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Does crypsis influence foraging patterns in a colour polymorphic Arctic fox population?

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Picture: Camera trap mounted on feeding station

Abstract

Seasonal coat colour moulting species moult to white winter fur for crypsis in snow-covered landscapes. Seasonal coat colour moulting occurs in birds and mammals; some are colour polymorphic; one of which is the arctic fox (*Vulpes lagopus*), having a blue and white colour morph. Camouflage, thermoregulation and physiology likely contributed to the evolution of this polymorphism. Climate change is expected to reduce snow cover duration in the Arctic, putting the white morph under pressure as periods of background mismatching may be prolonged. Through behavioural plasticity, animals can select environments that improve their crypsis level, but this mechanism has never been researched in Arctic foxes. Behavioural and phenotypic plasticity are expected to be vital for winter-white morphs to adapt to climate change but remain poorly understood. In this study, I aim to examine whether Arctic foxes are aware of their crypsis level. I thereby build upon the foundations of the camouflage hypothesis to investigate the potential presence of behavioural plasticity linked to crypsis level. I do this through camera trap images from feeding stations on Varanger. I predict conspicuous foxes use feeding stations more because of lowered foraging success (Foraging hypothesis), or alternatively, less to avoid predation at feeding stations (Predator avoidance hypothesis). Furthermore, I predict that conspicuous foxes will display a higher degree of nocturnal behaviour than cryptic foxes to avoid predation (Nocturnal behaviour hypothesis).

To investigate this, I analysed 193.715 camera trap images made at 19 feeding stations, scoring 61.950 pictures containing Arctic foxes taken during March, May, August, and December from 2018 until 2021, using the moulting stage, snow cover, and light hours as predictors. I found no compelling evidence to suggest that the two colour morphs use the feeding stations differently. The predicted change in winter detection rate in blue Arctic foxes was not found. Both colour morphs displayed strong nocturnal behaviour having a higher likelihood of presence during the night. To conclude, Arctic foxes appear unaware of their degree of crypsis and show no behavioural plasticity, as both colour morphs display similar foraging behaviour.

Keywords: colour polymorphism, seasonal coat colour moult, arctic fox, supplementary feeding, camouflage hypothesis, foraging, snow cover, climate change.

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1 Introduction

In the northern hemisphere, 21 species of mammals and birds go through seasonal coat colour (SCC) moulting from brown in summer to white in winter (Zimova et al., 2018). These species differ from other seasonal moulting species because of the seasonal colour change. They shift to a colour that makes them well camouflaged against the background, thereby achieving crypsis. SCC moulting is thought to have evolved independently in five bird and mammal families and is found in predators and prey (Zimova et al., 2018). Ten of these SCC moulting species are known to have winter colour polymorphism, having both winter-white and winter-brown phenotypes (Zimova et al., 2018). Monomorphic white populations typically occur in areas with a longer-lasting snowpack, whereas monomorphic brown populations occur in areas with shorter snow cover duration. Moreover, polymorphic populations are often found along the environmental gradient between such areas, where snow cover duration is more variable (Mills et al., 2018).

Two main hypotheses motivate the presence of colour polymorphism within populations of SCC species: the camouflage hypothesis and the thermoregulation hypothesis (Di Bernardi et al., 2021). The camouflage hypothesis assumes an advantage for camouflaged animals resulting in lower predation risk or, not mutually exclusive, improving their foraging success as they are harder to detect by prey. Winter white colour morphs are therefore expected to have a cryptic advantage over brown colour morphs during periods of snow cover. Conversely, dark morphs are expected to have a cryptic advantage in winter pelage when snow is absent. One example of a prey species with colour polymorphism is the snowshoe hare (*Lepus americanus*); as an important prey species for many predators, it is predicted to have strong selection for background matching. Zimova et al. (2016) showed that survival in snowshoe hares is significantly lower during background mismatching. Another example is the least weasel (*Mustela nivalis*). A study found that least weasels were more easily detectable by predators and, therefore, more vulnerable to predation during background mismatching (Atmeh et al., 2018).

Crypsis in predators is widely assumed to be beneficial for foraging success, but this has rarely been researched (Brechtbühl et al., 2010). No research on this topic has yet been conducted in the tundra ecosystem. In black-headed gulls (*Larus ridibundus*), impaired crypsis ability has been linked to reduced foraging success (Götmark, 1987). Moreover, another study found that

a colour polymorphic apex predator, the black sparrowhawk (*Accipiter melanoleucus*), adjusted its foraging activity spatially and diurnally to achieve a higher level of crypsis (Tate et al., 2016). Crypsis could thus be equally important for predators as for prey.

The thermoregulation hypothesis was proposed to explain the presence of winter brown colour morphs in colour polymorphic SCC moulting species inhabiting areas with snow cover in winter. The primary function of seasonal moulting in these animals is to facilitate the change of the fur's insulating capacities in response to the season's weather conditions. Di Bernardi et al. (2021) hypothesised that the dark morph might have higher fitness because of the possible thermoregulatory advantage of the darker-toned fur, weighing up against the disadvantage of appearing conspicuous in snow-covered landscapes. However, little evidence supporting this theory has been found (Di Bernardi et al., 2021). The thermoregulation hypothesis is beyond the scope of this study and will, therefore, not be explored further.

Climate change-induced changes in snow cover can affect SCC moulting species' ability to match their colour with the background and thus to achieve crypsis. In no region on Earth is the climate changing as rapidly as in the Arctic, with temperatures rising three to four times faster than the global average (AMAP, 2021; Jansen et al., 2020; Rantanen et al., 2022; Richter-Menge et al., 2020). Snow cover duration has declined significantly over the last decades and is expected to be reduced strongly in the future (Pulliainen et al., 2020). The quality and duration of snow cover affect the organisms living in tundra significantly. Such changes include increased exposure for subnivean prey, ice layers impeding herbivory, changes in mobility and many more mechanisms (Berteaux et al., 2017). The main proximate driver of seasonal moulting is photoperiod; therefore, earlier snowmelt due to climate change is not expected to trigger an earlier onset of spring moult, potentially leading to a prolonged camouflage mismatch (Zimova et al., 2018; Zimova et al., 2016). Background mismatching can decrease survival in SCC moulting species (Zimova et al., 2020). With inter-annual changes in the snowpack further amplified by climate change, SCC moulting species must adapt to remain camouflaged, potentially affecting proportions and distributions of colour polymorphism throughout polymorphic species.

Recently, two mechanisms have been proposed to facilitate crypsis in response to changing snow conditions. The first potential mechanism is phenotypic plasticity in moult timing in response to fluctuating temperatures and snow cover (Laporte-Devlyder et al., 2022). Zimova

et al. (2022) found evidence for earlier moulting in autumn and later moulting in spring in Arctic fox populations further north, with the two colour morphs responding differently. Over a long-term study on snowshoe hare, Oli et al. (2023) found evidence for phenotypic plasticity, most evident in autumn. The second mechanism could be adaptation in behaviour by using more cryptic environments corresponding to their fur colour. This would require that the animal is aware of its degree of crypsis. Although this mechanism was not found in snowshoe hares, it may apply to other SCC moulting species (Kumar et al., 2020).

The Arctic fox is a particularly interesting polymorphic SCC moulting species. The Arctic fox is a highly mobile arctic mesopredator with a circumpolar distribution (Poulin et al., 2021). It is both prey and predator and has a larger body size than any other SCC moulting species. The Arctic fox has two distinct colour morphs: white and blue. The “white morph” appears entirely white in winter, whereas the “blue morph” has a dark charcoal colour year-round; both morphs change their fur in summer to a brown colour that blends in with the background. White individuals are the most prevalent type, appearing well camouflaged against a snow-white background. The blue morphs are well hidden in coastal areas with little snow cover but appear conspicuous in a snow-covered landscape (Fuglei & Ims, 2008). Habitat use and dietary differences have been observed between the Arctic fox colour morphs (Pagh & Hersteinsson, 2008). Arctic foxes are often classified into two ecotypes: “lemming” and “coastal”. The coastal ecotype, which relies primarily on marine resources, is most prominent in ice-free coastal regions where lemmings are absent, such as Iceland, Svalbard, and West Greenland (Fuglei & Ims, 2008). The lemming ecotype is more prominent in inland areas, such as Siberia and Fennoscandia, where small rodents are the most significant resource, often mirroring their population densities (Dalén et al., 2005; Elton, 1942; Henden et al., 2009). In contrast, coastal Arctic fox populations have more stable density dynamics because of higher dependency on more temporally stable marine subsidies (Fuglei & Ims, 2008; Nater et al., 2021). White foxes are more associated with the “lemming ecotype” whereas blue foxes are often associated with the “coastal ecotype” (Fuglei & Ims, 2008). In Iceland, where lemmings are absent, a higher proportion of blue foxes is found in coastal areas (Hersteinsson & MacDonald, 1992). The relative proportions of the colour morphs can vary significantly between populations.

