









RESEARCH ARTICLE

A camera trap-based assessment of climate-driven phenotypic plasticity of seasonal moulting in an endangered carnivore

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Keywords

camera trapping, camouflage, climate change, colour polymorphism, phenological mismatch, phenotypic plasticity

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Editor: Marcus Rowcliffe

Associate Editor: Xuehua Liu

Received: 4 March 2022; Revised: 13 August 2022; Accepted: 29 August 2022

doi: 10.1002/rse2.304

Abstract

For many species, the ability to rapidly adapt to changes in seasonality is essential for long-term survival. In the Arctic, seasonal moulting is a key life-history event that provides year-round camouflage and thermal protection. However, increased climatic variability of seasonal events can lead to phenological mismatch. In this study, we investigated whether winter-white (white morph) and winter-brown (blue morph) Arctic foxes (*Vulpes lagopus*) could adjust their winter-to-summer moult to match local environmental conditions. We used camera trap images spanning an eight-year period to quantify the timing and rate of fur change in a polymorphic subpopulation in south-central Norway. Seasonal snow cover duration and temperature governed the phenology of the spring moult. We observed a later onset and longer moulting duration with decreasing temperature and longer snow season. Additionally, white foxes moulted earlier than blue in years with shorter periods of snow cover and warmer temperatures. These results suggest that phenotypic plasticity allows Arctic foxes to modulate the timing and rate of their spring moult as snow conditions and temperatures fluctuate. With the Arctic warming at an unprecedented rate, understanding the capacity of polar species to physiologically adapt to a changing environment is urgently needed in order to develop adaptive conservation efforts. Moreover, we provide the first evidence for variations in the moulting phenology of blue and white Arctic foxes. Our study underlines the different intraspecific selective pressures that can exist in populations where several morphs co-occur, and illustrates the importance of integrating morph-based differences in future management strategies of such polymorphic species.

Introduction

From freezing, snow-covered winters to milder, snowless summers, Arctic habitats show considerable variations from one season to the other. In order to adapt to such contrasted conditions, species that live at these latitudes evolved diverse strategies. By transitioning from a short summer coat to a denser winter pelage, moulting is a seasonal process that contributes to maintaining thermal balance. This mechanism evolved convergently in birds and mammals sharing similar environments [e.g. Arctic foxes (*Vulpes lagopus*), snowshoe hares (*Lepus americanus*),

short-tailed weasels (*Mustela erminea*), rock ptarmigans (*Lagopus muta*)], emphasizing the importance of external factors in its regulation (Beltran et al., 2018; Helm et al., 2013; Zimova et al., 2018). In addition to changes in the insulative property of the fur, moulting is often polychromatic, with a winter pelage typically pale (often white) during the snow-covered months and significantly darker (often brown) during summer, which provides year-round camouflage in tundra landscapes.

Although the dominating selective pressure remains contentious, camouflage is largely regarded as the preponderant function for a seasonally dichromatic moult (Davis

et al., 2019; Mills et al., 2018; Zimova et al., 2018). However, while background matching is a proven strategy to best achieve crypsis (Caro, 2005), seasonal coat colour change needs to be well timed in order to be efficient. The phenology of moulting is subject to strong photoperiodic influence (Beltran et al., 2018; Zimova et al., 2018). Because photoperiod does not differ between years, this underlying cue makes moulting-dependent species vulnerable to inter-annual climatic variability, with potentially serious fitness consequences (Thackeray et al., 2016; Visser & Gienapp, 2019; Walker II et al., 2019; Zimova et al., 2016). Accelerated rates of climate change over recent decades have promoted special attention to Arctic ecosystems where the effects of global warming are most pronounced (Bokhorst et al., 2016; Cooper, 2014; Post et al., 2019). At the forefront of these changes, milder temperatures in combination with reduced snow cover and duration are altering ecosystem dynamics (Bokhorst et al., 2016; Cooper, 2014; Parmesan, 2003). The ability to maintain well-timed climate-dependent circannual life history traits, such as reproduction, migration or moulting, is therefore paramount.

To date, the majority of studies on dichromatic moult have focused on species that are subject to intense predation (e.g. Atmeh et al., 2018; Imperio et al., 2013; King & Moody, 1982; Mills et al., 2013; Pedersen et al., 2017; Rust, 1962; Watson, 1963, 1973; Zimova et al., 2019). At the other end of the food chain, the Arctic fox presents an interesting case study of a medium-sized carnivore that changes colour twice a year. Along with their dimorphic seasonal coat, Arctic foxes also exist in two main colour phenotypes, white and blue. White morph individuals are fully white during the winter months and turn pale grey/brown on the dorsal side in summer, while blue Arctic foxes remain dark brown year-round, displaying only a slightly lighter blue shade in winter (Audet et al., 2002). Both morphs overlap in their distribution, and while the proportion of each phenotype varies between populations (Braestrup, 1941; Chesemore, 1968), the vast majority of the species' distributional range is polymorphic (Mills et al., 2018). Despite their higher trophic position, Arctic foxes are still subject to predation by larger predators (Frafjord et al., 1989; Landa et al., 2017; Pamperin *et al.*, 2009; Tannerfeldt et al., 2002). In this context, a conspicuous white fur on a contrasting snow-free background intensifies the threat of predation and adequate camouflage is essential (Montgomerie et al., 2001; Pedersen et al., 2017; Zimova et al., 2016). Alternatively, crypsis could also be advantageous for the Arctic fox to avoid detection by its prey, although studies on foraging success of cryptic predators are lacking in tundra habitats, where hunting is subnivean for a large part of the year (Bilodeau et al., 2013).

