalian and avian species in the northern hemisphere express a seasonal colour coat (SCC) making them white in winter periods and brown or dark in summer. Reduced number of snow-covered days causes an increasing camouflage mismatch between the white coat of animals expressing SCC and their winter background. Camouflage is thought to be the function of coat colour, lowering detectability by predators. Due to climate change, snow cover is expected to start later in autumn and end earlier in spring at high latitudes. Despite some observed species plasticity in timing of moulting, climate change is occurring at such a rate that plasticity is thought to be insufficient to cope with the changing environment. In this study, decoys resembling the average size of SCC species in Scandinavia were used to assess the difference in detection by predators between mismatched and matched individuals. Decoys were used in camera trap clusters consisting of three camera traps, one with no decoy, one with a white decoy and one with a brown decoy. Clusters were placed during periods of snow cover and after snowmelt to test how a camouflage mismatch affects detection by and interaction with predators in both open meadow habitats and closed forest habitats. Images from camera traps were classified, the data was analysed using generalised linear mixed models and survival analysis to determine which factor explained predator detection best and how being mismatched affected survival of decoys. I found that mismatched decoys attracted more predators in comparison to matched decoys. In addition to increased attraction of predators, survival probability of mismatched decoys decreased more rapid than matched decoys. This effect was stronger in closed forest habitats in comparison to open meadow habitats, hazard of being in open habitats was overall lower than in closed habitats. These results suggest that the decline of populations expressing SCC could indeed be caused by decreased survival due to mismatching camouflage. If adaptation, either morphological or behavioural, is not able to keep up with the rapidly changing environment, species expressing SCC will undergo increased predation pressure potentially causing rapid population declines.

Keywords: Climate change, snow cover, seasonal colour coat, crypsis, mismatch, camera trap, survival analysis.

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Abbreviations

SCC	Seasonal Colour Coat
GLMM	Generalized linear mixed model
SLU	Swedish University of Agricultural Sciences
RUG	University of Groningen

1. Introduction

Animals are subjected to changes in environmental conditions due to climate change, threatening global biodiversity (Walther e.a. 2002; Parmesan 2006; Bellard e.a. 2012). At high latitudes, where the increase in temperature and liquid precipitation period has been greatest, climate change results in an earlier onset of spring and late end of autumn (Parmesan 2006; Trenberth 2011; IPCC 2021). At high latitudes, from temperate to polar zones, animal species express specific seasonal and circannual traits to cope with harsh winter conditions (Varpe 2017). Traits such as hibernation, seasonal migration and colour coat moulting are expressed by animals to increase fitness in periods of low productivity and survival (Williams e.a. 2015; Varpe 2017; Zimova e.a. 2018). Shifts of these circannual and physiological traits are needed for animals from temperate to polar regions to adapt to changing conditions (Both e.a. 2006; Blix 2016; Zimova e.a. 2018).

Seasonal colour coat (SCC) moulting is a key trait used by at least 21 bird and mammal species in the Northern hemisphere to adapt to harsh winter conditions (Mills e.a. 2013, 2018). During SCC moulting, animals change their fur or plumage colour to white in autumn and brown or grey in spring (Mills e.a. 2018; Zimova e.a. 2018). SCC is a form of camouflage, or crypsis, functioning as a defence mechanism against predation in which animals use body colouration to lower the risk of being detected (Caro 2005; Di Bernardi e.a. 2021; Murali e.a. 2021). SCC is considered a form of camouflage called ‘background matching’, in which an animal will try to match its environmental background as much as possible but does not resemble it perfectly, as the background might change for moving animals (Caro & Koneru 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 e.a. 2017; Zimova e.a. 2018). However, crypsis is recognised as the main driver of winter colouration, as it provides a lower predation risk for prey and predation advantage for predators expressing SCC (Galeotti e.a. 2003; Caro 2005; Zimova e.a. 2018; Di Bernardi e.a. 2021). Nevertheless, little is known about selective pressure for seasonal colouration and how this is affected by a mismatching environment.

Earlier snowmelt in spring and late snowfall in autumn at high latitudes causes an increasing mismatch between the white winter coat colour of animals expressing SCC moulting and snow-covered habitat (Mills e.a. 2013; Kunkel e.a.

2016; Zhu e.a. 2019; Zimova e.a. 2020b; a). A mismatch between a trait such as SCC moulting and the favourable corresponding environment can result in negative fitness costs. Previous research on snowshoe hares *Lepus americanus* predicted that temporal mismatch between white hares and brown background in either spring or autumn will increase rapidly in this century (Mills e.a. 2013). If no evolutionary change in seasonal mould is observed, the expected decrease in snow cover duration will result in increased predation pressure on a variety of species expressing SCC (Mills e.a. 2013; Pedersen e.a. 2017; Atmeh e.a. 2018). Hence, models predicting winter colour phenotypes in individuals found snow cover and climate variables such as seasonality and temporariness of snow as most important covariates (Mills e.a. 2018).

Moulting of fur or plumage is, like other life events such as hibernation or migration, coordinated by internal circannual rhythms in combination with external cues, the most important one being photoperiod (Helm e.a. 2013; Zimova e.a. 2018; Melin e.a. 2020). Especially at mid-range and high latitudes, changes in photoperiod throughout the year are considered a dominant source of information for seasonal morphological, behavioural and physiological changes (Helm e.a. 2013). Different populations of species expressing SCC have adapted to moult at different photoperiods to optimise moulting according to their environment (Zimova e.a. 2020b). As photoperiod patterns are not changing with climate change, the optimal timing of populations to adapt to seasonal changing conditions is potentially mismatched (Bradshaw & Holzapfel 2007).

The most immediate way to cope with climate change is phenotypic plasticity (Zimova e.a. 2014). Moulting rates are suggested to be adaptive to snow cover and temperature, resulting in a decreased mismatch in warmer springs in comparison to colder springs (Mills e.a. 2013; Zimova e.a. 2014). However, plasticity linked to photoperiod is likely to be limited, to fully react to climate change (Visser 2008; Zimova e.a. 2014).

Despite the plasticity in moulting rate of species expressing SCC, as found in several species of the *Lepus* genus, climate change is expected to proceed too rapidly to prevent an increasing mismatch (Mills e.a. 2013; Quintero & Wiens 2013; Zimova e.a. 2020a). Under current temperature rise predictions, increasing mismatch is predicted to cause a steep decline in annual survival, threatening species and populations expressing SCC (Zimova e.a. 2016). Some subspecies of animals expressing SCC do not moult or moult to grey instead of white, such as *Mustela nivalis vulgaris* (Atmeh e.a. 2018; Giska e.a. 2019). With decreasing snow cover, these subspecies could have a selection advantage in comparison to subspecies that turn white (Atmeh e.a. 2018). Where various studies have mainly studied the consequences of SCC mismatch in terms of demography of wild populations, less is known about selection pressure in terms of predation. Previous research mainly used snowshoe hares as a study subject for climate-change induced

SCC mismatch, whereas species expressing SCC in Scandinavia are heavily understudied (Zimova e.a. 2014, 2020b; Wilson e.a. 2019). One of the species expressing SCC, the least weasel *Mustela nivalis*, occurs in boreal habitats throughout Scandinavia and the subspecies *Mustela nivalis nivalis* is characterised by a white winter coat (Hellstedt e.a. 2006; Atmeh e.a. 2018). Weasels are vulnerable to attacks by several mammalian and avian predator species and predation is considered an important mortality factor for their populations (Zub e.a. 2008; Ylönen e.a. 2019). Thus, increasing mismatch in SCC moulting is suggested to result in increased predation pressure and therefore selection. Weasels play an important role in regulation of small mammal communities in Fennoscandia and extinction of least weasel could have cascading effects on other species (Hanski e.a. 2001; Ylönen e.a. 2019). I used decoys resembling the average size of animals expressing SCC in Fennoscandia, therefore, the results from this study can be applied to a broader range of small animals expressing SCC in Fennoscandia such as mountain hare *Lepus timidus* or willow ptarmigan *Lagopus lagopus* (Hofmeester e.a. 2020; Melin e.a. 2020).

In this study, I experimentally tested how a camouflage mismatch of decoys resembling animals expressing SCC affected their survival. Additionally, I tested whether a difference in survival of decoys exists between different habitat types. The study took place during both periods of snow cover and snowmelt where camouflage mismatch shifted from brown during the period of snow cover, to white during the period after snowmelt. The experiment was conducted in two different types of habitats: open meadows and closed forest areas. I used camera traps to determine if an attraction difference exists between decoys. Camera traps are widely used in a broad range of ecological studies applications, such as phenological mismatch studies, and can monitor a broad range of predators (Meek e.a. 2016; Hofmeester e.a. 2020; Zimova e.a. 2020b). Both the number of predators captured on camera trap images and the interaction of predators with decoys were used to assess if predators are more likely to detect mismatched decoys and if so, whether this increases the probability of interaction with a decoy. Consequently, interactions with the decoy were used as events to calculate how a camouflage mismatch affects survival using survival analysis to determine how the survival probability of a mismatched individual differs from a matched individual.