The role of the camouflage hypothesis for the Arctic fox is unclear. As prey to other animals, the Arctic fox may benefit from a lower detection probability by predators. As a predator, the

Arctic fox could benefit from a cryptic advantage making it harder for prey to detect the fox while hunting. The Arctic fox could be expected to be less vulnerable to predation than other SCC moulting species, such as the least weasel (*Mustela nivalis*) or the stoat (*Mustela erminea*), because of its bigger size. However, it is still susceptible to predation by several predators, such as the golden eagle (*Aquila chrysaetos*) and the red fox (*Vulpes vulpes*) (Chevallier et al., 2016; Elmhagen et al., 2013; Jackson et al., 2023; Landa et al., 1997; Nyström et al., 2006; Tannerfeldt et al., 2002). Therefore, appearing conspicuous relative to the background can come with significant predation risk on the exposed Arctic tundra.

The role of crypsis in foraging behaviour has not been studied in Arctic foxes; one could expect that background mismatching could reduce foraging success. In winter, small rodents are primarily under the snow cover and, therefore, unable to visually detect an Arctic fox hunting (Bilodeau et al., 2013). Crypsis may be more critical for hunting alternative prey, such as rock ptarmigan (*Lagopus muta*), willow ptarmigan (*Lagopus lagopus*), and mountain hare (*Lepus timidus*). Nevertheless, during winter, Arctic foxes are mostly scavengers (Ims et al., 2017). A cryptic individual may suffer a lower degree of interference by predators while foraging than a conspicuous individual, it could be hypothesised that the crypsis level regarding their predators may be the most significant determinant of foraging success in hunting and scavenging. However, no research has yet examined this hypothesis.

To maximise crypsis level animals can adapt their behaviour by using environments in which they are more cryptic or by using these environments differently. An example of this is nocturnal foraging behaviour as a strategy to avoid predation. This behaviour has been found in many species across several taxonomic groups, including the Arctic fox (Eppley et al., 2016). They are predominantly nocturnal (Audet et al., 2002; Eberhardt et al., 1982; Thierry et al., 2020), but this is less prominent in a population where mesocarnivore competitors and other potential predators are absent (Fuglei et al., 2017; Thierry et al., 2020). This behaviour has yet to be compared between the two colour morphs, the role of crypsis in this nocturnal behaviour is, therefore, unknown. Background mismatching could cause the conspicuous morph to display more nocturnal behaviour, but therefore, the fox would need to be aware of its crypsis level.

This study focuses on an Arctic fox population on the Varanger peninsula, Norway (Fig. 1). The Arctic fox population on Varanger is classified as a population of the “lemming ecotype” (Ims et al., 2017). The high degree of colour polymorphism in this “lemming ecotype”

population is uncommon. These are commonly nearly all white individuals. It likely resulted from the release of blue foxes by the National Arctic fox conservation programme (Landa et al., 2022). This high degree of polymorphism offers excellent circumstances to assess foraging behaviour patterns in light of the camouflage hypothesis.

It is unknown if the Arctic fox has an awareness of its own crypsis level and if it has associated behavioural responses during background mismatching. In this study, I aim to provide the first insight into the degree of awareness of crypsis and associated behavioural plasticity in Arctic foxes. I provide the first comparison of seasonal and diurnal foraging patterns of two Arctic fox colour morphs in response to ambient snow cover and light conditions. I do this by analysing a large number of images from camera traps at feeding stations on the Varanger peninsula. I test if the colour morphs adapt their seasonal and daily foraging patterns to their crypsis level and, thus, if they show awareness of their crypsis level.

I predict two alternative responses to background mismatching. Firstly, I predict that during periods when a colour morph is subject to background mismatching, it will use the feeding stations more than during periods of crypsis because of a hypothesised reduction in foraging success (Foraging hypothesis). This may be caused by prey more easily detecting the Arctic fox, as well as that Arctic fox predators may detect the fox more easily and interfere with the foraging efforts. This could cause the Arctic fox to prefer the more readily-available feed from the feeding stations. In this case, I expect the blue colour morph to visit more regularly throughout the winter.

Alternatively, I predict that the colour morph subject to background mismatching will use the feeding station less regularly and with shorter visits than the cryptic colour morphs as a predator avoidance strategy (Predation avoidance hypothesis). As the feeding stations are located in exposed areas, the more detectable conspicuous morph may suffer an increased predation risk over the cryptic morph while using the feeding stations. Upon entering the feeding station, the Arctic fox is unaware of the surroundings, potentially increasing predation risk. Consequently, Arctic foxes could avoid feeding stations during background mismatching.

Furthermore, I predict that regardless of the validity of either of the hypotheses mentioned above, nocturnal behaviour will be displayed more strongly in foxes not achieving crypsis, as a predation avoidance strategy (Nocturnal behaviour hypothesis). During background

mismatching, it may suffer from increased predation risk and therefore choose to use a feeding station more during the night.

I test these hypotheses by examining the foxes' foraging patterns in relation to snow cover, the moulting stage, and by comparing seasonal and daily foraging patterns of both Arctic fox colour morphs.

2 Methods

2.1 Study area

Varanger peninsula is located at 70-71° North, 29-31 ° East (Fig. 1). The northern part is considered low-Arctic tundra, whereas the southern part of Varanger is considered sub-Arctic (Walker et al., 2005). Varanger has a relatively mild winter climate compared to other coastal tundra regions. Therefore, it could be a valuable region for predicting the effects of climate change on other tundra regions (Ims et al., 2017). In the future, Varanger is expected to receive increased amounts of precipitation during every season (Hanssen-Bauer et al., 2017). The snow season has shortened by three weeks in the last three decades, and this trend is expected to persist in the future (Hanssen-Bauer et al., 2017; Pedersen et al., 2021).

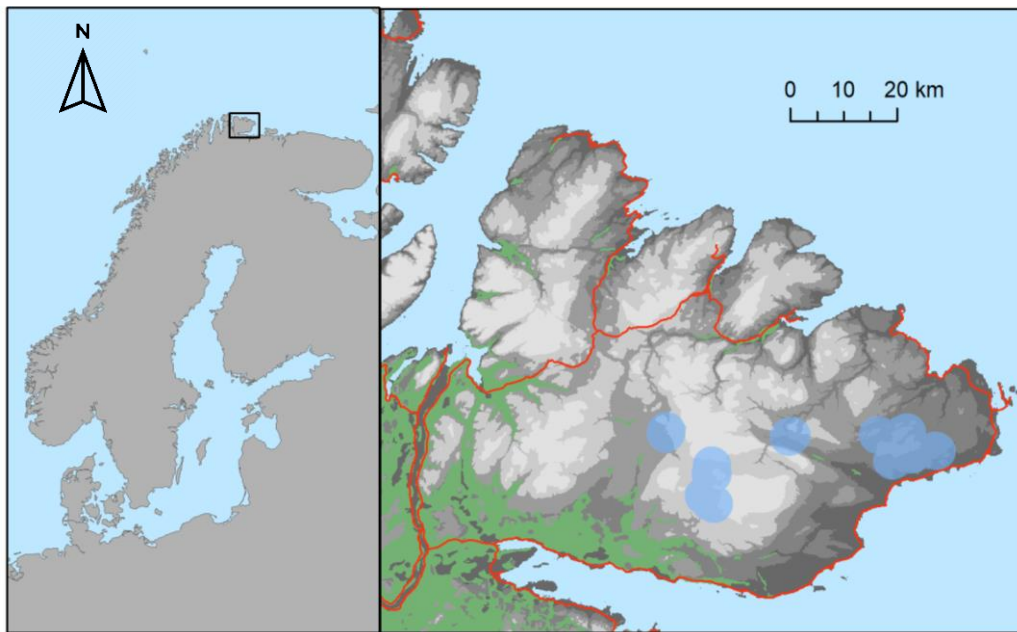


Figure 1: Map of the study area. The left panel shows the location of the Varanger peninsula in Fennoscandia, whereas the right panel shows the study area. The shaded areas indicate the approximate location of the supplementary feeding stations. The exact locations of the supplementary feeding stations are disclosed. Grey shading indicates elevation in 100 m intervals, green represents forest, and red lines roads.

2.2 Study population

The Arctic fox population on the Varanger peninsula is under intensive management as part of the National Arctic fox conservation programme (Eide et al., 2017), led by the Norwegian Institute for Nature Research (NINA) in collaboration with the State Nature Surveillance

(SNO). This programme was created to reverse the nationwide decline in Arctic fox numbers and likely saved the Varanger population from near extinction in 2017 (Ims et al., 2017). Three distinct management actions have been implemented on the Varanger peninsula: red fox culling, feeding station maintenance, and release of captive-bred Arctic foxes. Red fox culling has occurred since 2005 to reduce resource competition for the Arctic fox, and is still an important conservation tool in the area (Ehrich et al., 2022; Ims et al., 2017). Sixty-seven captive-bred foxes were released to supplement the population in January 2018-2020, of which 24 of the blue morph and 43 of the white morph (Ehrich et al., 2022), as part of a nationwide release programme (Landa et al., 2017). From 2017 onwards, 19 feeding stations designed by NINA have been set up on the Varanger peninsula to increase the released foxes' survival probability and reproductive capacity.