Phenotypic plasticity, 'the ability of individual genotypes to produce different phenotypes when exposed to different environmental conditions' (Pigliucci et al., 2006), allows for a rapid adaptive response to a changing environment, and has the potential to mitigate climate change-related stressors such as background mismatch, by allowing individuals to modulate the phenology of their moult.

In this study, we used camera trap images to test the capacity of Arctic foxes to physiologically adapt to inter-annual changes in environmental conditions, and quantified temporal variations in the progression and rate of their winter-to-summer moult. The influence of pertinent ecological factors was explored over an eight-year period in an inland polymorphic subpopulation of Arctic foxes in Norway. To date, no difference in the phenology of moulting has been characterised between white and blue Arctic foxes. We investigated both morphs and hypothesize that local year-to-year variations in moult phenology will be determined by annual climatic conditions, with the prediction that moulting in the spring occurs later and/or slower during colder years with longer duration of snow cover compared to warmer years with less snow cover.

Material and Methods

Study species

The Arctic fox population in Fennoscandia underwent a dramatic bottleneck in the late 19th century, mainly due to anthropogenic pressures (Angerbjörn et al., 2013; Landa et al., 2017). The species has been protected by law in Fennoscandia since 1928–1938 and subsequent mitigation measure such as red fox (*Vulpes vulpes*) culling and supplementary feeding have been carried out (Angerbjörn et al., 2013; Hemphill et al., 2020), followed by the initiation of the Norwegian Arctic Fox Captive Breeding Programme in 2005 (Landa et al., 2017). Through these conservation measures, the overall number of Arctic foxes has increased from 40–60 adult individuals in all of Fennoscandia in 2000 (Angerbjörn et al., 2013) to an estimated 273–338 adults in 2020 in Norway alone (Eide et al., 2020).

Although increasing in number, the Fennoscandian metapopulation is still distributed in small, isolated subpopulations and remains vulnerable (Henriksen & Hilmo, 2015). As global warming progresses, new challenges appear for the Arctic fox. Rodent cyclicality, a known driver of inland Arctic fox population dynamics (Angerbjörn et al., 1999; Strand et al., 1999), is expected to become increasingly irregular (Kausrud et al., 2008), leading to reduced Arctic fox reproductive success in the

absence of rodent peak years (Fuglei & Ims, 2008). Moreover, climate change has led to a northward expansion of larger competitors (Elmhagen et al., 2015; Norén et al., 2015). Among them, the red fox poses a major threat to the Arctic fox by being both a competitor for resources, but also imposing a substantial risk of predation on its smaller congener (Frafjord et al., 1989; Hamel et al., 2013; Tannerfeldt et al., 2002).

Study area

The study area comprised approximately 1,500 km² of Arctic fox habitat in south-central Norway (Fig. 1), located on the highest mountain plateau of Dovrefjell-Sunndalsfjella National Park (62°23'48" N 9°10'23" E). The landscape consists mainly of alpine tundra habitat, with an average altitude of 1,300 m asl. and peaks reaching 2,286 m asl. Snow usually covers the ground from November to May. Wolverines (*Gulo gulo*), golden eagle (*Aquila chrysaetos*) and red foxes are commonly found in the area (Bischof et al., 2020) and can be observed around the supplementary feeding stations on a regular basis (pers. obs.). Among the species of small rodents that occur locally, bank voles (*Clethrionomys glareolus*) and Norwegian lemmings (*Lemmus lemmus*) are the most abundant (Strand et al., 1999) and typically display a 3–5 year cyclicality (Ehrich et al., 2019; Framstad, 2021), with the last two peak years observed in the study area in 2014 and 2017 (Framstad, 2021).

Wildlife camera traps

The study area covers the subpopulation termed “Snøhetta”, and is one of the earliest release sites of the Captive Breeding Programme where juvenile Arctic foxes were reintroduced between 2007 and 2011 (Landa et al., 2017; Ulvund et al., 2021). Snøhetta is now home to one of the largest subpopulations of Arctic foxes in Norway, still supported by supplementary feeding (Eide et al., 2020; Ulvund et al., 2021). As part of the extensive monitoring scheme in place in the area, motion-triggered wildlife camera traps (PC800 HyperFire semi-covert camera trap, Reconyx Inc., Wisconsin, USA) were mounted on supplementary feeding stations in proximity to active Arctic fox dens (see Landa et al., 2017; Thierry et al., 2020). We used pictures and video footage from a recurring time frame from April to August 2011–2018 to identify and extract the date at which visiting foxes were reaching different stages of moulting. To ensure a maximum continuity of pictures covering the whole study period, 21 different feeding station sites of comparable climatic conditions were selected within Snøhetta. The relative positions of the cameras at the landscape scale

