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Global change biology

Colour moult phenology and camouflage mismatch in polymorphic populations of Arctic foxes

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Species that seasonally moult from brown to white to match snowy backgrounds become conspicuous and experience increased predation risk as snow cover duration declines. Long-term adaptation to camouflage mismatch in a changing climate might occur through phenotypic plasticity in colour moult phenology and or evolutionary shifts in moult rate or timing. Also, adaptation may include evolutionary shifts towards winter brown phenotypes that forgo the winter white moult. Most studies of these processes have occurred in winter white populations, with little attention to polymorphic populations with sympatric winter brown and winter white morphs. Here, we used remote camera traps to record moult phenology and mismatch in two polymorphic populations of Arctic foxes in Sweden over 2 years. We found that the colder, more northern population moulted earlier in the autumn and later in the spring. Next, foxes moulted earlier in the autumn and later in the spring during colder and snowier years. Finally, white foxes experienced relatively low camouflage mismatch while blue foxes were mismatched against snowy backgrounds most of the autumn through the spring. Because the brown-on-white mismatch imposes no evident costs, we predict that as snow duration decreases, increasing blue morph frequencies might help facilitate species persistence.

1. Introduction

One of the most common outcomes of climate change is phenological mismatches between the timing of life events and optimal environmental conditions [1–3]. A particularly striking phenological mismatch occurs in species displaying seasonal colour polyphenism where summer brown animals moult to white pelage to maintain camouflage against seasonally changing snow cover [4]. As climate change decreases duration of snow cover [5,6], at least 21 species of birds and mammals can become mismatched against brown backgrounds that make them more susceptible to predation [7–11].

As with other phenological mismatches, colour moulting species might be able to reduce camouflage mismatch via phenotypic plasticity in moult phenology [12]. Temperature- and snow-mediated plasticity in moult phenology has been observed in several colour moulting taxa including snowshoe hares (*Lepus americanus*) and mountain hares (*Lepus timidus*) [4,9,13,14]. Although this plasticity was adaptive, in the sense that moults tracked the temperature and snow each particular season, it was insufficient to meaningfully decrease camouflage mismatch during seasons with low snow cover [13,15–17].

Adaptive responses to camouflage mismatch may also be fostered by evolutionary shifts in moult phenology, or in the winter colour phenotype. Pelage colour phenology has been shown to covary with climate [15–17], implying that the timing and rate of seasonal pelage colour shape has been adaptively shaped by local snow duration and timing. However, this generality may be compromised in cases where small population size or relaxed selection pressure may compromise scope for evolutionary shift in a changing climate [13].

Adaptive evolution to camouflage mismatch might also occur via shifts towards genetically based winter brown phenotypes that undergo seasonal moults but their winter pelage is brown [18–21]. The distribution of winter white versus winter brown (commonly referred to as blue) morphs has been shaped by local snow duration and ephemerality across the northern hemisphere, leading to populations of all winter white morphs, all winter brown morphs, and polymorphic populations with both winter white and winter brown morphs [11]. As snow cover duration declines under climate change, blue morphs should better match their backgrounds and increase in frequency over time [11]. However, surprisingly little is known about the moults or camouflage mismatch in polymorphic populations of any colour moulting species.

Our objectives in this study were to quantify moult phenology, phenotypic plasticity and camouflage mismatch in two polymorphic populations of Arctic foxes in Sweden. Arctic foxes are the largest colour moulting carnivore [12] that presumably relies on seasonal camouflage to reduce the probability of detection by its predators (e.g. golden eagles) and possibly its prey as well (e.g. lemmings) [22–25]. First, we hypothesized that local climate determines moult phenology and predicted that foxes in the more northern, colder area would moult to winter pelage earlier in the autumn and to summer pelage later in the spring than foxes in the more southern, warmer area. Second, we hypothesized that annual temperature and snow mediate moult phenology and we predicted that foxes would moult earlier in the autumn and later in the spring during colder, snowier spring. Finally, we hypothesized that colour mismatch will differ across morphs, with white foxes experiencing no mismatch during winter but higher camouflage mismatch in spring and autumn compared to blue foxes due to the shortening snow season.