Figure 2: Supplementary feeding station on Varanger. The feeding stations consist of three barrels and are equipped with motion-triggered RECONYX Hyperfire PC800 camera traps. Picture: J.E. Knutsen.

The feeding stations are placed between 150 and 900 meters from known dens. They consist of three plastic barrels; the entrance consists of a plastic tube dimensioned to exclude the larger red fox from entering (Fig. 2). The feeding stations are filled with dog pellets approximately every month by SNO personnel. These feeding stations have all been equipped with motion-triggered RECONYX Hyperfire PC800 camera traps. The cameras were programmed to take pictures when motion was detected. For one trigger, a single picture, or a burst of two or three

pictures were taken. This was variable throughout the study period; additionally, a daily picture was made at a set time.

The Arctic fox is the only SCC moulting polymorphic species in the study area that displays winter colour polymorphism. Despite being SCC moulting polymorphic species, the stoat, the least weasel, and the mountain hare have winter white monomorphic populations on Varanger. The Arctic fox on the Varanger peninsula is found within a community of predators and scavengers of which the golden eagle, the wolverine and the red fox may prey on Arctic foxes (Ims et al., 2017; Jackson et al., 2023; Killengreen et al., 2012). Besides reindeer carrion in the winter, small rodents (lemmings and voles) are the most important food resources for foxes in the study area. The Arctic fox on Varanger belongs to two functional groups: the small rodent specialists and the scavengers. The former means that the Arctic fox depends on small rodent population dynamics (Ims et al., 2017). The study area has three small rodent species: the Norwegian lemming (*Lemmus lemmus*), the grey-sided vole (*Myodes rufocanus*), and the tundra vole (*Microtus oeconomus*) (Ims et al., 2017). The Norwegian lemming is the preferred prey of the Arctic fox, but foxes also prey on mountain hares, rock, and willow Ptarmigan.

2.3 Image classification

All images were manually processed in MapView Professional by RECONYX. I scored images taken during December, March, May, and August, from March 2018 to December 2021. These months represented a broad spectrum of snow and light conditions needed to examine differences in feeding station usage. December has mostly full snow cover and no daylight, March has full snow cover with both day and night, May has days with varying snow cover and mostly daylight, and August has no snow cover with long days and short nights. I recorded every Arctic fox detected by the cameras within these given months, except pictures taken in bursts of two or three; in that case, they were treated as one picture and the highest number of foxes was taken within the burst. For each fox, I recorded the colour morph, the moulting stage and snow cover. During the study period, I went through 193.715 camera trap images, scoring 61.950 pictures containing Arctic foxes. These sightings were recorded at 19 feeding stations over a total of 3505 detection days. In these images, 53314 foxes were of the white colour morph, and 11510 foxes were of the blue colour morph. An overview table can be found in Appendix III, table S1.

I developed a simple, subjective framework to estimate snow cover visually. Each image was assigned to one of three snow cover classes: full snow cover, partial snow cover and no snow cover. A three-category framework was chosen to suffice the precision needed for further analysis. A more detailed version would make the scoring process more time-consuming and less precise. More details and examples are provided in Appendix I. Laporte-Devlyder et al. (2022) developed a framework to obtain a moulting score for Arctic foxes detected on camera traps. This framework distinguishes seven different moult stages ranging from 100% winter fur to 0% winter fur and has clearly defined limits for each category. Further information about this moulting framework can be found in Appendix II.

2.4 Data analysis

I carried out all data analyses in R version 4.2.2 (R CORE TEAM, 2022) by means of Generalized Linear Mixed Models (GLMM) in the glmmTMB package (Brooks et al., 2017). I made predictive plots using the ggpredict function within the ggeffects package (Lüdtke, 2018). I assessed model fit based on diagnostics through “simulateResiduals” from the DHARMA package (Hartig, 2022). Unless otherwise stated in the results, the models were found to have a reasonably appropriate fit to the data. All estimates presented are given on the scale of the link functions of the GLMMs; i.e. log-scale for models based counts of detection and logit-scale for binary presence/absence or proportion data.

I designed several GLMM models to test the proposed hypotheses. With these models, I aimed to evaluate the hypotheses that the colour morph that appears conspicuous uses the feeding stations either more often because of lower hunting success (Foraging hypothesis), or less often as a strategy for predator avoidance (Predation avoidance hypothesis). To test these hypotheses, I first developed models to assess seasonal differences in feeding station usage by each of the two colour morphs by modelling the detection numbers for each month.

Next, I used only the month of May, the month with the most variation in snow cover and moulting stages. I tested the response in foraging behaviour of both morphs to the proportion of snow cover, the factor determining the level of crypsis. I did this to test if the Arctic foxes change foraging patterns in response to their level of crypsis. Moreover, the level of crypsis with respect to the snow cover in white foxes is dependent on their moulting stage. Therefore, I created an additional model for the white fox in May that also included the moulting stage.

This model could directly test if the white fox adapted its foraging behaviour to its level of crypsis.

Lastly, I hypothesised that the conspicuous colour morph displays more nocturnal foraging behaviour as a mechanism to avoid predation (Nocturnal behaviour hypothesis). Here I focused only on March and used the hours of daylight to predict the proportion of visits per day during daytime. This allowed me to directly test if the conspicuous blue morph had a higher proportion of detections during the night compared to its cryptic white counterpart.

I transformed the original snow score to numerical values on a 0-1 scale: full snow cover (1), partial snow cover (0.5), and no snow cover (0). Additionally, I transformed the moulting score from percentages to fractions. I aggregated the data from all the images to a data frame organised per day and feeding station; all data frames derived from this have the same structure, except for the daylight data frame. I then calculated the sum of detection for each morph. I split this original data frame into a data frame for each morph for the seasonal analysis and created a variable for the month. For the May models, I selected days in May. For each day and at each feeding station, I created a moulting score and a snow score. I did this by calculating the mean of all moulting score values and the mean of all snow values at each feeding station/day combination. Only moulting scores for the white fox were used to calculate this mean value. Hereafter, I interpolated the snow scores for days when no fox was detected, and consequently no snow was scored, by taking the average of the first snow value before and after the missing values at the corresponding feeding station. After I created a presence/absence score for both colour morphs. I derived the white fox moulting model data from this data frame by only selecting instances when a white fox was detected and then calculated the sum of white fox visits per feeding station/day combination. For the daylight model, I only selected days during March from the original data frame and split each feeding station/day combination into two rows, one for each colour morph. I then calculated the sum of each row's detections per night and day, using sunset and sunrise times obtained through the `suncalc` package (Thieurmél & Elmarhraoui, 2022). Lastly, I calculated the proportion of detections during daytime out of the total detections for each feeding station/day combination.

2.4.1 Seasonal comparison

I constructed two models to investigate seasonal differences in feeding station usage, one for each colour morph. The morphs were not combined in one model, as this led to a poor model fit. I created the white fox model based on 3179 days of detection and the blue fox model using 1535 days of detection over all feeding stations. Each model had the sum of detections per feeding station and per day as the response variable. I fitted both models with feeding station and year as nested random factors. Year was nested within feeding station, as foxes are expected to mainly visit the same feeding station throughout their lifespan. The nested random factors accounted for variation beyond the scope of this analysis, such as yearly population dynamics and rodent densities. I fitted the model with a truncated negative binomial distribution using the `truncated_nbinom2` function (Brooks et al., 2017). I compared the months using a Tukey posthoc test with the `tukeyHSD` function in the `stats` library (R CORE TEAM, 2022). I then used these models to predict the number of detections per day per feeding station for each month.

2.4.2 May models

After, I created two models, one for each colour morph, to investigate the effect of the proportion of snow cover on feeding station usage during May, to test for a behavioural response to crypsis level (Foraging hypothesis, Predation avoidance hypothesis). I used a data frame containing 1447 days of detection over all feeding stations. I fitted both models with a presence/absence score per day per feeding station as the response variable and this interpolated snow score as the predictor variable. As above, I fitted both models with feeding station and year as nested random factors. I fitted the model with a binomial distribution (Brooks et al., 2017). I then used these models to predict the probability of presence at varying proportions of snow cover using `ggpredict` (Lüdtke, 2018).

2.4.3 Moulting phenology

Next, I developed a model that included moulting stage for the white fox. I analysed the interactive effect of the moulting stage and snow cover on feeding station usage by white foxes through a model based on count data. I only used days with a white fox detection during May, 823 days over all feeding stations. I used the number of detections per day per feeding station as the response variable. I used snow and moulting as predictor variables, as well as the

interaction between them. I hypothesise that the moulting stage of the fox might alter its response to the snow cover. I again used the feeding station and the year as nested random factors. I fitted the model with a truncated negative binomial distribution using the `truncated_nbinom2` function (Brooks et al., 2017). I then used the model to predict the number of detections at varying snow cover levels for three distinct moulting categories (Fig. 5), 0%, 50%, and 100% winter fur, using `ggpredict` (Lüdecke, 2018).