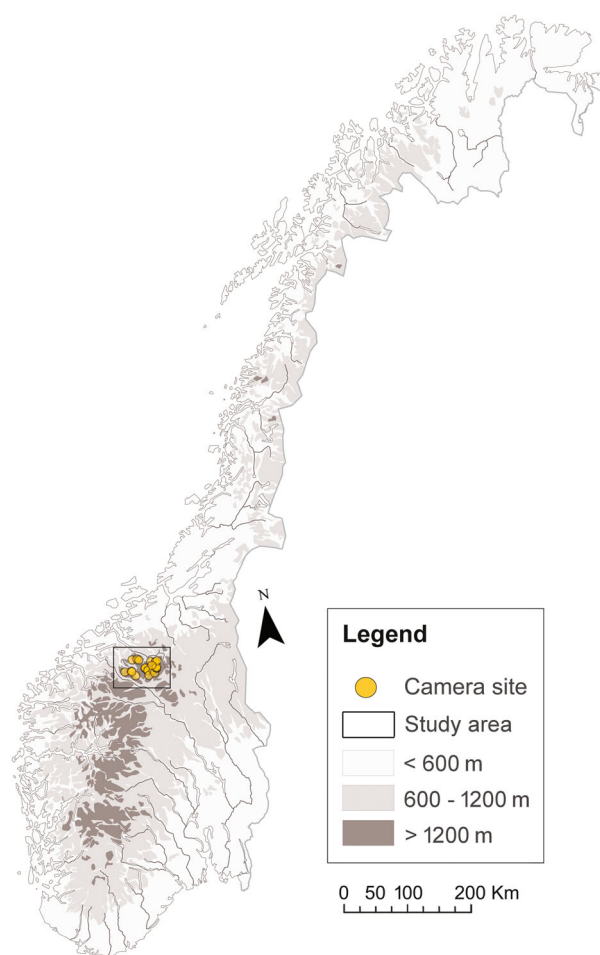


Figure 1. Map of Snøhetta study area with the position of the wildlife camera traps used in this study. Arctic foxes are endangered and protected by law in Norway, and sensitive data such as the exact location of dens, feeders, and camera traps are consequently shielded from public access and cannot be released. Map representation has therefore been kept to a coarse scale, and details related to the relative positions of the cameras are provided in the method section.

were such that the mean distance between closest neighbouring cameras was 3.56 km (SD: 2.73 km), with a minimum of 0.34 km, and a maximum of 8.93 km.

Moult phenology characterisation

To characterise the progression of the moult in wild Arctic foxes from camera trap pictures, we first established a standardized six-category protocol developed by Moberg (2017), ranging from full winter coat to full summer coat. Moulting was established as “initiating” when the first signs of shedding were apparent (at least 95% winter fur). Following onset, subsequent categories were set at 75%, 50%, 25% and 5% winter fur, and eventually,

moult was considered “complete” when no remaining patches of winter pelage were observed (0% winter fur) (Fig. 2; see Supporting Information S1 for the complete protocol). Individual Arctic foxes were identified based on physical characteristics (e.g. ear tags, scars, moulting patterns, timing of moulting) and assigned a unique ID number. Morph (white/blue), site and year of observation were additionally noted for each fox.

From the pictures, 188 Arctic foxes were identified, with a minimum of 13 and a maximum of 33 different individuals identified within a single year (Table 1). The pictures allowed us to establish a moulting progression score for a total of 882 independent moulting stages. Moulting stages were scored by the same person to ensure homogeneity in the dataset and pictures from different foxes at the same moulting stages were cross-validated.

Environmental variables

The study period included years where local environmental conditions varied considerably (Table 1). We included in the analysis three weather variables reflecting different aspects of the climatic conditions for a given year and relevant to moult phenology (following Atmeh et al., 2018; Mills et al., 2013; Pedersen et al., 2017; Zimova et al., 2014, 2016, 2019). The average temperature during spring moulting season (April–July), reflecting inter-annual temperature variations for all sites, was extracted at the closest weather station at relevant altitude (Hjerkinn II station, 1,012 m asl) (the Norwegian Meteorological Institute, 2021). We used two variables for snow – depth and duration, retrieved for each camera location.

Snow variables were collected from modelled snow water equivalent (SWE) (Saloranta, 2014) and interpolated into daily gridded 1×1 km resolution maps produced by The Norwegian Water Resources and Energy Directorate (NVE). For the days of interest, all snow variables were extracted from individual 1 km resolution cells within which a camera site was present, so that the scale of the snow data used matched the modelled snow products. Snow depth (mm) on May 1st was used as a measure of the amount of snow present, and reflecting the colour of the background just prior to moulting season. For inter-annual comparisons of the duration of the spring snow season, we used the number of days with continuous snow on the ground between January 1st and the first day when snow is absent for a minimum of 7 days. Following Zimova et al. (2019), this 7-day buffer ensured that we discarded any apparent early spring snowmelt followed by further snow events.