2. Materials and methods

(a) Study areas

This study was conducted in two areas in central Sweden: Vindelfjällen (66°N, 10°E) in Västerbotten County and Helags (62°N, 12°E) in Jämtland County. Both areas are open tundra and lie at similar elevation (approx. 1000 m.a.s.l.), but Vindelfjällen is located approximately 350 km north of Helags. This latitudinal difference leads to cooler temperature and longer duration of snow cover in the more northern Vindelfjällen population (electronic supplementary material, table S1). The arctic fox population in Sweden is highly fragmented and both areas are genetically isolated [26] with a possibility of local adaptations.

(b) Moult phenology monitoring

We monitored moult phenology of 89 Arctic foxes using remote camera traps placed on active Arctic fox dens (see electronic supplementary material for more details). Cameras operated during the main periods of autumn and spring moults from August to December in 2015 and 2016, and from April to August in 2016 and 2017. About half of the monitored foxes ($n = 41$ individuals) were ear-tagged with a unique combination of coloured tags as a part of a long-term monitoring project [27], facilitating individual identification from the photographs. The remaining foxes ($n = 48$ individuals) could also be individually identified based on a combination of den location, colour morph, shedding pattern and or old injuries.

We developed a standardized protocol (see electronic supplementary material) to visually identify the three stages of moult phenology in both colour morphs from photographs: (i) winter pelage (greater than or equal to 75% of body area has winter pelage), (ii) summer pelage (less than or equal to 25% of body area has winter pelage) and (iii) moulting pelage (all other instances). All photographs were classified by one observer (D.M.). All data can be accessed in Dryad [28].

(c) Statistical analysis

(i) Moult phenology

We used a hierarchical multi-nomial logistic regression analysis within a Bayesian framework to describe moult phenology and to quantify the effects of temperature and snow cover [16] (see electronic supplementary material for detailed description of the statistical framework). Briefly, we estimated the probability of a fox being in either summer (p_{summer}), winter (p_{winter}) or moulting (p_{molt}) pelage on each day using a multi-nomial logistic regression in R [29] with individuals coded as random effects.

To test whether moult phenology differed between colour morphs, we added to the model a fixed effect of colour morph (white and blue) on the probability of being in a certain pelage. The effect of the colour morph covariate overlapped zero in spring and autumn (electronic supplementary material, table S2), indicating the same moult phenology in both morphs. Therefore, we ran the following models using all individuals.

To test for differences in moult phenology across the two study areas, we added study area (Helags, Vindelfjällen) as a fixed effect. This also allowed population-specific estimates of approximate moult initiation and completion dates (see electronic supplementary material for more detail).

Finally, we investigated the effects of seasonal temperature and snow cover on moult phenology. Mean seasonal temperature (Temp) and snow water equivalent (= amount of snow; Snow) were calculated for each year at each fox den using TerraClimate dataset [30]. The seasons were defined as autumn (1 August—30 November) and spring (1 April—31 July) and encompassed the main periods when foxes underwent moults. We included either Temp or Snow as a fixed effect in univariate models to avoid problems associated with high correlation between the two variables (Pearson correlation coefficients $> |0.80|$ in all but one occasion).

To document moult plasticity at the individual level, we compared phenology of seven Vindelfjällen foxes whose moults were monitored throughout two spring seasons (no individuals were monitored in both autumn seasons). We plotted pelage observations of those individuals over time for visual assessment of the reaction norm in moult phenology.