2.4.4 Light hours

I then created a model to investigate the effect of changing light conditions on the diurnal foraging patterns of the colour morphs in March. I created the model based on 1194 days of detection over all feeding stations. I used the proportion of detections during daytime as the response variable. I used light hours and colour as predictors as an interactive term. As before, I fitted feeding station and year as nested random factors; additionally, I added crossed random factor for ID to improve the model fit. I assigned a unique ID to each row of the dataset, and this ID explained additional variation between observations that other predictor variables or random factors could not explain. This variable accounted for overdispersion in the model. I fitted the model with a binomial distribution (Brooks et al., 2017). Afterwards, I made predictions based on the model described above using `ggpredict` (Lüdecke, 2018), and plotted those against the proportion of daytime with daylight.

3 Results

For both Arctic fox colour morphs, the total number of detections varied considerably between and within months and years (Fig. 3). In the years 2018, 2019, and 2020 captive-bred individuals were released on Varanger, accounting for part of this variation. Moreover, there was a 15-fold difference in the number of white foxes detected between the minimum month (August 2018) and the month with the maximum number of detections (March 2019). The proportion of blue and white fox detections showed large variation in and between years, with the lowest proportion of blue foxes occurring in May 2020 (8.4%) and the highest proportion occurring in August 2019 (32.3%).

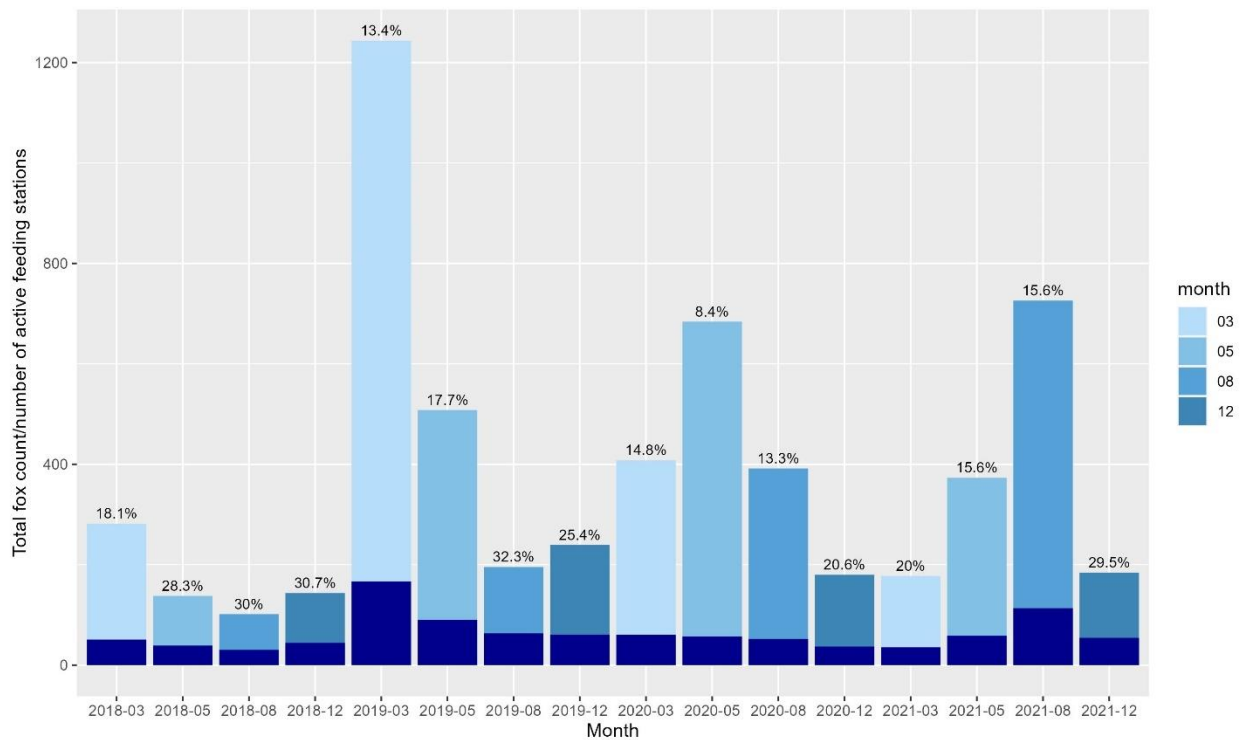


Figure 3 The total number of monthly detections (y-axis) of Arctic foxes of the two morphs throughout the study period. The total number of detections has been divided by the number of active feeding stations during the respective month. The y-axis contains the number of detections, and the x-axis contains the months of the study period. The dark blue part of each bar displays the number of blue fox detections, and the full height of the bar indicates the sum of all fox detection during that month. Above each bar, the percentage of blue fox detection out of all Arctic fox detections during the respective month is displayed.

3.1 Seasonal comparison

In the seasonal analysis, the predicted number of detections per day per feeding station showed considerable seasonal variation in both colour morphs (Fig. 4). In all the months, the predicted number of white foxes was higher than the predicted number of blue foxes. March had significantly fewer detections for both colour morphs than the other months (Appendix IV, S3). A Tukey posthoc test indicated that May had significantly more detections than December for the white fox (Estimate (est) = -9.11, 95% Confidence Interval (CI) [-13.26, -4.97], $p < 0.001$) but not for the blue fox (est = -1.06, 95% CI [-3.37, 1.25], $p = 0.64$) (Appendix IV, S4). All other pairwise month comparisons indicate similar patterns for both morphs (Appendix IV, S4). These findings do not support the proposed hypotheses (Foraging hypothesis, Predation avoidance hypothesis), as there are no consistent differences between the cryptic white morph and the conspicuous blue morph during winter. Both morphs use the feeding stations less in winter. No effect of the level of crypsis can be coupled to these results.

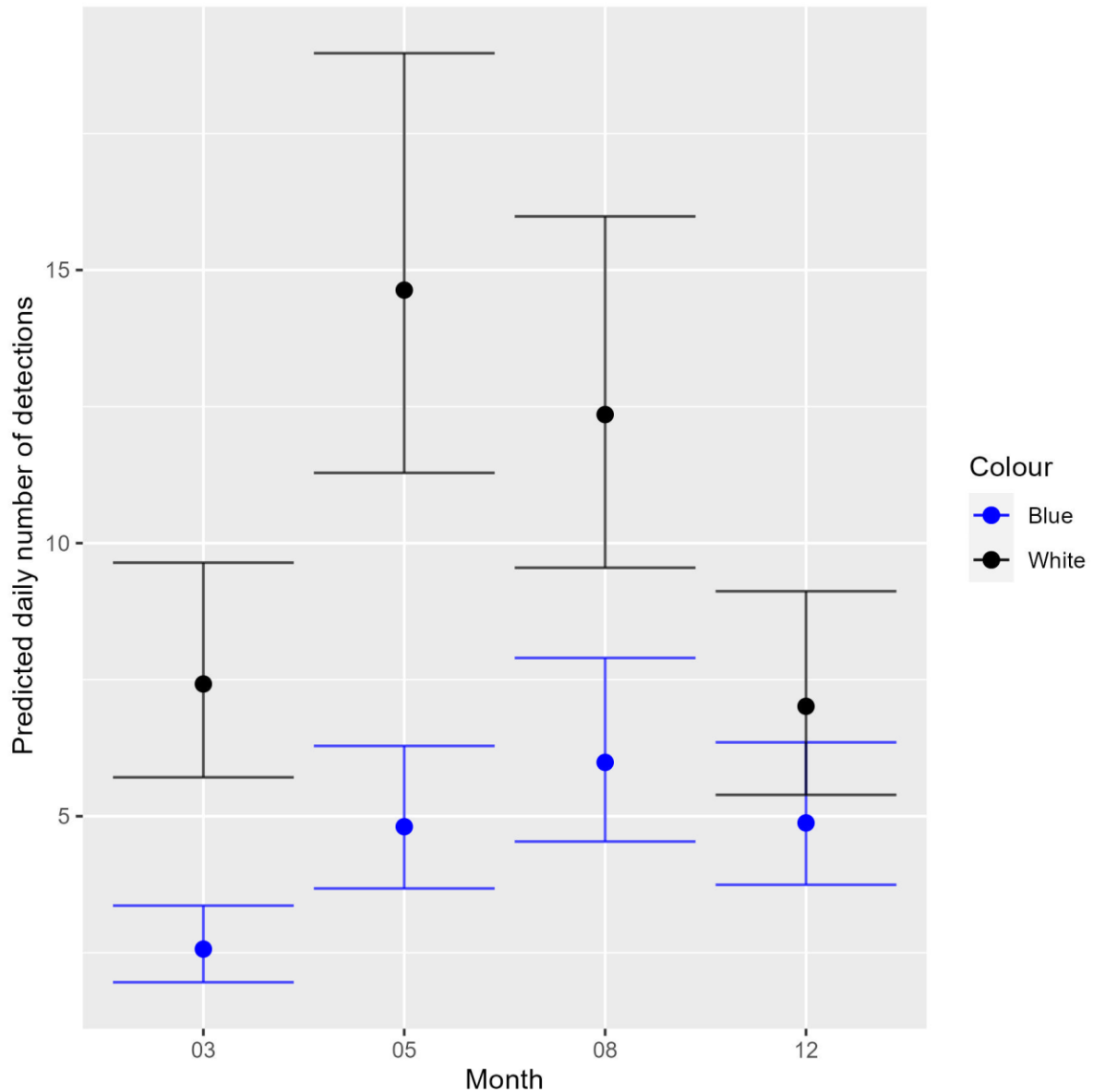


Figure 4: The predicted number of detections per day and feeding station for each month. The predictions for the blue colour morph are displayed in blue, whereas those for the white colour morph are shown in black. The y-axis shows the predicted number of visits per day and feeding station, and the x-axis shows the four months when pictures were scored. The error bars represent 95% confidence intervals.