Arctic foxes show a strong reproductive response to rodent abundance (Angerbjörn et al., 1999; Strand et al., 1999). An annual index of rodent density was therefore included in the analysis, expressed as a cycle phase value ranging from 1 to 4 (1 – low, 2 – increasing, 3 – peak, 4 – decreasing; following Angerbjörn et al., 2013) and estimated yearly from trapping data of three locally occurring rodent genera (*Lemmus*, *Myodes* and *Microtus* spp.) (Framstad, 2021).

Statistical analysis

All statistical analyses were carried out in R version 4.0.3 (R Core Team, 2020). Pairwise correlations among the

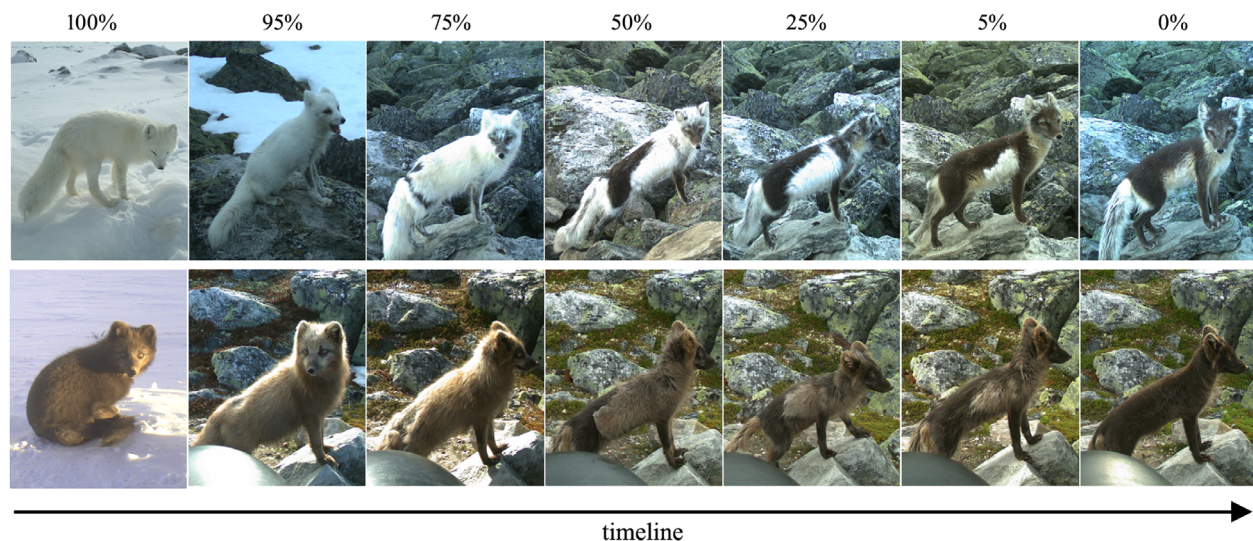


Figure 2. Spring fur moulting progression for Arctic foxes of the white (top row) and blue (bottom row) morphs. Moulting in spring progresses from full winter coat (100%) to full summer coat (0%).

TABLE 1. Annual environmental variables for the camera sites in the study area. For each year, the number of sites (*Camera sites*) where moulting events were recorded are given, along with the number of individual moulting Arctic foxes identified (*Individuals*) and the number of blue morph individuals in square brackets, the mean of the three climatic variables (*Temperature*, *Snow cover duration*, *Snow depth May 1st*), and the rodent cycle phase (*Rodent index* [1 – low, 2 – increasing, 3 – peak, 4 – decreasing])

Year	Camera sites (<i>n</i>)	Individuals (<i>n</i>) [blue morph]	Temp. (°C)	Snow cover duration (days)	Snow depth May 1st (cm)	Rodent index
2011	5	13 [5]	5.45	139	18.99	4
2012	8	33 [7]	4.17	174	94.82	1
2013	11	29 [7]	3.72	148	82.19	2
2014	7	23 [6]	5.68	151	68.34	3
2015	7	22 [6]	4.02	188	103.87	1
2016	8	27 [9]	4.62	154	85.97	2
2017	4	16 [6]	3.88	161	110.38	3
2018	7	25 [9]	5.52	147	89.41	4

climatic variables were first calculated based on local climatic data for the period between 2001 and 2020. All three variables showed a correlation coefficient greater than 0.70 and were therefore subsequently tested in three separate models.

To investigate differences in the timing and rate of spring moulting, we used a Linear Mixed Model (LMM) based on repeated observations of single individual foxes, with the *lmer* function from the *lme4* package (Bates et al., 2015). In order to use linear regression principles, we first converted the moulting progression scores (expressed as % of winter fur and ranging from 95% to 0%) to proportions, before performing a logit transformation. These proportions were then used as response variable in the models. Logit transformations are commonly performed in ecological studies to linearise sigmoid distributions of proportional data (Gibson, 2015), expressed as $\ln(p/(1-p))$, where p is a proportion (Warton & Hui, 2011). The timing and rate of the moulting events were both integrated in a single model, represented by the intercept values and the slope of the response curves respectively. We started from a full model, where moult scores were used as the dependent variable and date as main effect, with an interaction between date and any one of the climatic variables. Morph and rodent cycle phase were additionally integrated as explanatory variables. In all three models (one model per climatic feature), a random intercept and slope was fitted to the foxes' individual ID to allow for difference in individual responses, and random intercepts fitted to site and year. Year was used as a categorical random factor in the analysis, and the recorded dates of each moulting event, along with all climatic data, were treated as continuous variables. To avoid problems of convergence in the LMM analysis, we furthermore centre-scaled all continuous variables so that their means were 0 and standard deviations 1. Afterwards, we performed a stepwise removal of the non-significant relationships ($p > 0.05$), until only