Based on previous studies, I expected that a mismatch in camouflage results in higher detectability by predators in comparison to matching camouflage due to contrasting decoy coat and background (Zimova e.a. 2016, 2018). Furthermore, as previously stated, reduced detectability of predators is considered one of the main drivers of SCC (Mills e.a. 2018; Zimova e.a. 2018). Hence, mismatched decoys are expected to attract more predators. Detectability is expected to be higher in open meadow habitats in comparison to closed forest habitats as detection probability by predators is lower when more obstacles are present within a habitat or the

background is more complex (Wheatley e.a. 2020; Murali e.a. 2021; Rowe e.a. 2021). In addition, I expect closed habitat to be mainly dominated by mammalian predator species, such as red fox *Vulpes vulpes* and pine martens *Martes martes*, who are predominantly olfactory hunters and are therefore expected to be less attracted by decoys (Ruzicka & Conover 2011; Díaz-Ruiz e.a. 2016; Willebrand e.a. 2017). In the open habitats, more avian predators are expected to forage, which rely on visual cues (Potier e.a. 2018; Heninger e.a. 2020). Hence, I expect the effect of camouflage mismatched decoys to be larger in open habitats in comparison to closed.

2. Material & methods

2.1 Study Area

The study was conducted in the area surrounding the Röbbäcksdalen field station of the Swedish University of Agricultural Sciences, south-west of Umeå, Sweden (N 63.811°/E 20.242°). The area is characterised by agricultural fields in the south to north-west from the field station and some patches of boreal forest on the north and east sides of the area (figure 1). Agricultural fields in the study area consisted of a variety of meadows with different crops, from here on regarded as open habitats, and small patches of boreal forests as closed habitats. For open habitat, pastures managed by livestock grazing were selected (figure. 1). Boreal forests in Fennoscandia are mainly dominated by coniferous spruce species, such as European spruces *Picea abies* and Scots pine *Pinus sylvestris*, silver birch *Betula pendula* and downy birch *Betula pubescens* (Huuskonen e.a. 2021). Potential predator species in the area consist 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.

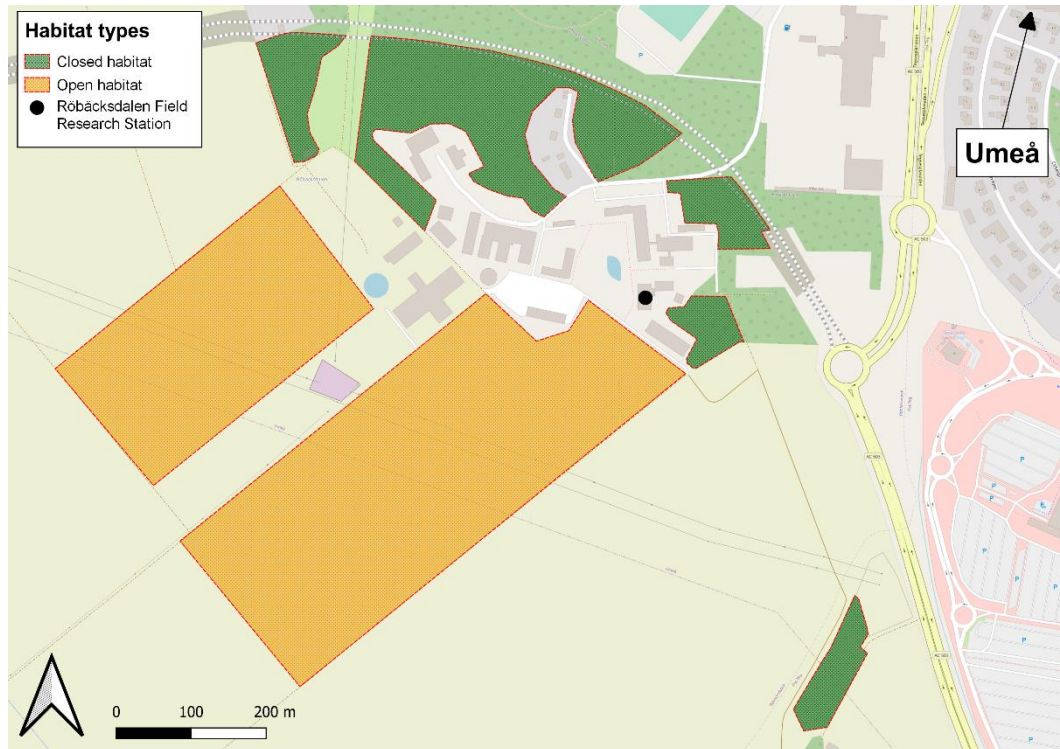


Figure 1: The study area and used fields in Röbbäcksdalen south-west of Umeå. The map was constructed in QGIS 3.10 (QGIS.org 2021) and uses as background map © OpenStreetMap.

2.2 Camera trapping design

A total of 18 camera traps (RECONYX® HyperFire 2™) were used to monitor 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 can be investigated as well as interactions, specifically in studying predator-prey interactions (Caravaggi e.a. 2017; Smith e.a. 2020). I deployed clusters consisting of three cameras (figure 2). Within each cluster, cameras were placed 20 meters apart: one control with no decoy, one with a white decoy and one with a brown decoy. I 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 ground, aimed in northern direction and angled to be parallel with the slope of the ground (Meek e.a. 2014; Apps & McNutt 2018). Cameras were set to take ten consecutive pictures with no delay after triggering. No quiet period was scheduled to fully monitor behaviour of the animal triggering a camera.

A total of twelve decoys, six brown and six white, were made using rough 'hairy' fabric of white and brown colour (appendix: figure 8). The fabric was cut into pieces of 50 by 20 centimetres, and one end on the long side was filled with pillow stuffing to mimic a head. Size of the decoys resembles a variety of species expressing SCC in Scandinavia and fits somewhere between a mountain hare and

stoat *Mustela erminea*. Decoys were attached to an aluminium stick 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 (appendix: figure 9). Decoys were placed five meters in front of the camera without any obstacles in between (figure 2).

Three clusters were placed per habitat type, open and closed, during each recording round. Each cluster was ideally placed at least 100 meters apart during a recording round to secure independent observations between sites. However, this proved unfeasible in forest habitats so there a minimum of 70 meters was used (Meek e.a. 2014). Each recording round lasted for roughly two weeks, starting on the 2nd of March, and lasting for five rounds. During recording rounds, cameras were regularly visited to ensure that decoys were not removed, still visible and cameras were properly functioning to minimize downtime of the cameras (appendix: table 6). After each recording round, memory cards of cameras were replaced, and clusters were moved at least 30 meters to a new location to assure no overlap between clusters. However, due to the lack of space in the closed forest habitat in the last recording round, distance between clusters at different times was set to 15 meters. The limited space between clusters in the same rounds or between rounds should not influence the data as spatial autocorrelation between camera trapping deployments is minimal even at low distances between clusters (Kays e.a. 2021; Kolowski e.a. 2021) When relocating a cluster, treatment order (i.e., control, white decoy, and brown decoy) was changed randomly to control for an effect of place within clusters.

Table 1: Species expressing SCC that are present in Fennoscandia, their trophic level and average body size. Data was obtained from the Animal Diversity Web using the Qaarvark tool (<https://animaldiversity.org/>)

Common name	Latin name	Trophic level	Average body length (mm)
Mountain hare	<i>Lepus timidus</i>	Prey	520
Least weasel	<i>Mustela nivalis</i>	Prey, predator	190
Stoat	<i>Mustela erminea</i>	Prey, predator	250
Willow ptarmigan	<i>Lagopus lagopus</i>	Prey	356

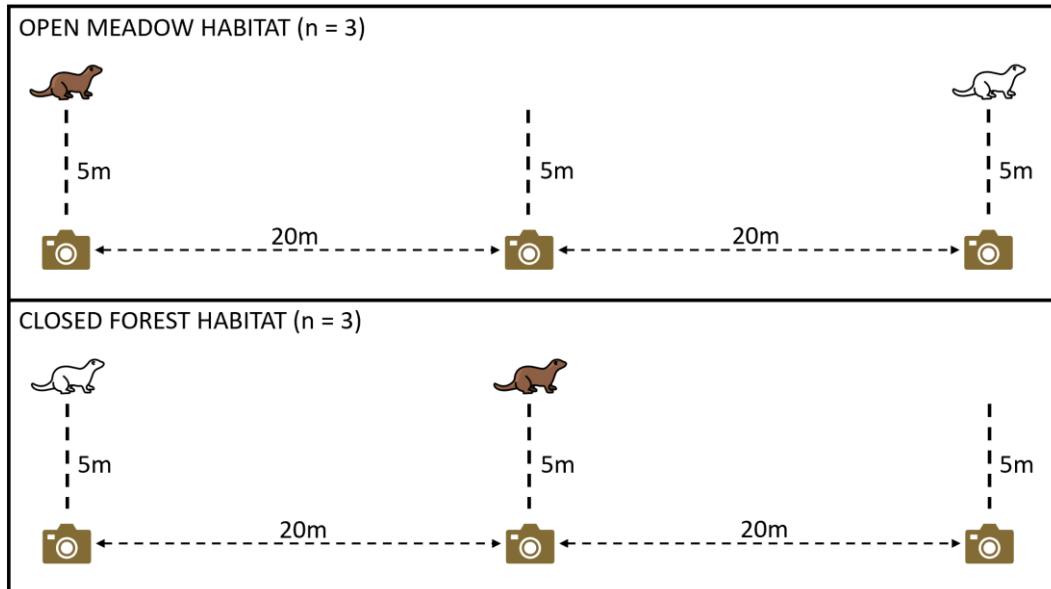


Figure 2: Experimental design to assess the difference in predator attraction between decoys of different colours. Each sampling cluster of three cameras and two models was repeated three times per habitat types ($n = 3$). Decoys were placed in random order. Sampling periods consisted of periods of snow cover and periods after snow melt.