3.2 May models

To further investigate for behavioural differences related to crypsis level, models during May were analysed. There was a significant increase in the probability of detecting a white fox at higher proportions of snow cover (Fig. 5) (est = 0.69, 95% CI [0.15, 1.2], $p < 0.05$) (Appendix IV). The May model for the blue Arctic fox detected a positive but non-significant response to

a higher proportion of snow cover (est = 0.30, 95% CI [-0.28, 0.89], $p = 0.3$) (Appendix IV). These results do not support the hypothesis that the more conspicuous blue fox would use the feeding stations more at higher snow cover levels (Foraging hypothesis), nor does it support the hypothesis of decreased use to lower predation risk (Predation avoidance hypothesis). The increased probability of detecting a white fox does not provide strong support for hypotheses either, as the moulting stage was not included in this model. Therefore, the crypsis level at these snow cover levels is unknown. Furthermore, this trend is expected to be linked to natural prey availability.

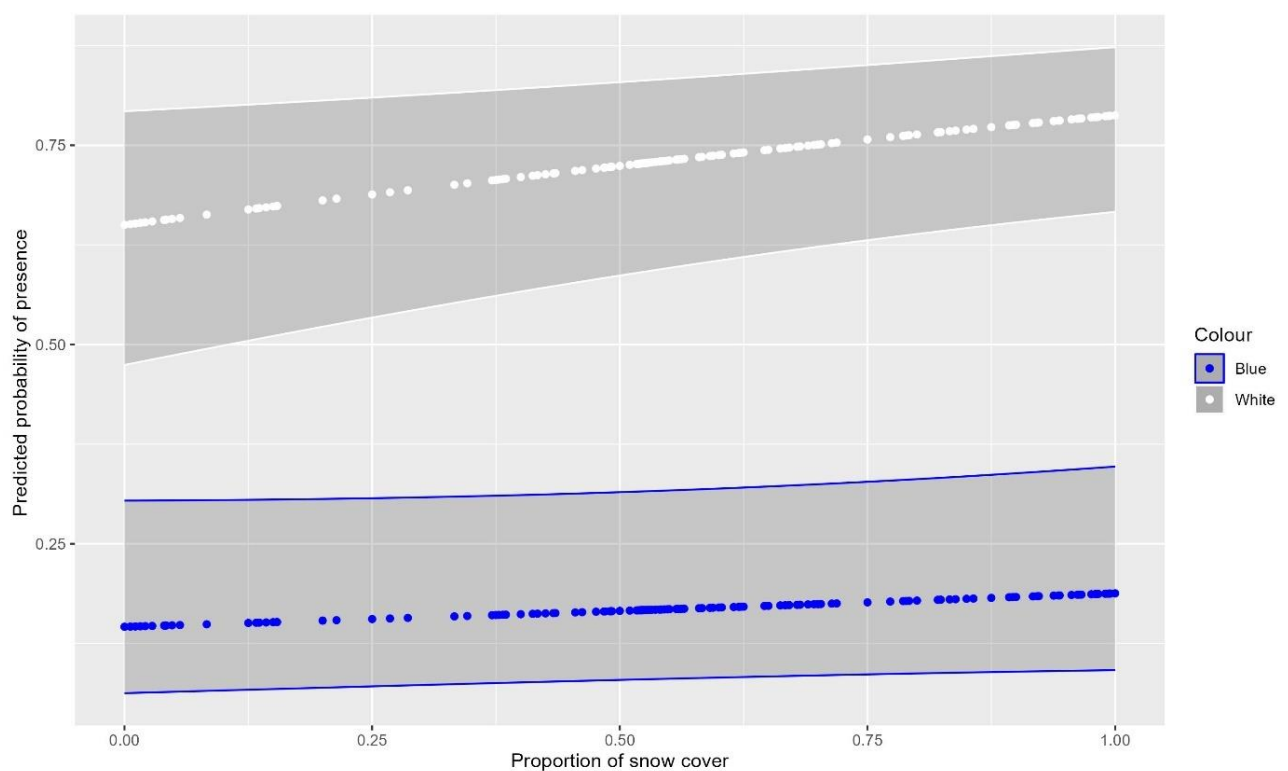


Figure 5: The predicted probability of the presence of both colour morphs in response to different snow cover levels in May. The x-axis shows the proportion of snow cover, and the y-axis shows the predicted probability of detection. The blue dots represent the blue colour morph, the white dots represent the white colour morph. Both responses were fitted with 95% confidence intervals.

3.3 Moulting phenology

When considering a possible interaction between snow cover and moulting stage for white foxes, the positive effect of snow cover was less clear and only close to significant (Fig. 6) (est = 1.20, 95% CI [-0.01, 2.40], $p = 0.052$) (Appendix IV). There was no significant effect of moulting (est = -0.36, 95% CI [-1.30, 0.59], $p = 0.5$). Moreover, there was no significant

interactive effect of snow cover and moulting stage (est = -0.91, 95% CI [-2.30, 0.48], $p = 0.2$), therefore, the response in foraging behaviour appears to be the same regardless of the moulting stage. The hypothesised effects (Foraging hypothesis, Predation avoidance hypothesis) of a response in the number of detections resulting from background mismatching were not observed.

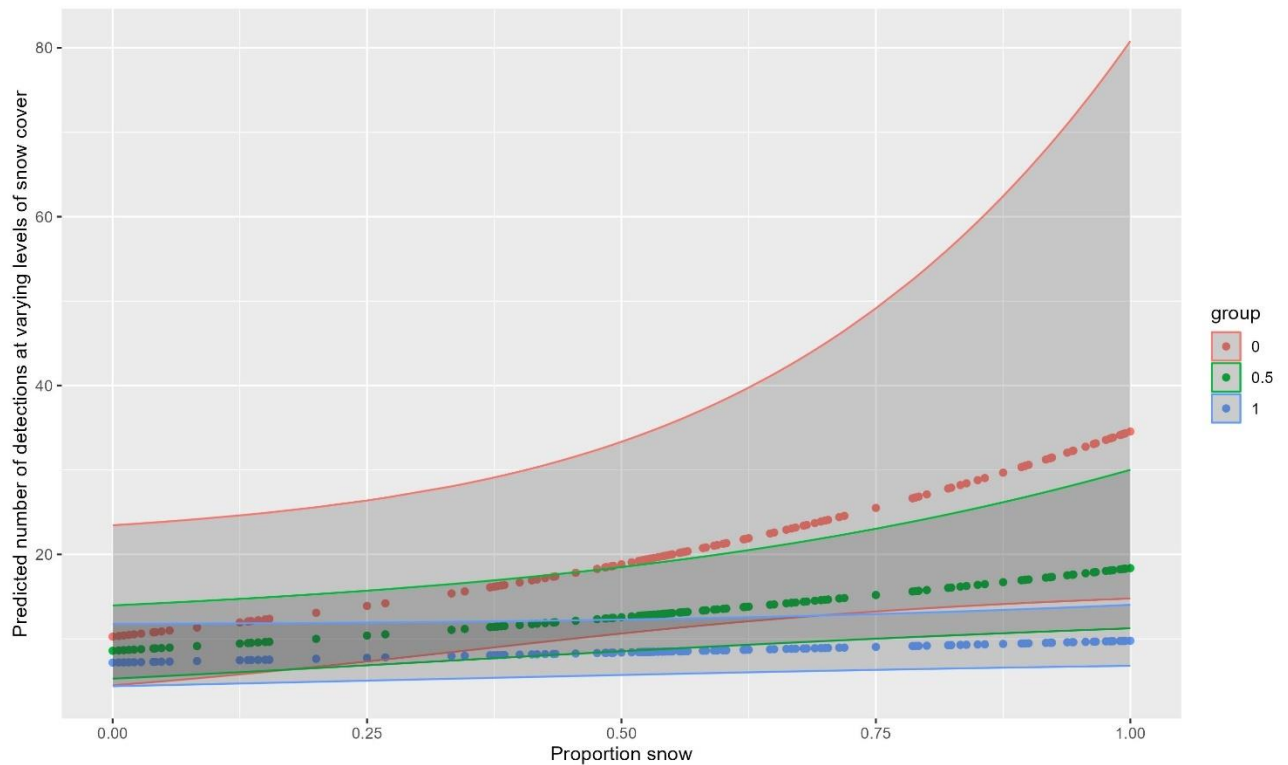


Figure 6: Predicted number of white fox detections at varying snow cover levels for three moulting categories during May, based on the white fox May moulting model, including an interaction term for snow and moulting. Predictions are shown for three moulting categories: Summer coat (0), moulting progression halfway (0.5) and full winter coat (1). All lines are fitted with 95% confidence intervals.