significant regressions remained. All tests of significance were based on type II Wald χ^2 from analyses of deviance using the *car* package (Fox & Weisberg, 2019), and the goodness-of-fit of the best candidate models evaluated with Nakagawa's R^2 (Nakagawa et al., 2017). Estimated effects with confidence intervals, for illustration (Fig. 3), were calculated using the *effects* package (Fox & Weisberg, 2019).

Results

The phenology of moulting in spring showed substantial variation between years at the population level. The duration of snow on the ground was identified as the factor best explaining variation in both the timing ($\chi^2 = 34.12$, $df = 1$, $p < 0.0001$) and rate ($\chi^2 = 26.98$, $df = 1$, $p < 0.0001$) of moulting, with a Nakagawa's marginal R^2 value of 0.662. Transition to the summer coat occurred earlier and was completed faster in years where the duration of snow cover was shorter (Fig. 3). Accordingly, a progressive shift towards later and slower rates of moulting was observed as the number of days with continuous snow on the ground increased (Fig. S2). Temperature was also significantly correlated to timing ($\chi^2 = 11.04$, $df = 1$, $p < 0.001$) and rate ($\chi^2 = 14.02$, $df = 1$, $p < 0.001$), with a Nakagawa's marginal R^2 value of 0.650; whereas snow depth had no significant effect on either timing ($\chi^2 = 0.03$, $df = 1$, $p = 0.87$) or rate ($\chi^2 = 2.24$, $df = 1$, $p = 0.13$) of moulting.

For the best fitted model, an analysis of variance (ANOVA) coupled with a Tukey post-hoc test established 2011 and 2015 as the 2 years with the greatest inter-annual differences in snow duration (mean difference of 51.43 days of continuous snow, $p < 0.0001$), with fewer days with continuous snow cover in 2011 compared to the long winter in 2015 (Table 1). These two climatically extreme years corresponded also to the largest shift in moult timing and rate, resulting in a 3- to 6-week