2.3 Image processing

Camera trapping data were processed and analysed using the open-source application Trapper (Bubnicki e.a. 2016). Pictures of the camera traps were uploaded in Trapper as JPGs. Pictures of the same deployment that were taken within 15 minutes of the previous picture were grouped into one single sequence or ‘event’ (Meek e.a. 2014, 2016; Hofmeester e.a. 2020). For each picture, the following attributes were determined: is empty (True/False), observation type (human/animal/vehicle), species, count, interaction with decoy (True/False), camouflage mismatch of decoy (match/mismatch), and snow cover (%).

If an animal was simply observed in the picture without interacting with the decoy, interaction was put as ‘false’. If an animal was observed interacting with the decoy through detection behaviour such as observing, sniffing, taking, urinating, or attacking, interaction was put as ‘true’ (appendix: figure 10) (Atmeh e.a. 2018). Camouflage mismatch of the decoy depended on the amount of snow or bare ground surrounding the decoy. If a white decoy was standing in a snow-covered area with a radius of roughly two meters, it was classified as matching camouflage, otherwise, camouflage was set as mismatch. I applied the same principle for brown decoys but with bare ground instead of snow cover resulting in a match. Snow cover was roughly estimated based on each picture in multiples of 10%.

Camouflage mismatch of decoys with no predator presence was determined based on either images of other non-predator animals or time-lapse imagery. If the

majority of the time (> 50%) a decoy was mismatched with its environment, it was set to mismatch for the whole deployment and vice versa for matched decoys.

2.4 Statistical analyses

All analyses were conducted using R version 4.1.2 in R studio 2021.09.1 (R Core Team 2021; RStudio Team 2021).

2.4.1 Differences between deployment treatments

The difference in predator visits between camera traps with different treatments (control/match/mismatch) was used to determine if decoys attract predators both in general and when mismatched. A generalized linear mixed model (GLMM) with Poisson distribution was used to assess if treatment affected the number of predator visits using the R packages: *Lme4* and *LmerTest* (Bates e.a. 2015; Kuznetsova e.a. 2017, 2020). The model contained the number of visits as response variable, treatment, habitat, as fixed effects, the log of camera effort as offset and camera cluster as a random intercept. No model selection was conducted as the model contained a limited set of covariates and the full model was the most relevant for the research question. Model outcome predictions as visit probability between treatments were visualised using the R add-on package *Jtools* to control for the variance created by clusters (Long 2021). Differences in the presence of predator species between deployments of different treatments was tested using a Tukey's post-hoc test using the *multcomp* package (Hothorn e.a. 2008).

2.4.2 Decoy interaction

To test which effects explain variation in interaction of predators with decoys a GLMM with binomial distribution was used using the R packages: *Lme4* and *LmerTest* (Bates e.a. 2015; Kuznetsova e.a. 2017, 2020). Interaction between a predator and the decoy (0 = no interaction, 1 = interaction) was used as response variable and camouflage (match / mismatch) as fixed response variable and cluster ID as random intercept. In addition, the same model was used but for mammalian and avian predators separated, as these groups might react differently to decoys based on foraging strategies. Again, no model selection was conducted. Model outcome predictions as interaction probability were visualised using the R add-on package *Jtools* to control for the variance created by clusters (Long 2021).

2.4.3 Survival analysis

I used survival analysis to assess whether a mismatch between camouflage and background resulted in a lower survival probability. Survival or time-to-event

analysis is a statistical analysis using the time as outcome variable until an event occurs (Bischof e.a. 2012, 2014; Kleinbaum & Klein 2012). Survival analysis uses ‘events’ to analyse survival over time; in this study the interaction of a predator with a decoy is considered as an event as this provides the highest certainty that a predator has detected a decoy. Survival analysis uses censoring to use data in which no event has occurred (Kleinbaum & Klein 2012; Bischof e.a. 2014). In this study, right-censoring is used for deployments with decoys which have had no interaction with predators, even if a predator was captured on camera. If a decoy had multiple predator interactions, I reset the time of the event after each interaction creating a theoretical new decoy. I did this to use data of decoys which had multiple interactions with predators to increase sample size. Time to event for these decoys is set to be the time from one interaction to the next interaction. I also analysed without repeated interactions to see if a different pattern in survival is observed. In addition to survival analysis with only interaction, I conducted survival analysis where predator visits, so not only interactions, were considered as events. This is done to see if a similar pattern is found compared to the survival analysis with only interactions and results are not dependant on the interpretation of an ‘event’. In this analysis, deployments with no predator visit or interactions were right-censored.

Analyses were conducted using the R add-on package *Survival* (Therneau & Grambsch 2000). The packages *Survminer* and *ggplot2* were used to visualise survival using Kaplan-Meier curves and summarise survival analysis results (Kassambara e.a. 2021; Wickham e.a. 2021). I conducted two versions of the survival analysis. First, I tested the difference of matched and mismatched decoys independent of habitat. Second, I tested the difference between matched and mismatched 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, hazard ratios for camouflage and habitat were calculated to assess the difference in risk between habitats and matched and mismatched decoys.

3. Results

3.1 Camera trap data

During the camera trapping period, cameras recorded a total of 97 603 pictures of which empty pictures, animal pictures, human and vehicle pictures were respectively 78.3%, 11.8%, 4.0% and 5.9%. Of the animal pictures, 87.4% and 12.6% were non-predator and predator pictures, respectively.

During the fourth round, the poles to which the cameras were attached in the open habitat fell over and caused the cameras to rapid-fire roughly 20 000 empty pictures. These empty pictures have not been uploaded and classified in Trapper. I excluded all the data of the fifth round from the analysis, partially due to the poles in the open habitat that had fallen over causing them to rapid-fire many empty pictures and fieldwork of farmers in the meadows affecting the experimental set-up. Pictures from the closed habitat have been uploaded and classified in Trapper but due to technical difficulties, the results of this round have not been added to the analysis. In total, four rounds of data have been used in the analysis in both open and closed habitats.

In total, predator species visited mismatched decoys most often ($n = 50$), followed by control deployments ($n = 44$) and matched decoys ($n = 44$). In closed habitat more predator events were recorded ($n = 100$) in comparison to open habitat ($n = 38$). The most recorded avian predator was Hooded crow *Corvus cornix* in both habitats ($n = 55$). For mammalian predators this was red fox ($n = 25$) (table 2).

Snow cover remained relatively high in both closed and open habitat until the middle of April (figure 3). Hereafter, snow quickly started to melt creating more habitats with bare ground. Closed habitat showed higher variation in periods of snow cover and bare ground in comparison to open habitat.

Table 2: The total number of predator visits recorded by camera traps for both habitat, treatment, and camouflage. In general, the greatest number of predator visits were detected in closed habitat. Of the avian predators Hooded Crows visited deployments the most, for mammalian predators most visits were red fox.