3.4 Light hours

Furthermore, no differences were observed with the daylight model, both colour morphs had similar responses to the proportion of daylight, with a higher probability of being detected during daytime as hours of daylight increased, but still with the vast majority of detections occurring during the night-time (Fig. 7) (est = 0.58, 95% CI [0.29, 0.87], $p < 0.001$) (Appendix IV, S2). There was no significant difference between the colour morphs (est = 0.56, 95% CI [-3.30, 4.40], $p = 0.8$), nor was there a significant effect of the interaction term between light hours and fur colour (est = -0.05, 95% CI [-0.38, 0.28], $p = 0.8$). Both colour morphs showed a

clear tendency towards nocturnal foraging behaviour. These results do not support the nocturnal behaviour hypothesis that the more conspicuous blue colour morph would be more nocturnal than the cryptic white morph, as both morphs mostly use the feeding stations at night.

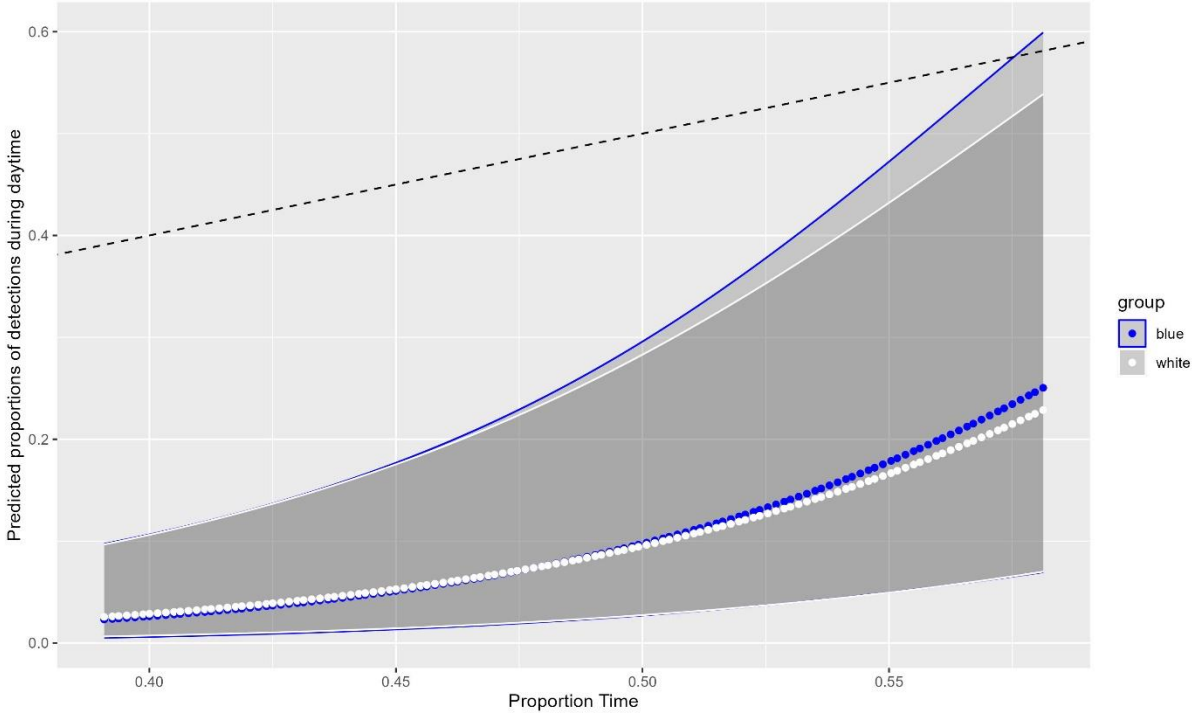


Figure 7: The predicted proportion present during daytime is plotted against the proportion of light hours in a day during March. The x-axis contains the proportion of time in the day with daylight, and the y-axis contains the predicted proportions of detections during the daytime. The blue dots correspond to the predicted proportions of the blue fox, and the white dots correspond to the white fox. The dashed line represents the expected proportions of detections during the daytime, given that no bias towards nocturnal behaviour is present. The grey surfaces indicate the confidence intervals of the predictions. The model had an acceptable but not perfect fit. Both lines are fitted with 95% confidence intervals.

4 Discussion

The data derived from the feeding station monitoring enabled me to test if Arctic foxes of either colour morph respond behaviourally to their level of crypsis. Overall, there was no evidence for such a behaviour. Contrary to my expectation that the conspicuous colour morph would use the feeding station more frequently (Foraging hypothesis) or would avoid them to minimise predation risk (Predation avoidance hypothesis), the seasonal models did not indicate large seasonal differences in feeding station usage between the morphs. Both colour morphs displayed strong nocturnal foraging patterns, but no difference based on crypsis level was found, opposing my hypothesis (Nocturnal behaviour hypothesis).

Firstly, I tested for a behavioural response to the level of crypsis in both morphs (Foraging hypothesis, Predation avoidance hypothesis) through seasonal models in which I compared the average daily count of Arctic foxes per feeding station throughout the year. The cryptic white morph was detected significantly less frequently in December compared to August. In contrast, the conspicuous blue morph was not detected significantly less in December (Fig. 4). Nevertheless, both morphs were detected significantly less in March. Overall, both Arctic fox morphs used the feeding stations less frequently during the winter than during the summer. A factor making the interpretation of the seasonal models more challenging is the release of captive-bred foxes in January of the years 2018, 2019, and 2020. Sixty-seven Arctic foxes have been released over these years (Ehrich et al., 2022; Landa et al., 2017). The release of these foxes, in combination with natural population dynamics, make it more challenging to compare seasonal difference, as they might be due to population fluctuations rather than behavioural differences.

The lower detection numbers in winter may be explained by the reduced energy demands of the Arctic fox in winter (Audet et al., 2002; Thierry et al., 2020). Moreover, increased fur insulation (Prestrud, 1991; Scholander & Hock, 1950), reduced activity and lower basal metabolic rate (Fuglei & Øritsland, 1999; Fuglestad et al., 2006) all work towards this lower energy requirement during winter. For both colour morphs, May and August are the months with the most detections, when the metabolic rate is expected to be higher. In May, Arctic foxes reproduce, and in August, pups also use feeding stations. Another factor potentially explaining fewer arctic fox detections is the increased availability of carrions in winter, providing an alternative resource. On Varanger, a considerable reindeer population remains in the area in

winter in some years, and the mortality rate is estimated to be high (Ims et al., 2017). The lowered metabolic rate, combined with some degree of cub mortality and increased availability of reindeer carrions, and a generally smaller population, likely explain most of this reduction in detection numbers in winter.

Hereafter, I tested the behavioural response to crypsis level hypotheses (Foraging hypothesis, Predation avoidance hypothesis) by directly assessing the response to different snow cover levels in May. In contrast to the blue morph, the level of crypsis at varying snow cover proportions in the white morph depends upon its moulting stage. First, I tested for a behavioural response in both morphs in May, irrespective of the moulting stage (Fig. 5). The white fox showed a significantly higher probability of detection with increasing snow cover, opposing my prediction. It could be argued that this is due to a behavioural adaptation to crypsis, but I predict this is more likely due to increased availability of natural prey, such as lemmings, upon snow melt. Moreover, this model did not include the moulting stage. Therefore, it cannot be linked to a behavioural response to crypsis. Despite a lack of significance, a similar but weaker trend appeared to occur in the conspicuous blue morph. These results could further be explained by the Arctic fox experiencing its largest decrease in body fat between March and April due to harsh winter conditions and elevated energy needs related to reproduction in May (Prestrud & Nilssen, 1995; Thierry et al., 2020), possibly making overall feeding station usage during snow cover in May more essential than during other periods of the year. These May models did not support the hypotheses that Arctic foxes would adapt foraging behaviour to crypsis level, as the conspicuous colour morph did not adapt its foraging behaviour in response to snow conditions. Moreover, in the moulting model, there was no evidence of an effect of the moulting stage on feeding station usage, not on its own nor depending on snow cover. The model did not uncover a significant increase in detections at higher snow cover levels in white foxes. However, this effect was close to significant. Overall, no behavioural adaptation to the level of crypsis was found. Similar to the finding by Kumar et al. (2020) in snowshoe hares, these models do not indicate a response in behaviour in Arctic foxes due to camouflage mismatching. The lack of camouflage did not lead to either of the predicted adaptations in foraging behaviour. Therefore, it appears unlikely that Arctic foxes have a sense of awareness concerning their level of crypsis.