(ii) Camouflage mismatch

Camouflage mismatch was derived from daily presence or absence of snow at each den and the daily modelled pelage colour of each fox. Snow was considered present at a camera site when the 500 × 500 m area surrounding each den was greater than 50% snow covered [31]. White morph foxes were classified as being white when their pelage had $p_{\text{winter}} \geq 60\%$ and as being brown when $p_{\text{summer}} \geq 60\%$ as these thresholds included mostly white or brown foxes, respectively, when compared to observations [13,16].

We considered two types of mismatch: (i) white-on-brown mismatch occurred when foxes were white and snow was

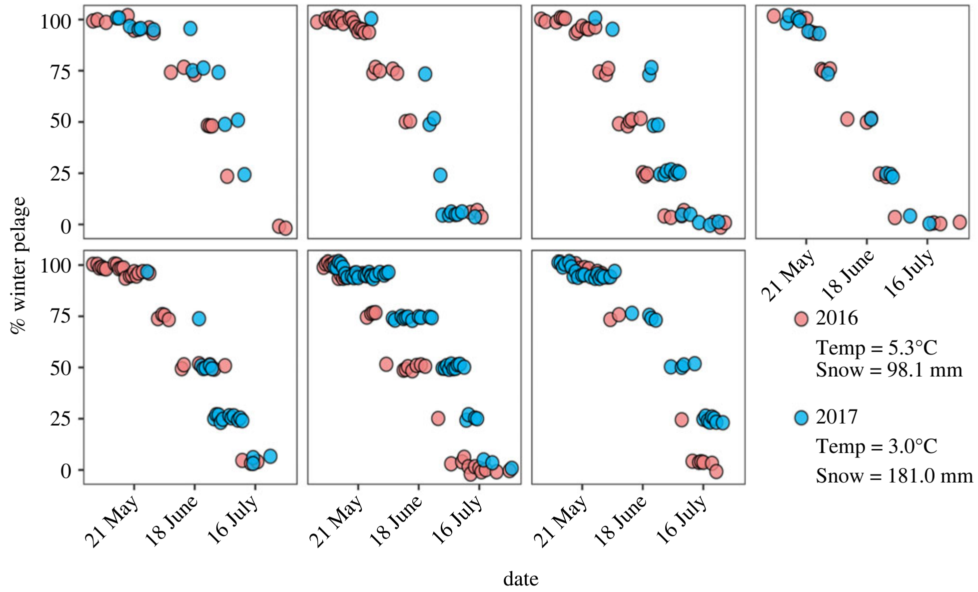

Figure 1. Spring moult phenology reaction norms of four blue (top row) and three white (bottom row) individual Arctic foxes monitored in Vindelfjällen over multiple springs. Annual average spring temperature (Temp) and snow water equivalent (Snow) for each year are given in bottom right corner.

Table 1. Effect of study area (Helags, Vindelfjällen), mean seasonal temperature (Temp) and mean seasonal amount of snow (Snow) on Arctic fox moult phenology in two study areas in Sweden. Given are mean effect size and 95% credible interval (CRI) estimates for slopes based on univariate models. Values reflect standardized data. Asterisks indicate CRIs not overlapping zero.

covariate	spring estimate	autumn estimate
area (Helags)	−6.82* (−10.88, −3.31)	4.46* (1.50, 7.99)
Temp	3.71* (2.64, 4.96)	−2.21* (−3.49, −1.16)
Snow	−4.17* (−5.55, −2.88)	−1.95* (−3.75, −0.48)

absent and (ii) brown-on-white mismatch occurred when foxes were brown and snow was present (figure 2) [16]. White foxes could experience both types of mismatch as they display seasonal polyphenism. Blue foxes could only experience brown-on-white mismatch as they are always brown. We note that our measures of mismatch were merely proxies of mismatch as perceived by human observers as opposed to Arctic fox prey and predators.

To understand the variation in mismatch between morphs, we calculated the proportion of autumn (1 August—30 November), winter (1 December—31 March) and spring (1 April—31 July) days that each morph experienced mismatch (no mismatch occurs during the summer). The proportion of each mismatch type occurrence was calculated as the count of days when individuals experienced mismatch, divided by the total number of days within each season.