Habitat	Treatment	Camouflage mismatch	Common Raven	Domestic Dog	Hooded Crow	Red Fox	Domestic Cat	European Badger	Short-eared Owl	Sum
Closed	Control	control	0	13	10	9	6	2	0	40
	Brown	Match	0	1	4	2	6	0	0	13
	Brown	Mismatch	0	6	13	8	2	1	0	30
	White	Match	0	1	5	2	3	2	0	13
	White	Mismatch	0	0	0	0	0	4	0	4
Open	Control	control	0	0	3	1	0	0	0	4
	Brown	Match	0	0	9	0	0	0	1	10
	Brown	Mismatch	0	1	2	2	0	0	7	12
	White	Match	1	1	5	1	0	0	0	8
	White	Mismatch	0	0	4	0	0	0	0	4
			1	23	55	25	17	9	8	138

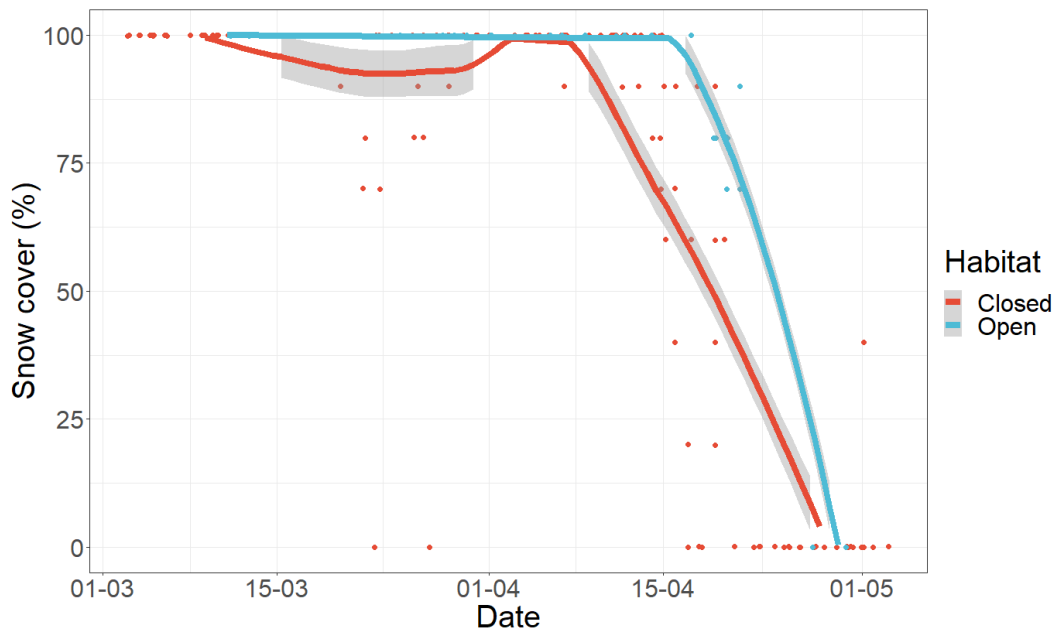


Figure 3: Snow cover in both closed and open habitat during the study period. Trends were created using the 'loess' function. Each data point is the maximum snow cover per day per deployment.

3.2 Decoy attraction

Mismatching camouflage of decoys was found to be the most important factor explaining an increase in predator captures on cameras (table 3). Decoys of either white or brown colour that were mismatched with their environment attracted more predators in comparison to both decoys that matched with their environment (Tukey HSD, $p = 0.018$) and the control with no decoy (Tukey HSD, $p = 0.098$) (figure 4). On average, deployments with matched decoys attracted fewer predators in comparison to control deployments within the same cluster ($\bar{x} = -0.16$), whereas mismatched decoys attracted more predators ($\bar{x} = 0.78$). Deployments in open habitats attracted on average fewer predators ($\bar{x} = 1$) in comparison to closed habitats ($\bar{x} = 3$).

Table 3: Effects of various fixed effects on the number of predators captured on camera traps per deployment. The model was constructed as a GLMM using the above-mentioned fixed effects in addition to cluster ID as a random effect. Control treatment is the intercept.

Predictor	Estimate	SE	z	p-value
Camouflage mismatch (No)	-0.1561	0.2188	0.5948	0.4757
Camouflage mismatch (Yes)	0.4119	0.1998	2.062	0.0392 *
Habitat (Open)	-1.1128	0.6005	-1.853	0.0639 .
Log(Cam_effort)	0.8163	0.5948	1.372	0.1700

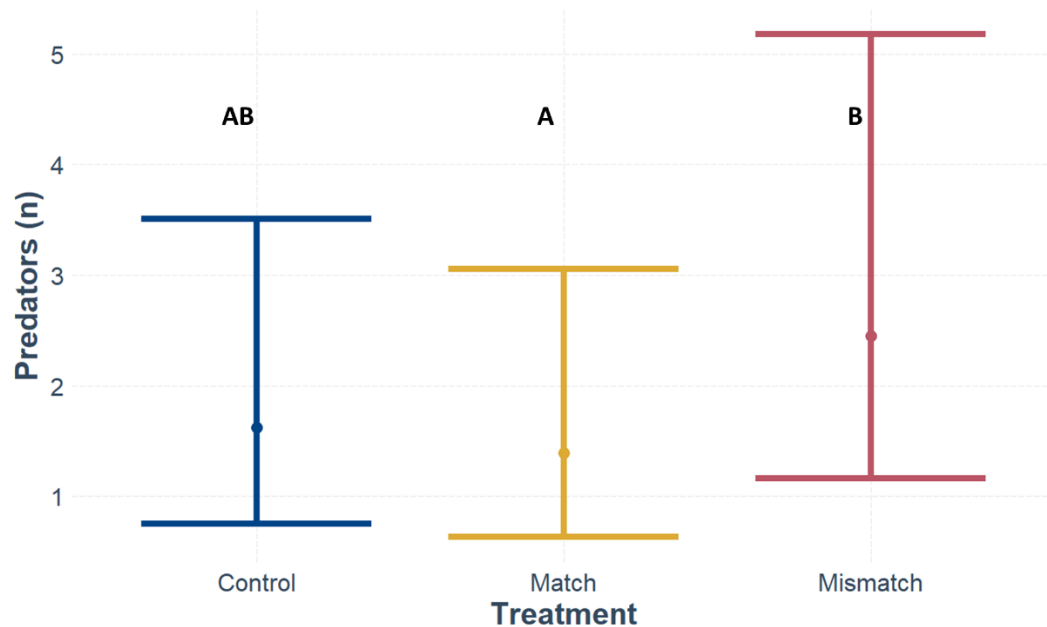


Figure 4: Predicted differences in the number of predator visits for cameras with a control treatment, matched decoys, and mismatched decoys based on the GLMM. Mismatched decoys attracted more predators on average in comparison to matched decoys (Tukey HSD, $p = 0.018$) and control but with little evidence (Tukey HSD, $p = 0.098$). No difference was found between the control treatment and matching decoys (Tukey HSD, $p = 0.755$).

3.3 Decoy interaction

No evidence was found that predators were more likely to interact with mismatched decoys ($n = 9$) in comparison to matched decoys ($n = 4$) (GLMM, $z = 0.951$, $p = 0.342$). Interactions with decoys did not differ between matched and mismatched decoys, for either mammalian (GLMM, $z = 0.764$, $p = 0.445$) or avian predators (GLMM, $z = 0.312$, $p = 0.755$) (figure 5).

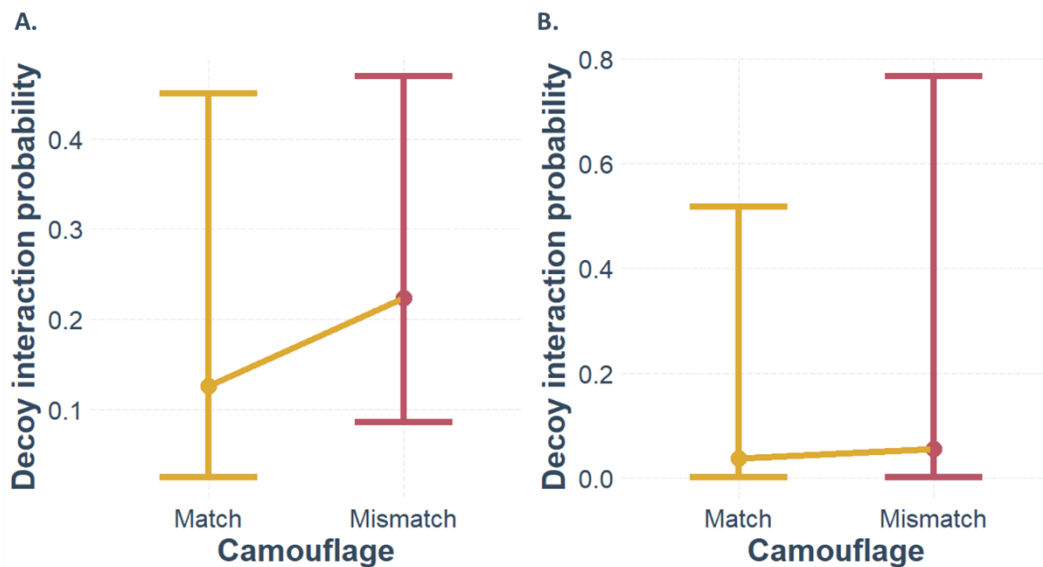


Figure 5: Probability of a predator interacting with a decoy for both mammalian (A.) and avian (B.) predators based on the GLMM. No evidence was found for a higher probability of interacting with a decoy when mismatched (mammalian predators: $p = 0.445$. avian predators: $p = 0.755$).