Lastly, I tested the hypothesis that lack of crypsis would result in higher rates of nocturnal foraging behaviour because of the increased need for predator avoidance (Nocturnal behaviour

hypothesis) (Fig. 7). Although no differences were found between the cryptic white morph and the conspicuous blue morph, both showed a clear tendency towards nocturnal foraging behaviour. These results align with other studies concluding that Arctic foxes are predominantly nocturnal as a strategy for predator avoidance (Audet et al., 2002; Eberhardt et al., 1982; Thierry et al., 2020). Arctic foxes in Varanger face danger from red foxes, wolverines, and golden eagles. Golden eagles can form a considerable threat to Arctic foxes (Jackson et al., 2023). Therefore, I hypothesise that this nocturnal behaviour is an essential behavioural pattern of foxes on Varanger. Based on these results, the role of crypsis in this behaviour is hard to define as both colour morphs display a similar rate of nocturnal behaviour.

Overall, this study's results support the recent theory that there is no evident cost of a background mismatch for blue Arctic foxes compared to their white counterparts (Zimova et al., 2022). This study found no evidence for behavioural adaptations to the level of crypsis, and in extension, a sense of awareness in Arctic foxes of its level of crypsis appears unlikely. Furthermore, this study provides no evidence to suspect that supplementary feeding stations could be skewing the balance of the colour polymorphism in Arctic foxes in favour of either colour morph. The results do not indicate a more substantial need for blue foxes to use supplementary feeding stations during periods of mismatching. Despite a lack of evidence for differences in behaviour related to crypsis between the colour morphs, a higher breeding propensity resulting in higher fitness has been documented for blue foxes in other sub-populations in Norway (Di Bernardi et al., 2021). The mechanisms behind this are poorly understood and remain a topic of discussion (Di Bernardi et al., 2021; Tietgen et al., 2021).

Further supporting the findings by Di Bernardi et al. (2021) is a recent study that predicts an evolutionary shift towards brown colour morph populations in response to climate change because of predicted pre-adaptation to conditions with reduced snow cover (Zimova et al., 2022). The study suggests that the brown-on-white mismatch does not seem to outweigh the possible benefits of brown pelage in Arctic foxes. This cannot be attributed to a fitness discrepancy between wild and captive-bred individuals, as wild-born foxes perform equally well as captive-born foxes in the wild (Landa et al., 2022).

Aside from the camouflage hypothesis, the associated behavioural responses and the thermoregulation hypothesis, general for polymorphic SCC moulting species, other mechanisms driving colour polymorphism in Arctic foxes could explain these potential fitness

discrepancies. A single Mendelian gene determines fur colouration in Arctic foxes, the MC1R gene (Adalsteinsson et al., 1987; Tietgen et al., 2021; Våge et al., 2005). In some conditions, blue colour morphs may have a selective advantage over their white counterparts (Laporte-Devyllder et al., 2022) due to potential differences in aggressiveness between the colour morphs linked to pleiotropy in the melanocortin system (Ducrest et al., 2008; Mafli et al., 2011; Roulin & Ducrest, 2011; Tietgen et al., 2021). Higher aggressiveness could increase the foxes' ability to compete with the larger red fox. Another fitness advantage may be the higher spermatozoa count and concentration in the semen of blue Arctic foxes, which could benefit them in reproduction (Stasiak et al., 2019).

To fully comprehend the impacts of long-term supplementary feeding and the implications of climate change on the proportion of polymorphism in Arctic fox populations, more research needs to be done to improve our understanding of drivers and behavioural differences associated with polymorphisms in SCC moulting populations.

4.1 Study Design

It is essential to understand the limitations of the dataset to understand the results' reliability and the overall study's value. One of the strengths of this dataset is that it directly links the moulting stage of a detected fox to the background. As a result, every data point where a fox was detected has information on background matching. Another strength of the dataset is its size; with over sixty thousand fox detection observed during 16 months, the dataset is robust. With such a high sample size, behavioural differences were likely to be detected if present. However, the dataset also has two main weaknesses.

The primary weakness in this dataset is its lack of information on the moulting stage and the snow cover during moments of absence of a fox at a feeding station. A study based on relative visiting frequencies was deemed most appropriate to address the research questions. As a study based on individual identification of Arctic foxes could have limited the temporal scope of this study as that process is more time intensive. Furthermore, this method is less precise because of potential misidentifications. The models mostly explain the presence of arctic foxes but provide little explanation for their absence. Interpolating the moulting scores of the arctic foxes was considered, but this option was ruled out due to significant variation in moulting progression between individual foxes (Laporte-Devyllder et al., 2022).

The other main limitation of this study is that the foraging conditions are unnatural. The feeding stations offer a resource available year-round and are designed to exclude resource competitors such as the red fox. The primary consideration is whether the Arctic fox displays the same foraging patterns with this artificial non-living feeding resource as under entirely natural conditions. Currently, it is unclear how important the feed from the supplementary feeding stations is to the overall diet of the Arctic foxes on Varanger. Nevertheless, it is thought to play significant role in their diet, as shortly after the feeding station's introduction, the population's reproductive patterns were decoupled from the small rodent cycle (Ehrich et al., 2022). It is unclear if Arctic foxes prefer this artificial resource over their natural ones as this it is more readily available. Hence, assessing a response in the foxes' foraging behaviour is more challenging, as feeding stations might be the preferred resource regardless of crypsis level. This uncertainty factor in the study makes it harder to make precise predictions about the expected responses of the foxes under the foraging and the predator avoidance hypotheses.

4.2 Future research

Here I propose multiple research ideas that could aid future research on colour polymorphism in Arctic foxes and potentially also in other species. Future camera trap-based studies can benefit from (semi)automated image scoring through machine learning (Fennell et al., 2022). Such methods can dramatically reduce the time and effort spent on analysing images. Although (semi)automated workflows cannot yet estimate characteristics such as the moulting stage, they could significantly reduce the workload of similar studies by identifying images containing the species of interest. Furthermore, future studies on this topic could benefit from using techniques such as passive integrated transponder (PIT) tags to link moulting scores to individuals (Thierry et al., 2020). To monitor snow cover remote sensing options may be a less labour-intensive alternative for snow score but may conversely reduce the level of site-specific information compared to a score based on images. The moulting scores are the most significant obstacle for such a follow-up study as they can only be obtained through visual assessment. Therefore, a combination of a camera trap along such a PIT tag-reader could provide a moulting score that can be linked to every fox individually, offering a better insight into individual differences in behaviour in response to crypsis level. This alternative study design could, with a higher degree of precision, re-test the conclusion drawn from the results in this study and determine with more certainty that a behavioural response to background mismatching is absent.

Another interesting research method could be to fit Arctic foxes of both colour morphs with GPS collars. This could enable researchers to track both morphs' spatial and temporal habitat use. Combined with daily remote sensing data on snow cover, one could investigate if colour morphs use areas that suit their crypsis needs more. Moreover, GPS tracking could indicate if the conspicuous colour morph might stay closer to its den than the cryptic colour morph to lower its predation risk. GPS tracking data could simultaneously provide a tool for other Arctic fox studies in the region that go beyond the scope of this study.

5 Conclusion

This study represents a first attempt to assess the presence of behavioural plasticity in response to crypsis level in a colour polymorphic mesopredator. The results do not indicate differences in feeding station usage, suggesting no differences in foraging (Foraging hypothesis) or predator avoidance strategies (Predation avoidance hypothesis, nocturnal behaviour hypothesis). Only an increase in feeding station usage by white Arctic foxes at higher proportions of snow cover was found. However, I predict this is not linked to the level of crypsis but rather due to more natural prey becoming available when the snow melts. Furthermore, both Arctic fox colour morphs display a high rate of nocturnal foraging, likely due to predation risk.

Recent developments in the research of colour polymorphism in Arctic foxes suggest that the shift to an increased proportion of blue foxes in Fennoscandia could be due to behavioural or physiological differences between the colour morphs rather than the thermoregulation or the camouflage hypotheses (Di Bernardi et al., 2021; Zimova et al., 2022). Based on the findings of this study, there is no clear indication of behavioural differences between the two colour morphs. Similar to the snowshoe hare, the Arctic fox displays no behavioural plasticity in response to background mismatching (Kumar et al., 2020). Therefore, the Arctic fox appears unaware of its crypsis level. As a consequence of the absence of a behavioural response to a camouflage mismatch, the white colour morph will likely be under increased pressure as climate change will prolong periods of background mismatching, potentially shifting colour polymorphism in Arctic foxes more towards blue dominant populations (Zimova et al., 2022).