3. Results

(a) Moult phenology

We determined moult phenology of 89 foxes based on 1881 independent moult observations in two study populations (electronic supplementary material, table S3). Moult phenology differed between the populations (table 1), with foxes in Vindelfjällen, the colder, more northern study area, moulting about a week earlier in the autumn and about two weeks later in the spring than foxes in Helags (electronic supplementary material, figure S1). Both spring and autumn moults took on average 48 days.

Moult phenology was mediated by temperature and snow cover. On average, moults occurred earlier in the autumn and later in the spring during colder and snowier years (table 1). This trend was consistent with phenology reaction norms; six out of the seven foxes that were observed over two springs delayed moults during the colder and snowier year (figure 1).

(b) Camouflage mismatch

Blue foxes experienced high levels of brown-on-white mismatch, being constantly mismatched against snow throughout the winter and up to 39%, and 72% of all autumn, and spring days, respectively (figure 2). White foxes experienced low levels of mismatch with white-on-brown mismatch occurring less than 7%, and brown-on-white mismatch occurring less than 3% of all spring and autumn days (figure 2). White foxes matched completely throughout the winter.

4. Discussion

(a) Moult phenology

Here we quantify for the first time the moult phenology and camouflage mismatch in Arctic foxes and in any polymorphic populations of seasonal colour moulting species. Foxes differed in moult phenology between the two study areas, with foxes in the colder, more northern Vindelfjällen population moulting to white earlier in the autumn and to brown later in the spring (electronic supplementary material, figure S1). This finding is consistent with our predictions and with findings from other species [15,16].

Also as predicted, seasonal temperature and snow cover mediated the annual variation in moult phenology in both seasons (table 1) [4,9,13–17]. The effect of weather on spring moult phenology was also evident on the individual level as six individuals moulted to summer pelage later in the

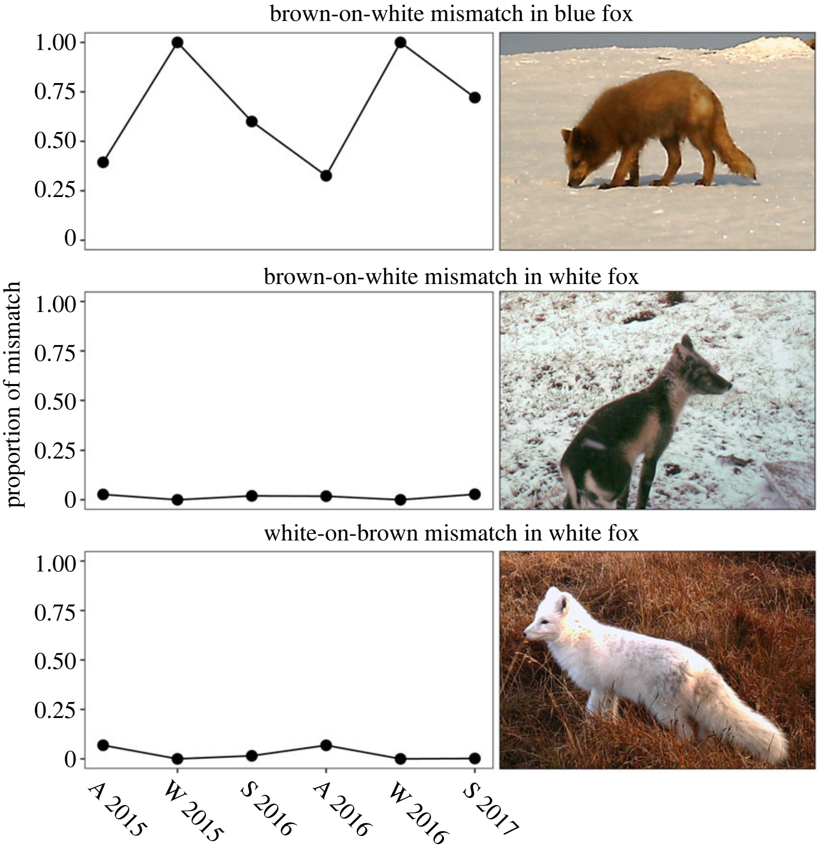

Figure 2. Proportion of days with camouflage mismatch during each season. Photos depict examples of each mismatch type for blue and white colour morphs. 'A' stands for autumn, 'W' for winter and 'S' for spring.