3.4 Decoy survival

There is some evidence that camouflage mismatched decoys showed a faster-decreasing probability of daily survival in comparison to camouflage-matched decoys (figure 6, $p = 0.09$). For mismatched decoys survival after 2 days was 0.69 whereas the probability of survival of matched decoys was 0.96 on the second day. The hazard ratio for mismatched decoys was 3.05 times higher in comparison to matched individuals ($z = 1.844$, $p = 0.065$, table 4). In addition, the hazard ratio for decoys was 3.7 times lower for decoys in open meadow habitats in comparison to decoys in closed forest habitats ($z = -1.989$, $p = 0.047$, table 4). When eliminating repeated measures (i.e., decoys with multiple events) a similar effect is found for camouflage ($z = 1.828$, $p = 0.067$) and a less strong but no evident effect of habitat ($z = -1.250$, $p = 0.2$) (appendix: figure 11, table 7).

When separated into four categories based on camouflage and habitat, differences in survival and hazard ratios are observed between categories (figure 7,

table 5). There is moderate evidence that the mismatched decoys in closed habitats had a survival probability of 0.5, whereas survival probability of the other decoys ranged from 0.92 to 1.0 ($z = 2.050$, $p = 0.04$, figure 7). In comparison to matched decoys in open habitat, hazard ratio of mismatched decoys was 3.4 times higher. A similar effect but weaker evidence was found when repeated measures were removed from the analysis ($z = 1.732$, $p = 0.0833$) (appendix: figure 12, table 8). When not only interactions between predators but also predator visits are used as events in the survival analysis, stronger evidence for a similar pattern is found but with lower effect sizes in terms of hazard ratios (appendix: figure 13 & 14, table 9 & 10).

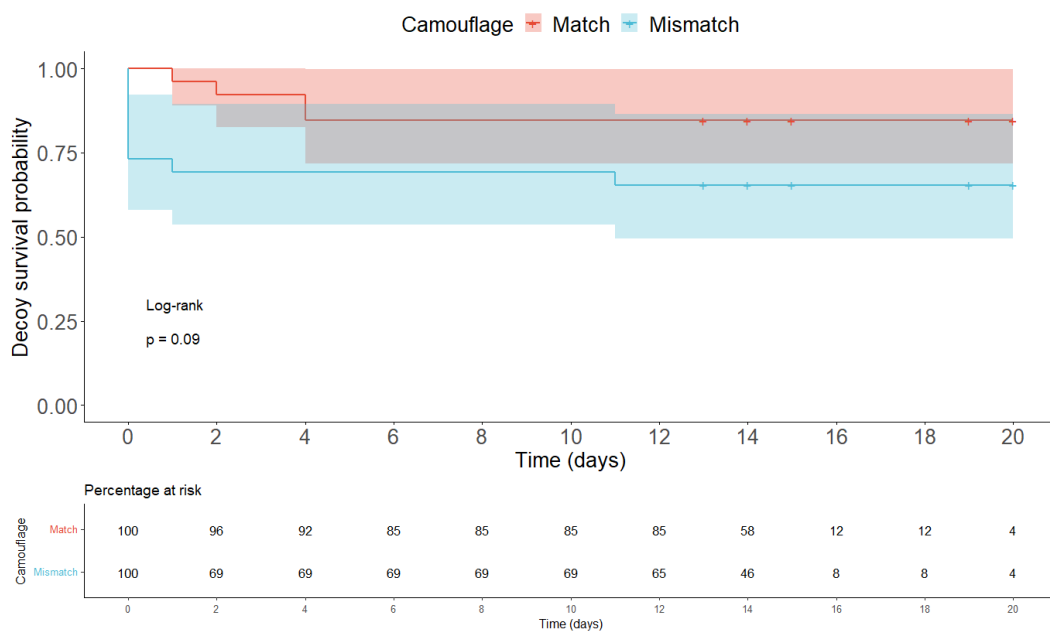


Figure 6: Kaplan – Meier curves for the survival of matched and mismatched decoys using predator interactions. Shaded bands depict 95% confidence intervals. The lower survival table shows the percentage of the population at risk over the course of time.

Table 4: Relative hazard ratio of mismatched decoys in comparison to matched decoys and decoys in open habitat in comparison to closed habitat based only on predator interactions.

Characteristic	HR ¹	95% CI ¹	p-value
<i>Camouflage</i>			
Match	—	—	
Mismatch	3.05	0.93, 9.95	0.065
<i>Habitat</i>			
Closed	—	—	
Open	0.27	0.07, 0.98	0.047

¹ HR = Hazard Ratio, CI = Confidence Interval

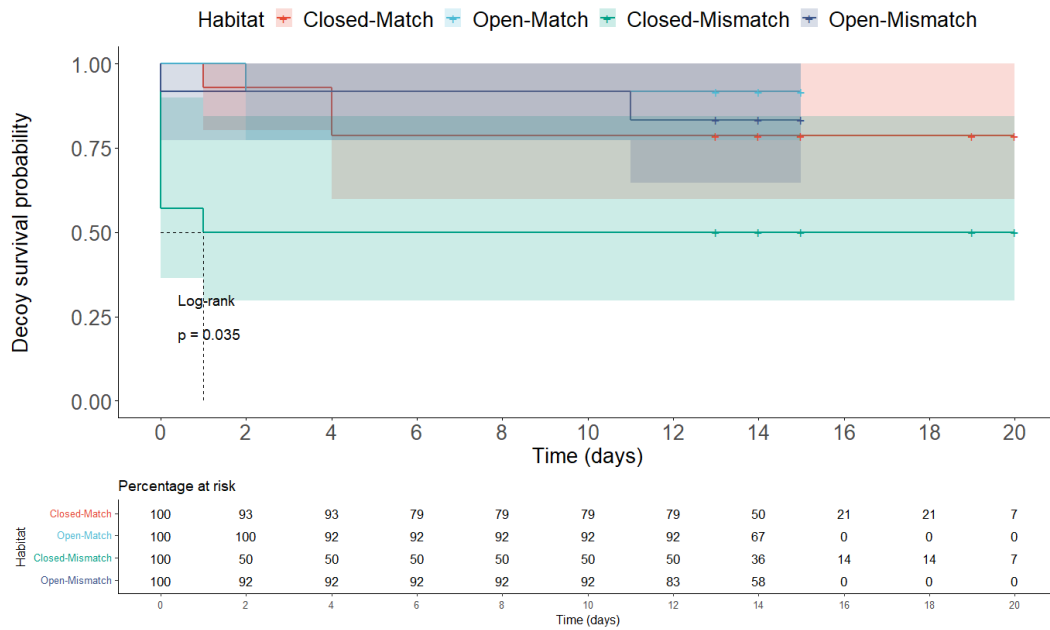


Figure 7: Kaplan-Meier curves for matched and mismatched individuals in open and closed habitat separated using predator interactions. Shaded bands depict 95% confidence intervals. The lower survival table shows the percentage of the population at risk over the course of time. Mismatched individuals in closed habitat showed a strong decrease in survival probability in comparison to the other three categories.

Table 5: Hazard ratios of both matched and mismatched individuals in both closed and open habitats. Hazard ratios are relative to matched in the closed habitat. There is some moderate evidence that mismatched decoys in closed habitat was 9 times higher in comparison to matched decoys in open habitat.

Characteristic	HR ¹	95% CI ¹	p-value
Camouflage * Habitat			
Open Match	—	—	
Open Mismatch	2.08	0.19, 23.0	0.5
Closed Match	2.64	0.27, 25.4	0.4
Closed Mismatch	8.99	1.10, 73.3	0.04

¹ HR = Hazard Ratio, CI = Confidence Interval

4. Discussion

Decreasing snow cover at high latitudes causes animals expressing SCC moulting to have an increasing period of camouflage mismatch with their environment. Here, I tested how a camouflage mismatch in decoys of different colours affected their chance of being detected by predators and how this affected their survival. I found that a mismatch between decoys, resembling animals expressing seasonal colour moults, and their environment increases attraction of potential predator species and subsequently decreases decoy survival. Cameras fitted with mismatched decoys captured more predator visits in comparison to matched decoys. Furthermore, deployments in the closed forest habitat attracted a higher number of predators in comparison to the deployments in the open meadow landscape. No evidence was found that predators, in general, were more likely to interact with mismatched decoys in comparison to matched decoys. In addition, neither mammalian nor avian predators were more likely to interact with decoys. Nevertheless, the survival analysis of predators interacting with decoys showed that survival probability decreases faster for mismatched decoys in comparison to matched decoys. There is moderate evidence of an overall faster decrease in survival for mismatched decoys in closed habitats in comparison to matched decoys in closed habitats, and all decoys in open habitats.

4.1 Increased attraction of mismatched decoys

As predicted, camouflage-mismatched decoys had an overall higher number of predator visits in comparison to the camouflage-matched decoys (figure 4). Even though the difference in the number of predator visits was not significantly different from the control deployments, there is still an indication that camouflage mismatch causes increased detectability and attraction by predators (table 2). This result is in line with previous research, where mismatched decoys, mimicking moths, mice and least weasel, were more often visited or detected by predators in comparison to models that matched their environmental background (Cuthill e.a. 2005; Vignieri e.a. 2010; Atmeh e.a. 2018). This is especially the case with Atmeh e.a. (2018), who found camouflage mismatch to be the most significant predictor explaining predator detection in a similar set-up, using brown and white decoys resembling least weasel.