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Appendix I

Snow protocol

Snow (90% or more snow cover)

This level of snow cover contains mostly snow. The ground is fully covered by snow; only some objects can be uncovered, for instance, larger rocks or shrubs above the snow layer.



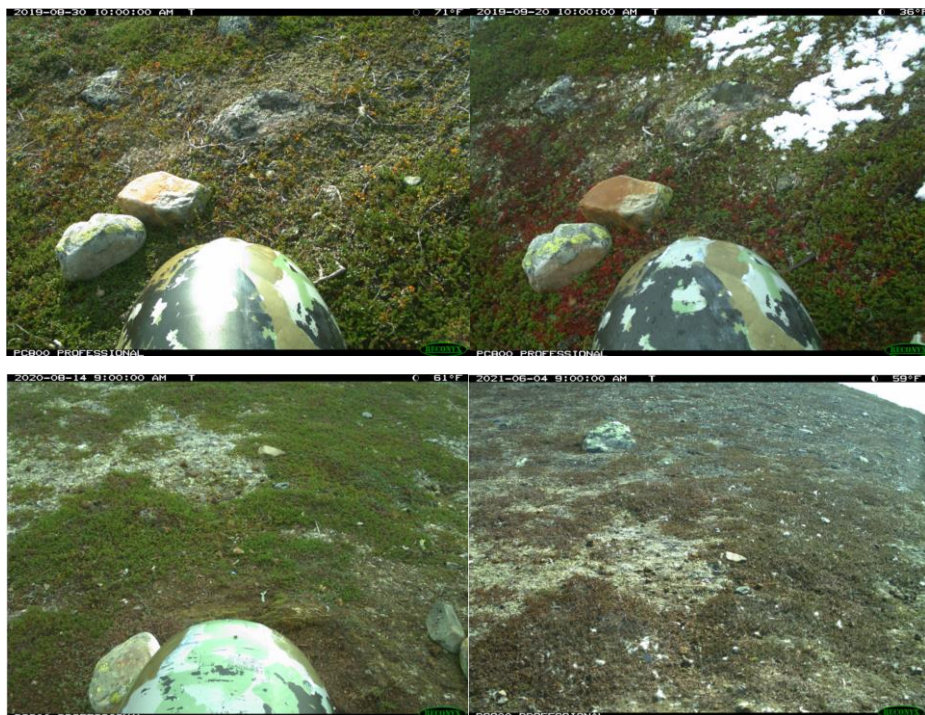
Partial snow cover (between 10% and 90% snow cover)

The most varied snow cover category ranges from 10% snow cover to 90% snow cover. This score can be allocated when more than larger rocks or shrubs are exposed. The lower limit is defined as 10% or more snow cover.



No snow (10% or less snow cover)

The upper limit is 10% snow cover; here, the cut-off is made when the vast majority of the ground is not covered in snow. Some small patches are allowed as the feeding station may provide more shade than under natural circumstances.

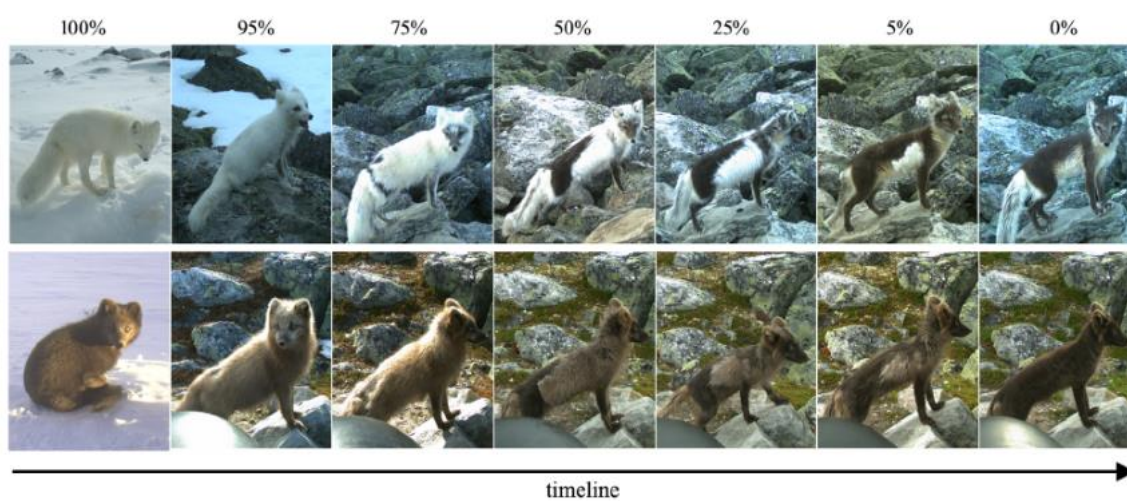


Appendix II

Moult protocol

This seven-category moult framework was adapted from (Laporte-Devlylder et al., 2022).

Figure S1: Moult score framework with seven categories ranging from 100% winter fur to 0% winter fur, adapted from (Laporte-Devlylder et al., 2022)



Appendix III

Table S1: Overview table of materials. This table lists an overview of the total fox detections per colour, along with the number of active feeding stations (the decimals are a result of some feeding stations not being active for the duration of the entire month) and the total number of pictures taken during each month of monitoring.

Overview of materials						
year	month	White fox detections	Blue fox detections	Active feeding stations	Total pictures taken	Detection Days
2018	03	1956	435	8.6	7963	262
2018	05	1155	455	5.8	5471	178
2018	08	1009	432	5.6	6903	176
2018	12	1296	575	8.2	6507	255
2019	03	6287	976	11.7	16208	362
2019	05	4993	1085	12.0	20393	370
2019	08	2008	962	12.4	9341	385
2019	12	2476	849	11.9	7394	361
2020	03	1976	348	14.2	7443	440
2020	05	7799	727	15.1	19905	469
2020	08	4490	689	13.6	12275	373
2020	12	2399	630	14.7	7463	444
2021	03	1175	299	13.0	5790	404
2021	05	3714	700	14.0	17591	430
2021	08	9001	1665	16.7	32170	516
2021	12	1961	827	15.0	7448	465

Appendix IV

Table S2: Model outputs of models based on ambient light, snow cover and moulting stage. Intsnow refers to daily values for snow cover combining observed values with interpolated values for the days without observations. The model outputs contain predictor estimates, 95% confidence intervals and p-values.

Characteristic	Beta	95% CI [†]	p-value
White fox moult model			
snow	1.2	-0.01, 2.4	0.052
moulting	-0.36	-1.3, 0.60	0.5
snow * moulting	-0.91	-2.3, 0.48	0.2
Light hour model			
light_hours	0.58	0.29, 0.87	<0.001
colour			
colourwhite	0.56	-3.3, 4.4	0.8
light_hours * colour			
light_hours * colourwhite	-0.05	-0.38, 0.28	0.8
Blue fox May model			
intsnow	0.30	-0.28, 0.89	0.3
White fox May model			
intsnow	0.69	0.15, 1.2	0.012

[†] CI = Confidence Interval

Table S3: Model outputs of the seasonal models. Both models were fitted with the month of March as the intercepts. The model outputs contain predictor estimates, 95% confidence intervals and p-values.

Characteristic	Blue fox seasonal model			White fox seasonal model		
	Beta	95% CI [†]	p-value	Beta	95% CI [†]	p-value
month						
03	—	—		—	—	
05	0.63	0.40, 0.86	<0.001	0.68	0.53, 0.83	<0.001
08	0.85	0.60, 1.1	<0.001	0.51	0.35, 0.67	<0.001
12	0.64	0.41, 0.88	<0.001	-0.06	-0.22, 0.10	0.5

[†] CI = Confidence Interval

Table S4: Tukey posthoc test comparing the number of detections per day and per feeding station between months in the dataset for both colour morphs. The table includes the difference, lower and upper confidence limit, and an adjusted p-value.

Tukey posthoc blue fox					Tukey posthoc white fox				
	diff	lwr	upr	p adj		diff	lwr	upr	p adj
05-03	2.731266	0.3875932	5.0749391	0.0146926	05-03	7.313570	3.3826898	11.2444505	0.0000108
08-03	4.677503	2.3452052	7.0098002	0.0000017	08-03	4.172869	0.3181279	8.0276096	0.0277911
12-03	1.668006	-0.6071705	3.9431821	0.2346555	12-03	-1.799260	-5.9640154	2.3654949	0.6831053
08-05	1.946237	-0.4202599	4.3127330	0.1486887	08-05	-3.140701	-6.9769424	0.6955396	0.1518711
12-05	-1.063260	-3.3734813	1.2469607	0.6372798	12-05	-9.112830	-13.2604687	-4.9651921	0.0000001
12-08	-3.009497	-5.3081769	-0.7108169	0.0043257	12-08	-5.972129	-10.0476792	-1.8965787	0.0009681