colder and snowier spring, with up to 20-day differences between the 2 years (figure 1). This supports conclusions previously made based on other species' population mean phenologies (as opposed to individuals tracked over multiple years; but see [17]), that phenotypic plasticity can alter moult phenology across years.

(b) Camouflage mismatch

Contrary to our prediction that white colour morphs would experience the most mismatch, camouflage mismatch was relatively low in white foxes. This might be because snow duration during each season was similar to the average duration that foxes experienced over the past 30 years at both sites (i.e. within 6 days of the 1986–2015 mean snow duration; electronic supplementary material, figure S2) and to which foxes' moult phenology and its plasticity have adapted to historically. However, snow duration is expected to decrease by on average 21 days within our study areas by the end of the century [32]. Unless white Arctic foxes are able to adaptively track the declining snow cover, white-on-brown mismatch will increase, potentially leading to selection against the white morph as observed in other colour moulting species [7–9] and other species displaying colour polymorphisms [33–36].

Blue foxes by definition could not experience white-on-brown mismatch, but they were mismatched brown against snowy background most of the autumn through the spring. Despite this surprisingly high occurrence of brown-on-white mismatch, blue fox frequencies have been increasing in some Scandinavian populations, including at our Helags study area [19,37]. Although the proximate factors driving these trends are likely complex and not well understood (e.g. camouflage, thermoregulation, immune response and genetic rescue effects) [19,37], our results suggest that brown-on white mismatch does not significantly penalize or outweigh the potential benefits of the blue morph phenotype [19,38].

5. Conclusion

Climate change is expected to lead to drastic declines in snow cover across much of the Northern Hemisphere [5,6], threatening the persistence of species adapted to cold, snowy winters [39–45]. For example, colour moulting species that moult to white pelage in the winter experience camouflage mismatch with snowless backgrounds [4]. Studies to date have documented increased mortality when mismatched [7–9] and limited ability of these species to adapt via phenotypic plasticity [15–17] and evolution in moult phenology [13]. Although little is known about populations of colour moulting species that are polymorphic in winter colour, they might play an important role in facilitating adaptation to increasingly snowless backgrounds [11]. We argue that blue morphs of colour moulting species are pre-adapted for increasingly snowless future and their frequencies are likely to increase under climate change. While this might lead to the loss of seasonal colour polyphenism in some or all populations of colour moulting species, such evolutionary shift might enable the persistence of these species and their ecological roles in the changed environments [11].

Ethics. Trapping and handling procedures were carried out following the Swedish law and the Swedish Board of Agriculture (Jordbruksverket) and the ethical board (Umeå djurförsöksetiska nämnd, ethical permits: A130-07, A131-07, A36-11, A18-14 and A19-14) and the Swedish Environmental Protection Agency (Naturvårdsverket, permit: 412-7784-07 NV, NV-01959-14).

Data accessibility. Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.djh9w0w3n [28].

Additional information are provided in the electronic supplementary material [46].

Authors' contributions. M.Z.: conceptualization, formal analysis, funding acquisition, investigation, methodology, visualization, writing—original draft and writing—review and editing; D.M.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft and writing—review and editing; L.S.M.: conceptualization, funding acquisition, supervision and writing—review and editing; A.J.D.: formal analysis, methodology and writing—review and editing; A.A.: conceptualization, funding acquisition, resources, supervision and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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