These findings show that background matching camouflage plays an important role in the detection of prey species and should be optimised by prey when trying to be conspicuous for predators (Caro & Koneru 2021). Some species (e.g., ptarmigans) have adapted behavioural changes to cope with increasing camouflage mismatch. Rock ptarmigans *Lagopus mutus* soil their white plumage in periods of mismatch to reduce attraction by predators (Montgomerie e.a. 2001). Other well-studied behavioural adaptations are active background matching as seen in SCC performing willow ptarmigans, but as well in other bird species (Steen e.a. 1992; Stevens e.a. 2017). Nevertheless, snowshoe hares have shown no behavioural change to the increasing mismatch (Zimova e.a. 2014). One of the general main functions of camouflage or crypsis is considered to be a mechanism to decrease detection by predators and therefore decreasing predation risk and increasing potential survival (Stevens & Merilaita 2009; Zimova e.a. 2018; Stevens & Ruxton 2019). This principle is also considered to be one of the main drivers for SCC moulting in general, in addition to other functions such as thermoregulation (Zimova e.a. 2018). The difference in predator visits between matched and mismatched decoys supports this idea, as predators were less likely to visit deployments fitted with a matched decoy in comparison to mismatched decoys.

4.2 Decrease in survival with mismatching camouflage

No evidence was found for a higher probability of interaction with mismatched decoys by either mammalian or avian predators (figure 5). A low number of interactions between predators and decoys causes the sample size to be too low to reliably show effects. Possibly, predators that detected a decoy noticed it not to be a real prey when near and therefore decide to avoid the decoy (Akcali e.a. 2019). A low number of avian predator detections might be partially explained by bird species being captured less often on camera traps in comparison to mammalian species (Blake e.a. 2011; Naing e.a. 2015; Akcali e.a. 2019). In general, the number of birds of prey and owl species was low in the study area during the study period, due to timing of migration from wintering grounds (Kjellén & Roos 2000). Furthermore, avian predators, such as raptors, tend to be more attracted to moving prey (Lawrence e.a. 2018; Akcali e.a. 2019). Mammalian predators tend to hunt less efficiently, often foraging for food over large areas, making them more likely to approach decoys by chance and being attracted (Willebrand e.a. 2017). I expected mammalian predators to be less attracted to the decoys as they rely on olfactory cues when foraging (Ruzicka & Conover 2011; Díaz-Ruiz e.a. 2016). However, the higher number of mammalian predator visits and interactions in comparison to avian predators does suggest that sight might play an important role in mammalian predator foraging.

When applying the interaction of predators with decoys in survival analysis, I found that there is moderate evidence that camouflaged decoys have a higher survival in comparison to uncamouflaged mismatched decoys (figure 6). After two days, mismatched decoys reached a survival probability of 0.69 whereas matched decoys had a survival probability of 0.96. Previous research done by Zimova e.a. (2016), found that mismatched snowshoe hares experienced a weekly survival decrease of 7%. The lower effect size found by Zimova e.a. (2016) is expected as their study was conducted on alive animals which express anti-predator behaviour. Despite the sample size of predators interacting with de decoys being low, the results presented indicate how animals expressing SCC decrease in survival with earlier onset of snowmelt and the therefore increasing camouflage mismatch. When not only predator interaction but also detection (i.e., being near a decoy) is taken into consideration, a similar but smaller difference between match and mismatch is found. This shows that survival decrease of mismatched decoys does not depend on the interpretation of an ‘event’ but a pattern that is observed independent from the interpretation of what is considered as an event in the analysis. The same applies to analysis without repeated interactions of a predator with the same decoy. One could state that a predator would return to a decoy out of interest. However, studies looking at habituation of predators to unrewarding olfactory cues, show that predators are less likely to be attracted to cues which are non-rewarding (Latham e.a. 2019; Norbury e.a. 2021).

Despite the use of decoys, which will not be a realistic representation of natural predator-prey interaction, the results confirm previous studies performed on Snowshoe hare showing decreased survival with increasing background mismatch (Zimova e.a. 2016; Wilson e.a. 2019).

4.3 Differences between habitats

In contrast to my expectations, I found weak evidence that decoys in closed habitat attracted more predator visits per deployment in comparison to open habitat (table 2). The hazard ratio of decoys placed in the open habitat was almost four times lower in comparison to decoys placed in closed habitat, independent of matching or mismatching camouflage (table 4, figure 7). Difference in survival between matched and mismatched decoys in open and closed habitat was stronger in closed habitat in comparison to open (table 5, figure 7).

Due to a difference in background complexity, the negative effect of mismatching background camouflage would be expected to be lower in a more heterogeneous habitat as a forest in comparison to a more homogeneous area such as an open meadow (Merilaita 2003; Stevens & Merilaita 2009; Rowe e.a. 2021). Nevertheless, both predator attraction and survival decrease were highest in closed habitat. However, due to a possible difference in predator composition between

both habitats and a difference in habitat preference of predators, chance of predators detecting decoys in closed habitat might be higher. This idea is supported by the higher number of camera captures of predators in closed habitat in comparison to open habitat and the effect of habitat on survival of decoys resulting in a higher hazard in closed habitat. In Northern Sweden, most avian predators are migratory (Kjellén & Roos 2000; Calladine e.a. 2012). Avian predators rely on visual cues and prefer to forage in open landscape (Potier e.a. 2018; Heninger e.a. 2020). Therefore, I expected them to have a large impact in the open habitat. Hence, the low number of interactions in the open landscape could be explained by birds of prey not being present in the study area until late April when birds of prey return to the study area. Red foxes show a preference for closed habitat in comparison to open habitat, which could explain the relative high number of mammalian predators in the closed habitat (Díaz-Ruiz e.a. 2016; Willebrand e.a. 2017). A difference in predator composition between open and closed habitats could explain the difference in survival probability between the habitats.

The lower survival probability in closed forest habitat in comparison to open meadow habitat would suggest that mismatched individuals should shift their habitat from closed to open habitat. Open landscape is often avoided by small prey to find shelter for predators (Blanchard e.a. 2018). However, animals expressing SCC in northern Sweden might benefit from the lack of avian predators in open habitat during winter and will have a higher chance of survival there instead of closed habitat. Nevertheless, little evidence has been found for behavioural changes in animals expressing SCC except for ptarmigans (Steen e.a. 1992; Montgomerie e.a. 2001; Zimova e.a. 2018, 2020a).

4.4 Study limitations and further research

Despite this study showing moderate evidence that confirms the idea that a camouflage mismatch in SCC animals increases their chance of being predated, the study also presents limitations.

Low sample size in the amount of predator visits and interaction with decoys limits the statistical strength of some analyses. Therefore, some of the results presented here are more an indication of an effect instead of clear evidence. Hence, I would suggest increasing the number of clusters over a greater area or to expand the study period to increase predator visits and interactions as these factors in camera trap studies are considered as important factors increasing detection probability by cameras (Stokeld e.a. 2015; Hofmeester e.a. 2019). In addition, I would propose to execute the study in areas further removed from human settlement as some predator species tend to change their activity with increasing human disturbance (Díaz-Ruiz e.a. 2016). Pine martens, a widely distributed predator in Scandinavia, avoid human settlements (Lindström e.a. 1995; Goszczyński e.a.

2007). Hence, the high human activity in the study area can have a reducing effect on predator densities and activity. When reproduced further away from human activity and settlements, I expect the differences in predator composition between open and closed habitat to be lower (Díaz-Ruiz e.a. 2016).

Poles, to which cameras were attached in open habitat, tended to fall over in periods of heavy wind or snowmelt. Resulting in relatively high downtime in periods of snowmelt. I was not able to place poles in the ground during the study as the ground was frozen solid. Therefore, I would recommend placing poles in the ground in late summer or early autumn when replicating this study in a comparable climate. The upside of poles being placed on pedestals is that they can be displaced. This feature will be lost when placing poles before the ground freezes. However, this will not be a problem if enough poles and cameras are accessible to maintain a high sampling size. In addition, I would recommend to pin decoys more firmly in the ground. Some animals, especially red squirrel *Sciurus vulgaris*, tended to displace the decoys. This forced me to regularly visit the study site to make sure everything was still in place, making the study sometime unnecessary labour intensive. The handling of decoys by me or by red squirrels is also a factor that could be taken into consideration as it could provide an odour to the decoys, attracting more predators such as red foxes.

Lastly, as seen in figure 3, the majority of the data is collected in a period of snow cover. Thus, mismatched decoys are brown decoys in a white background. This is not considered as the most realistic scenario, as climate change is expected to increase mismatch between white individuals in periods of little to no snow cover in both autumn and spring (Mills e.a. 2018; Zimova e.a. 2018; Hofmeester e.a. 2020). With this argument in consideration, I present evidence in this study on 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 almost half of the year snow cover remains present in northern Scandinavia, subspecies that do not turn white will have a lower survival in comparison to subspecies that do turn white (Irannezhad e.a. 2017). Therefore, I do not expect selection on no SCC moulting but more selection on the ability to adapt.