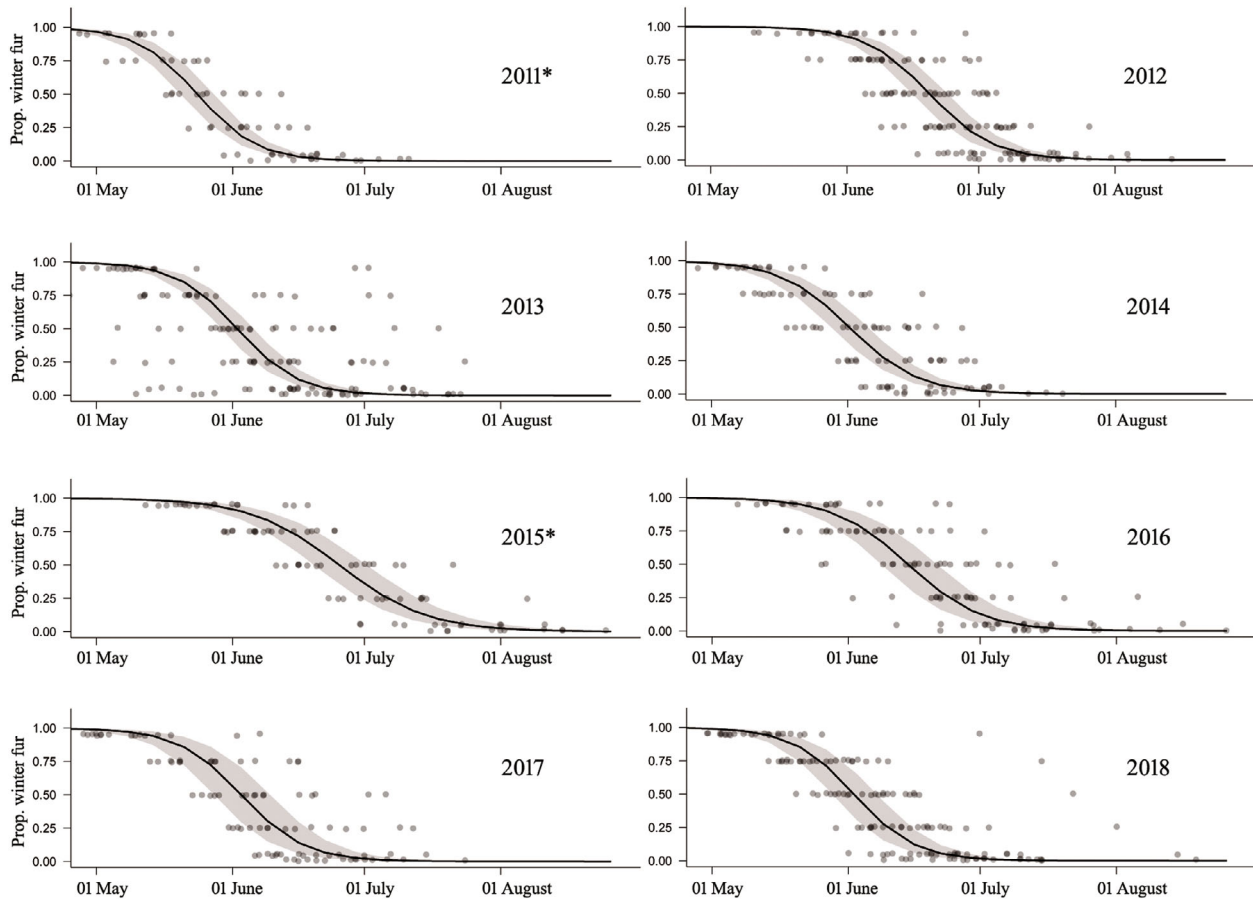


Figure 3. Progression curves of the Arctic foxes' spring moult phenology for each year between 2011 and 2018. Each point aligned along the same moulting stage corresponds to a single individual fox. In order to ease visual interpretation, the logit transformed response variable (% winter fur) has been plotted back to its original scale and predictor variables are presented using unscaled, uncentred values. Stars (*) indicate the 2 years with extreme short (2011) and long (2015) durations of snow cover.

difference in mean population initiation and completion dates. In 2011, the onset date of moulting was early in May (May 7th \pm 1.99 days) and moulting was completed in late June (June 23rd \pm 3.21 days). In contrast, spring moulting in 2015 initiated in late May (May 27th \pm 2.37 days), and the population's mean completion date was in the beginning of August (August 1st \pm 4.35 days) (Fig. S3).

A significant difference in moult timing was established for the blue and white morphs (snow duration model: $\chi^2 = 5.529$, $df = 1$, $p = 0.0187$; temperature model: $\chi^2 = 5.553$, $df = 1$, $p = 0.0184$), with white foxes moulting earlier than blue. Further analysis on the median dates of moulting (50% winter fur) in years of extreme snow and temperature values demonstrated this difference to be largely driven by the warmest years (2011 and 2018), where white individuals reached 50% of winter fur loss 10 days earlier than blue on average (Fig. 4a. *t*-test;

$t = 2.2644$, $df = 18.291$, $p < 0.05$), while no difference was detected for the coldest years (2012 and 2015, Fig. 4c. *t*-test; $t = -0.5501$, $df = 17.795$, $p = 0.59$) nor for years of intermediate weather conditions (2013, 2014, 2016 and 2017, Fig. 4b. *t*-test; $t = -1.0533$, $df = 46.206$, $p = 0.30$).

Discussion

Remote camera trapping has been used for some time to answer biological questions; however, very few studies utilized this means of investigation to look at phenological events across time or space (e.g. Hofmeester et al., 2019; Zimova et al., 2019). Images from the wildlife cameras yielded data of high temporal resolution, as typically required when looking at phenology, and allowed us to investigate plasticity at the population level. As illustrated here, the use of remote technologies offers great potential to investigate the resilience of endangered species in their

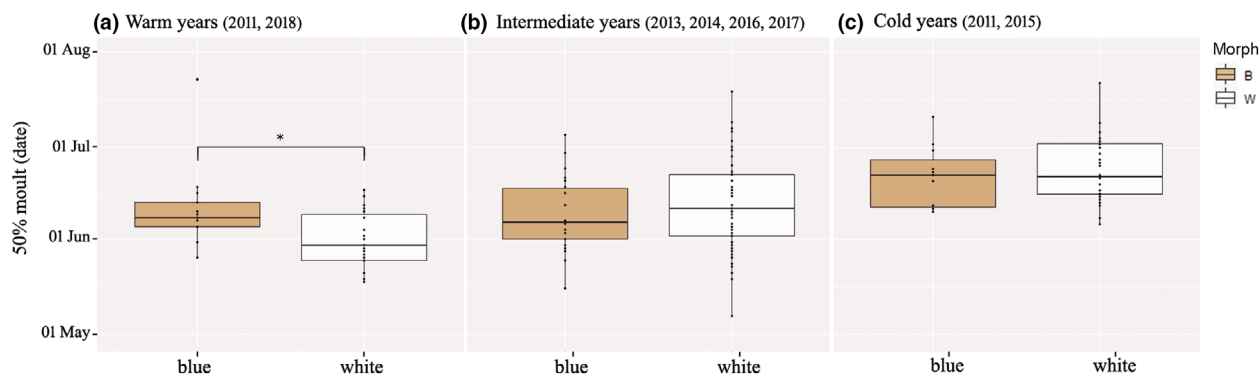


Figure 4. Median date of moulting (50% winter fur) for both morphs of Arctic foxes. Points represent single individuals. (a) For the 2 years with particularly short snow cover durations and high temperatures (2011 and 2018), white foxes moulted 10 days earlier than blue foxes on average ($p < 0.05$). (b) For years of intermediate snow cover durations and temperatures (2013, 2014, 2016 and 2017) there was no significant difference, nor for the 2 years with particularly long snow cover durations and low temperatures (2012 and 2015) (c).

natural environment, while minimizing stress and disturbance that could otherwise arise from repeated intensive fieldwork efforts, which was of particular relevance in our study.