4.5 Implication for our understanding of the system

Overall, I present some evidence in this study that climate change induced mismatch between animals expressing SCC and their background results in lower survival. The results presented here allow us to have a better understanding on how climate change will affect animals expressing SCC and the potential consequences it has for their survival. The negative effect of camouflage mismatch of animals expressing SCC has already been widely documented in several species such as: mountain hare, snowshoe hare, least weasel, willow, and rock ptarmigan (Steen e.a.

1992; Imperio e.a. 2013; Zimova e.a. 2016; Pedersen e.a. 2017; Atmeh e.a. 2018). However, quantifying the amount of impact in an experimental set up has been rarely documented, as presented in this study. With the predicted scenarios, the mismatch between white colour morph and background is only expected to increase (Mills e.a. 2013).

As photoperiod is not changing with climate change, phenotypic plasticity through environmental factors such as temperature would be ideal for animals expressing SCC to reduce their mismatch by adapting the timing of moulting (Visser 2008; Visser e.a. 2010). However, as phenotypic plasticity in the onset of SCC is limited, animals expressing SCC will undergo a decrease in survival resulting in decreasing populations or even disappearance from certain regions (Atmeh e.a. 2018; Zimova e.a. 2018; Kumar e.a. 2020). As a result, disappearance of species expressing SCC will have indirect effect on the system in which they reside. For example, reduced numbers or disappearance of least weasel from the boreal forests of Fennoscandia could have effect on vole cycles with unknown consequences (Ylönen e.a. 2019). However, it is expected that least weasel will not disappear but a shift in subspecies will change the spread of subspecies *M. n. nivalis* to a higher abundance of *M. n. vulgaris* which stays brown in winter in areas with little annual snow cover (Atmeh e.a. 2018; Ylönen e.a. 2019). Nevertheless, I show that individuals showing no winter coat will have a severe survival disadvantage during most of the year in northern Sweden due to the high number of days with snow cover. Hence, the future of species expressing SCC might therefor be heavily dependent on their ability to adapt to the changing environment, either behavioural or morphological. When no change is observed, the demographic consequences might be grim (Zimova e.a. 2016).

Observations of limited phenological shifts in several species expressing SCC indicate that protection of these species will not reduce their decrease in survival (Zimova e.a. 2014, 2020a; Atmeh e.a. 2018). It will be important to map if some populations show adaptability and protect those, so they can potentially spread over a larger area. In areas where snow cover is already limited, it is expected that subspecies that do not turn white during winter will have selective advantage and replace sub populations that do express SCC (Atmeh e.a. 2018). In areas where snow cover remains widely present throughout the year, populations are needed to adapt, either physiological or behavioural. Alternatively, as there is variation in timing of moulting between subpopulations, maintaining gene flow between populations of different latitudes might provide genetic variation resulting in selection for individuals with decreased mismatch (Zimova e.a. 2020b). However, more empirical data and research will be needed to assess the effectiveness (Hoffmann & Sgrò 2011).

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Appendix



Figure 8: A white and brown decoy as used in the experimental set up of the study, roughly 20 cm wide and 50 cm in length.

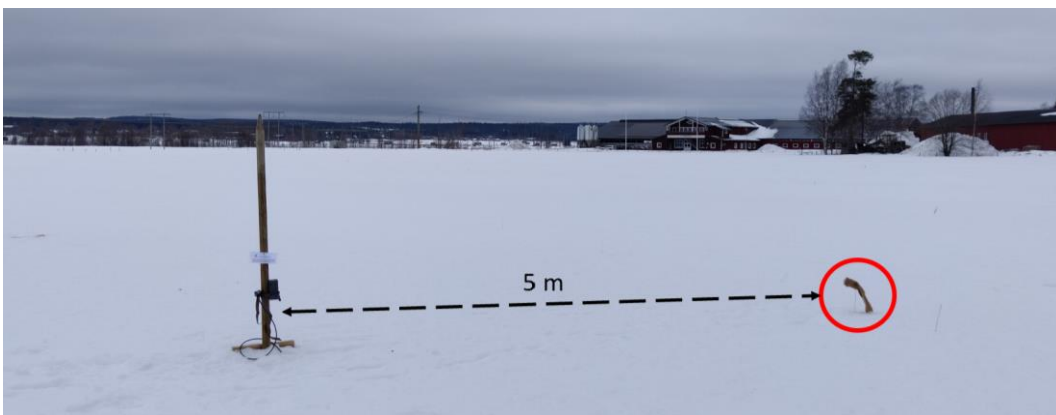


Figure 9: Experimental design. A brown model exposed in an open meadow habitat with snow cover.



Figure 10: From top left to bottom right: domestic dog rolling on a brown decoy in snow covered closed habitat, short-eared owl observing a brown decoy in bear ground open habitat, Eurasian badger sniffing a white decoy in closed habitat with no snow, a red fox approaching brown decoy in open habitat in period of snow cover.

Table 6: Camera trapping effort per treatment in habitat during the study period.

Habitat	Treatment	Cameras (n)	camera trapping (days)	down time (days)
<i>Closed</i>	Brown	12	184	0
	White	12	184	0
	Control	12	184	0
<i>Open</i>	Brown	12	168	46
	White	12	168	50
	Control	12	168	44

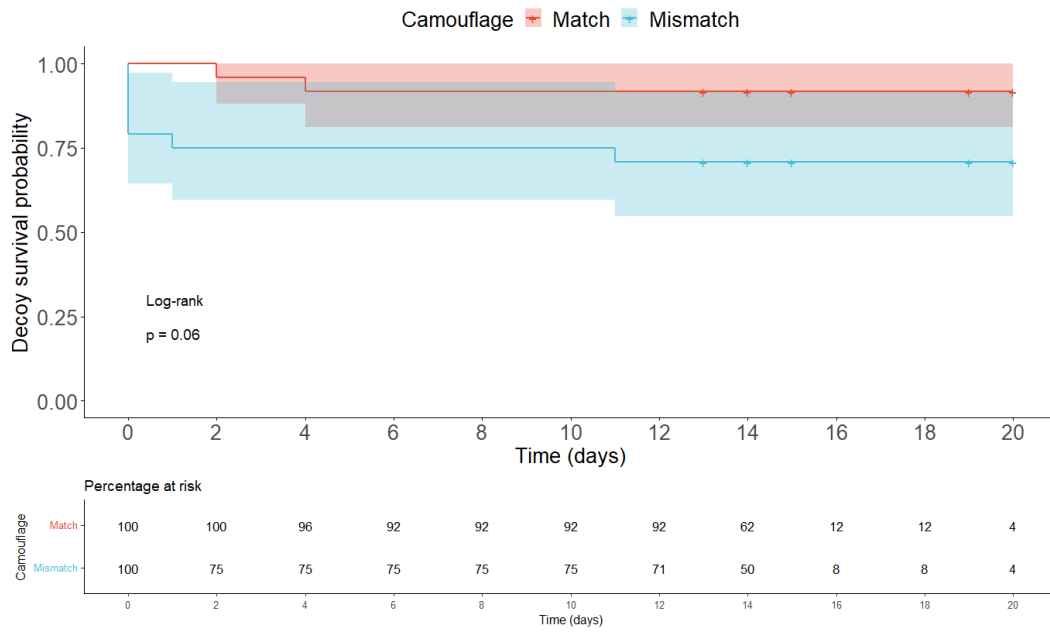


Figure 11: Kaplan-Meier curves depicting survival probability of matched and mismatched decoys, without repeated measures. Shaded bands depict 95% confidence intervals. The lower survival table shows the percentage of the population at risk over the course of time. The number of events is $n = 2$ and $n = 7$ for matched and mismatched decoys respectively.

Table 7: Relative hazard ratio of mismatched decoys in comparison to matched decoys and decoys in open habitat in comparison to closed habitat without repeated predator interactions. There is some weak evidence for a higher hazard for matched decoys, the lower hazard in open habitat is less evident.

Characteristic	HR ¹	95% CI ¹	p-value
<i>Camouflage</i>			
Match	—	—	
Mismatch	4.35	0.90, 21.0	0.068
<i>Habitat</i>			
Closed	—	—	
Open	0.41	0.10, 1.65	0.2

¹ HR = Hazard Ratio, CI = Confidence Interval

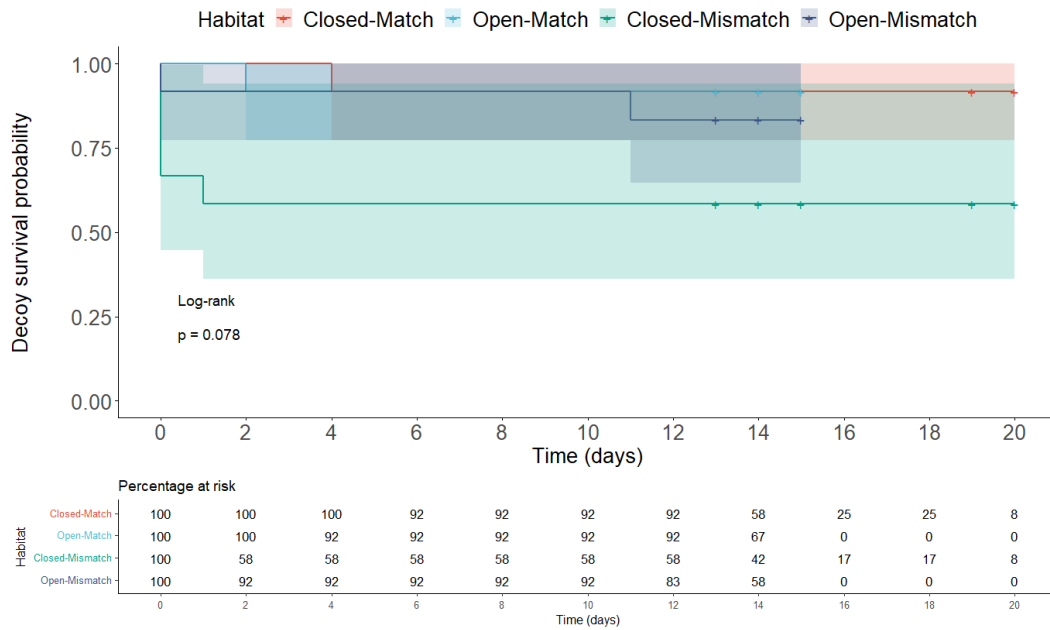


Figure 12: Kaplan-Meier curves depicting survival probability of matched and mismatched decoys in open and closed habitat. Shaded bands depict 95% confidence intervals. The lower survival table shows the percentage of the population at risk over the course of time. The number of events per group were $n = 1$, $n = 1$, $n = 5$, and $n = 2$ for closed-match, open-match, closed-mismatch, and open-mismatch respectively.

Table 8: Hazard ratios of both matched and mismatched individuals in both closed and open habitats without repeated interactions. There is weak evidence that the mismatched decoys had a 6.7 times higher hazard ratio closed habitat in comparison to matched decoys in open habitat. There was no evidence for a difference between the other three groups.

Characteristic	HR ¹	95% CI ¹	p-value
Camouflage * Habitat			
Open Match	—	—	
Open Mismatch	2.08	0.19, 22.9	0.5
Closed Match	0.99	0.06, 15.8	>0.9
Closed Mismatch	6.68	0.78, 57.4	0.083

¹ HR = Hazard Ratio, CI = Confidence Interval

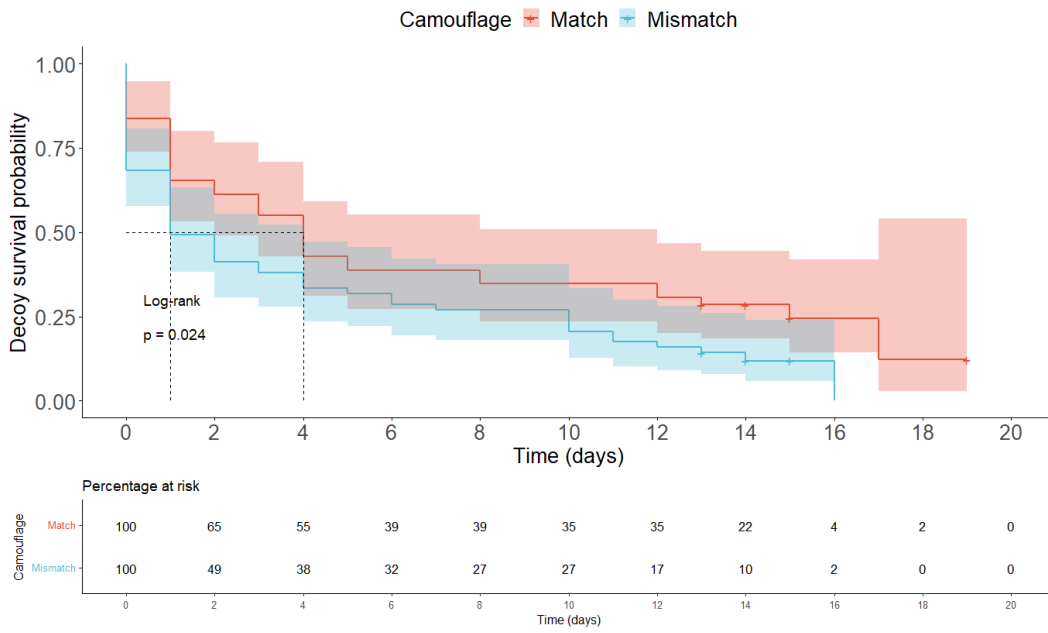


Figure 13: Kaplan – Meier curves for the survival of matched and mismatched decoys using both predator visits and interactions. Shaded bands depict 95% confidence intervals. The lower survival table shows the percentage of the population at risk over the course of time. Mismatched and matched decoys were visited 56 and 37 times respectively. Mismatched decoys had a faster decrease in survival probability in comparison to matched.

Table 9: Relative hazard ratio of mismatched decoys in comparison to matched decoys and decoys in open habitat in comparison to closed habitat based on both predator visits and interactions.

Characteristic	HR ¹	95% CI ¹	p-value
<i>Camouflage</i>			
Match	—	—	
Mismatch	1.61	1.05, 2.45	0.027
<i>Habitat</i>			
Closed	—	—	
Open	0.53	0.34, 0.84	0.006

¹ HR = Hazard Ratio, CI = Confidence Interval

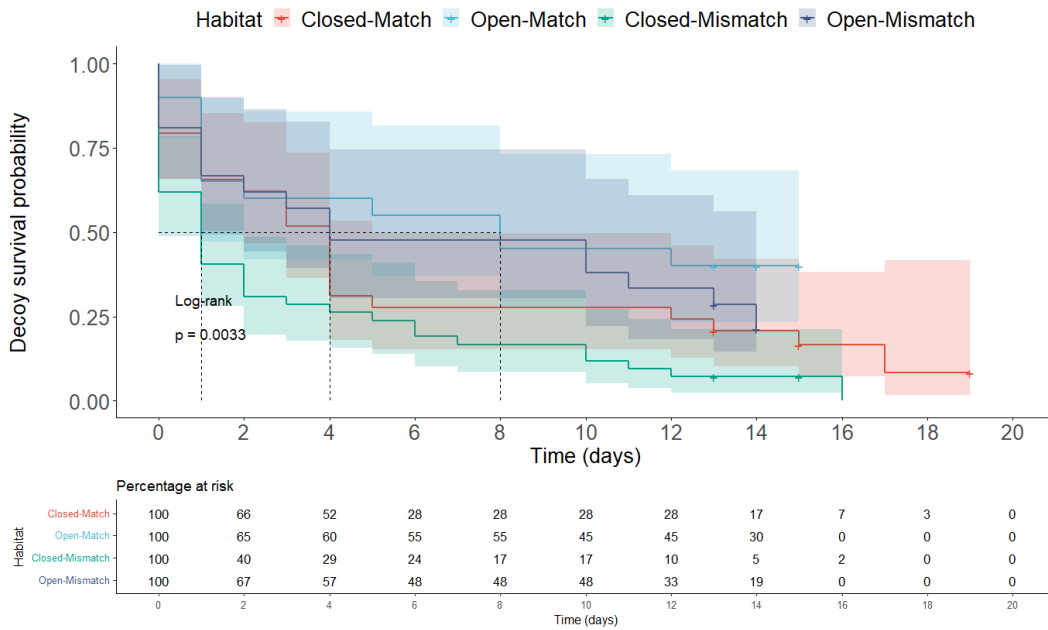


Figure 14: Kaplan-Meier curves for matched and mismatched individuals in open and closed habitat separated using both predator interactions and visits. Shaded bands depict 95% confidence intervals. The lower survival table shows the percentage of the population at risk over the course of time. Mismatched decoys in closed habitat showed the fastest decrease in survival, whereas matched decoys in open habitat showed highest probability of survival.

Table 10: Hazard ratios of both matched and mismatched individuals in both closed and open habitats using both predator visits and interaction. There is strong evidence that the mismatched decoys had a 2.8 times higher hazard ratio in closed habitat in comparison to matched decoys in open habitat. There was no evidence for a difference between the other three groups.

Characteristic	HR ¹	95% CI ¹	p-value
Camouflage * Habitat			
Open Match	—	—	
Open Mismatch	1.4	0.66, 2.96	0.4
Closed Match	1.66	0.83, 3.33	0.2
Closed Mismatch	2.84	1.48, 5.45	0.002

¹ HR = Hazard Ratio, CI = Confidence Interval