Our results show strong evidence of plasticity in the timing and rate of spring moulting at the population level. Moulting was mediated by exogenous factors, with seasonal values of snow cover duration and temperature affecting the moult phenology in the predicted direction. The strongest relationship was the progressive shift towards later and prolonged moulting as the number of days with snow on the ground increased and when temperatures remained cold far into the spring. Our results fall in line with previously established evidence of climate-driven plasticity for coat changes of other seasonally moulting mammals (King & Moody, 1982; Mills et al., 2013; Rust, 1962; Watson, 1963; Zimova et al., 2014, 2019) and birds (Kiat & Sapir, 2017; Watson, 1973) found at high latitudes. The interplay between exogenous cues and intrinsic factors of regulation remains largely unknown; however, both snow duration and temperature have been found to impact the phenology of multiple life history events (Caro, 2005; Mortensen et al., 2015; Réale et al., 2003). Similar to our results, studies conducted on snowshoe hares showed that both the rate of fur replacement (Mills et al., 2013; Zimova et al., 2014) and the initiation time (Zimova et al., 2019) of the white-to-brown moult were affected by those two factors.

Studies of moulting species have often opposed the camouflage hypothesis with the thermoregulation hypothesis as ecological drivers of a dichromatic coat change (Caro, 2005; Galeotti et al., 2003; Stuart-Fox et al., 2017), although some complementarity has been suggested (see Zimova et al., 2018). Disentangling the relative importance of camouflage vs. thermoregulation for fur

colouration was outside the scope of this study; however, our results provide empirical evidence that a combination of these factors could act as major driving forces of seasonal moulting in the Arctic fox, with different selective costs associated with respective colour morphs. For organisms that moult from a dark summer coat to a white winter coat, as is the case with white morph Arctic foxes, the camouflage hypothesis offers strong theoretical and empirical grounding. At first glance, the observed plasticity of the population in response to snow cover duration strongly leans towards camouflage as being the main *raison d'être* behind seasonal moulting. White Arctic foxes remain white substantially longer when snow cover persists for a relatively long period of time, providing them with a substantial crypsis advantage. Conversely, in a snowless landscape, the conspicuous white fox faces a greater pressure to moult to avoid detection, and should *a priori* transform earlier/faster to its summer pelage than blue individuals. The difference observed between morphs in this study rigorously supports this hypothesis, with white foxes completing their moult earlier than blue morphs in years with particularly warm temperatures and a short snow cover duration. On the other hand, if phenological plasticity of the moult was only driven by selective pressures related to camouflage, then there should be a clear advantage for the white morph being cryptic year-round. Polymorphism in nature remains uncommon (Galeotti et al., 2003; Roulin, 2014) and morphs that have increased risks of mismatch (e.g. blue morph arctic foxes in a snow-covered environment) are usually found at decreasing proportions or only in marginal numbers (Atmeh et al., 2018; Mills et al., 2018; Pedersen et al., 2017). Opposite to that idea, recent findings showed that having a brown pelage in a snow-covered environment does not confer a fitness disadvantage, with even slightly higher survival and reproduction rates for

the blue morph (Di Bernardi et al., 2021). The proportion of blue foxes in inland Norway has been on the rise for the past 15 years (Di Bernardi et al., 2021), suggesting that ultimate causes complementary to crypsis are at play. The vast majority of animals that change colour seasonally show a clinal variation in winter colour phenotypes, with a clear gradient from complete winter brown to complete winter white populations as latitudes increase (Mills et al., 2018). Sympatry of winter white and winter brown animals (e.g. snowshoe hares and least weasels [*Mustela nivalis*], respectively) has mostly been associated with differences in the selective pressures on fur colouration due to contrasting life-history strategies, and mainly in relation to camouflage against predation (see Davis et al., 2019). The co-occurrence of blue Arctic foxes with their white conspecifics however cannot be associated with diverging life cycles or opposing trophic positions. In the context of background matching, the duration of snow cover could be expected to have little impact on the spring moult phenology of these individuals that remain brown year-round. Nevertheless, blue arctic foxes moulted significantly later when the duration of snow cover was prolonged, demonstrating the same patterns of variation as the white morph.

Asides from a lighter colouration, the winter pelage of seasonally moulting mammals displays changes in density and length (Underwood & Reynolds, 1980), providing a far better insulation against the cold than the shorter summer coat. Because it is most dense on body parts that are in direct contact with the ground, the winter fur of Arctic foxes is most efficient in insulating them from snow (Prestrud, 1991). Parts, such as the head, the ears, or the distal end of the legs, not in contact with the snow surface, show only minor changes in density from summer to winter (Prestrud, 1991; Underwood & Reynolds, 1980). Consequently, and consistent with the findings of the present study, not only temperature-, but also snow-driven plasticity confers a clear advantage for the animals, regardless of their fur colouration, bringing thermoregulation to centre stage in seasonal moulting for both blue and white Arctic foxes.

Although the crypsis advantage of the white phenotype remains evident in the presence of snow, the functional efficiency of a white winter coat is undermined under climate change scenarios. Zimova et al. (2018) predicted a decline of winter white morphs as possible adaptation to the global shortening of winter seasons, echoing the increase in blue morph individuals observed in inland Norway (Di Bernardi et al., 2021). Moreover, with the widespread increase of earlier snowmelt, environmental plasticity in the timing of moulting does not necessarily reduce the frequency of mismatches in the absence of additional behavioural response (e.g. moving away from a

brown snowless patch when having a white coat) (Kumar et al., 2020). In this regard and in the context of global warming, direct or indirect selection on phenotypic traits genetically associated with fur colouration might favour dark phenotypes, and topple the adaptive benefit of camouflage. The blue colour, caused by a single gene (MC1R) found in a region of high gene density (Tietgen et al., 2021), is inherited as a simple Mendelian trait and dominant to the white morph (Våge et al., 2005). Genomic regions implicated in melanogenesis have been found to confer increased resistance to stress (Ducrest et al., 2008; Roulin & Ducrest, 2011), higher immunity (Fedorka et al., 2012), and a better regulation of climate-induced physiological processes (Roulin et al., 2005). Although it has yet to be established, the pleiotropic effects of these genes might constitute a selective advantage to blue over white morph Arctic foxes as suggested by Di Bernardi et al. (2021) and Tietgen et al. (2021). As part of the behavioural syndromes generated by the melanocortin system (Ducrest et al., 2008), darker individuals often also show enhanced aggressiveness and tend to be better competitors than their white conspecifics (Maffi et al., 2011; Roulin et al., 2005). Accordingly, with the recent northward expansion of the red fox (Elmhagen et al., 2015; Norén et al., 2015), blue Arctic foxes might be better equipped to contend with the intraguild competition imposed by this larger carnivore. Morph distinction between blue and white Arctic foxes is seldom considered, and further investigation on how behaviour and physiology covary with fur colouration is necessary to shed light on any significant differences between the two morphs.

Our study constitutes a first attempt to integrate highly variable interannual variation in the characterisation of environmentally driven phenological plasticity of blue and white Arctic foxes in the wild. The circumpolar distribution of the species places this tundra specialist in habitats where conditions fluctuate, and substantial variations in several life-history traits have been reported (Audet et al., 2002; Eide et al., 2011; Fuglei & Ims, 2008; Nater et al., 2021). Accordingly, local responses to climate could arise, including differences in the adaptive flexibility of moulting phenology. Changes in the local conditions could also lead to contrasted selection pressures on fur colouration. Supplementary comparative studies conducted in populations where resource availability and predation pressure contrast are needed to determine possible inter-population differences and understand the scale at which this phenomenon operates.

Conclusion

We showed that Arctic foxes are capable of modulating the phenology of their moult in response to local

variation of snow cover duration and temperature. Our results contribute to the growing body of evidence that rapid adaptation to a changing climate is possible in many organisms thanks to sufficient phenotypic variation and plasticity (Beltran et al., 2018; Mortensen et al., 2015; Zimova et al., 2014, 2019). The plasticity reported in this study offers potential for the Arctic fox to cope with challenges imposed by climate change. Understanding a species' capacity to physiologically adapt to a changing environment is central to conservation planning and contributes to identifying priority measures in future decision-making. Our results highlight moreover the intraspecific variations that exist in polymorphic populations, providing important insight and basis for integrating morph-based differences in conservation programmes, for instance, planning captive breeding and release of Arctic foxes into the wild, with the aim of restoring a species population that could cope with future climate variability.

Acknowledgements

We thank the Norwegian Nature Inspectorate, Lesja Fjellstyre, Oppdal Bygdeallmenning, Dovre fjellstyre, and Sundal fjellstyre for servicing the camera traps that provided the data used in this study. The Norwegian Captive Breeding Programme for Arctic Fox (contract 19087015), which was the basis for this study, was funded by the Norwegian Environment Agency.

Author Contributions

LLD, KRU, LRE, NEE and CRJ conceived the ideas and designed the study; LLD, OO and CRJ developed the methodology; LLD, KRU, LRE and CRJ collected the data and contributed to data curation; LLD analyzed the data with help from OO for statistics and visualization of the results; AL, NEE and ØF coordinated the long-term National programmes for captive-breeding and monitoring of Arctic fox in Norway that provided data for this study; NEE and AL led to the acquisition of the financial support for this project; CRJ, NEE and OO supervised the research activity planning and its execution; LLD led the writing of the manuscript; all authors contributed critically to the drafts and gave final approval for publication.

Data Availability statement

Data supporting the findings of this study are available within the article and its supplementary information files. Datasets on moult phenology, relevant metadata and R scripts, used herein for coding of statistical analysis and graphing, are available online from the Dryad Digital

Repository (<https://doi.org/10.5061/dryad.xd2547dhm>) (Laporte-Devyllder et al., 2022).

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Supporting Information

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

Appendix S1 Supporting Information.

Appendix S2 Supporting Information.