










Fitness and fur colouration: Testing the camouflage and thermoregulation hypotheses in an Arctic mammal

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Abstract

1. Selection for crypsis has been recognized as an important ecological driver of animal colouration, whereas the relative importance of thermoregulation is more contentious with mixed empirical support. A potential thermal advantage of darker individuals has been observed in a wide range of animal species. Arctic animals that exhibit colour polymorphisms and undergo seasonal colour moults are interesting study subjects for testing the two alternative hypotheses: demographic performance of different colour morphs might be differentially affected by snow cover with a cryptic advantage for lighter morphs, or conversely by winter temperature with a thermal advantage for darker morphs.
2. In this study, we explored whether camouflage and thermoregulation might explain differences in reproduction and survival between the white and blue colour morphs of the Arctic fox *Vulpes lagopus* under natural conditions.
3. Juvenile and adult survival, breeding propensity and litter size were measured for 798 captive-bred and released or wild-born Arctic foxes monitored during an 11-year period (2007–2017) in two subpopulations in south-central Norway. We investigated the proportion of the two colour morphs and compared their demographic performance in relation to spatial variation in duration of snow cover, onset of snow season and winter temperatures.
4. After population re-establishment, a higher proportion of blue individuals was observed among wild-born Arctic foxes compared to the proportion of blue foxes released from the captive population. Our field study provides the first evidence for an effect of colour morph on the reproductive performance of Arctic foxes under natural conditions, with a higher breeding propensity of the blue morph compared to the white one. Performance of the two colour morphs was not differentially affected by the climatic variables, except for juvenile survival. Blue morph juveniles showed a tendency for higher survival under colder winter temperatures but lower survival under warmer temperatures compared to white morph juveniles.

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5. Overall, our findings do not consistently support predictions of the *camouflage* or the *thermoregulation hypotheses*. The higher success of blue foxes suggests an advantage of the dark morph not directly related to disruptive selection by crypsis or thermoregulation. Our results rather point to physiological adaptations and behavioural traits not necessarily connected to thermoregulation, such as stress response, immune function, sexual behaviour and aggressiveness. Our findings highlight the need to explore the potential role of genetic linkage or pleiotropy in influencing the fitness of white and blue Arctic foxes as well as other species with colour polymorphisms.

KEYWORDS

apparent survival, Arctic fox, camouflage, capture–mark–recapture models, colour polymorphism, fitness, reproductive performance, snow cover

1 | INTRODUCTION

Animal colouration is shaped by multiple selection pressures including camouflage, communication and thermoregulation (Caro, 2005; Galeotti et al., 2003; Zimova et al., 2018), and has been correlated to fitness traits in many species (Brommer et al., 2005; Gratten et al., 2008; Kappers et al., 2020; Morosinotto et al., 2020; Roff & Fairbairn, 2013). Body colour often matches the typical habitat background in which the animal occurs and background matching can change with seasons. Many species of arctic vertebrates, such as rock ptarmigan *Lagopus muta*, snowshoe hare *Lepus americanus* and ermine *Mustela erminea*, have evolved a seasonally dimorphic coloured coat, displaying a white coat during winter and brown during summer (Caro, 2005; Delhey, 2019; Nowak & Walker, 1999). However, the selective pressures for fur colouration, and especially fur polymorphism in Arctic mammals, remain unclear.

A camouflage advantage can result in lower predation risk for prey species or conversely higher hunting success for predators, and crypsis has been widely recognized as the main ecological driver of animal colouration (Galeotti et al., 2003; Zimova et al., 2018). In addition to the selective advantage of camouflage, a potential role of thermoregulation as an ecological driver of coat colouration has been proposed and has received mixed empirical support (Caro, 2005; Clusella Trullas et al., 2007; Stuart-Fox et al., 2017). Thermoregulation is modulated by a complex set of physical, biological and behavioural factors (Stuart-Fox et al., 2017), and a thermal advantage of darker individuals has been observed both in ectotherms (reptiles, Clusella Trullas et al., 2007) and endotherms (birds, Roulin & Ducrest, 2011; mammals, Ciurej et al., 2020; Ducrest et al., 2008; Hetem et al., 2009). For reptiles and other ectotherms, the thermal advantage has been linked to skin colouration via the thermal melanism hypothesis (Forsman, 1995). Darker body surfaces heat faster and reach higher temperatures than pale surfaces due to greater absorption of solar radiation, faster heat gain and reductions in metabolic rate (Clusella Trullas et al., 2008; Geen & Johnston, 2014). In birds, two early studies found that dark

plumages had lower reflectance and higher heat gain (Hamilton & Heppner, 1967; Lustick, 1969), but these pioneering investigations were conducted in laboratory conditions with feather colouration modified by artificial selection and experimental dyeing. Studies on mammal species have not found any connection between colour and heat gain, but found influences of other optical and structural properties of the coat affecting heat gain, irrespective of coat colouration (Walsberg, 1983; Walsberg & Schmidt, 1989; Walsberg & Wolf, 1995). Furthermore, increased insulation may restrict the heat flow from/into an organism leading to a negligible effect of colour in the thick plumage and fur of arctic birds (Beasley & Ankney, 1988) and mammals (Dawson et al., 2014; Walsberg, 1991). On the other hand, some physiological properties related to the genes for melanin have been linked to a thermal advantage of darker morphs in colder temperatures, such as behavioural strategies in barn owls *Tyto alba* (Dreiss et al., 2016), differences in metabolic rates among different colour morphs of owls (Mosher & Henny, 1976; Roulin et al., 2005) and energy homeostasis in laboratory mice *Mus musculus* (Cone, 2006; Dreiss et al., 2010). Furthermore, stress response, sexual behaviour and aggressiveness have also been associated with colouration in different endotherm species (Ducrest et al., 2008; Roulin & Ducrest, 2011; San-Jose & Roulin, 2017).

Arctic species, such as the Arctic fox *Vulpes lagopus*, that exhibit colour polymorphisms and undergo seasonal colour moults, are interesting models for testing the relative importance of background matching as a camouflage tactic versus a role for thermoregulation in fur colour polymorphism. Species that undergo colour moult are of special relevance because long-term climate change has the potential to cause a mismatch in the seasonal camouflage that results in higher predation risk (Atmeh et al., 2018; Melin et al., 2020; Mills et al., 2013; Zimova et al., 2016). The Arctic fox has two colour morphs: white and blue. White foxes are fully white in winter and pale brown in summer while blue foxes remain dark brown year-round, with lighter colouration in the winter (Audet et al., 2002). Fur colouration in the Arctic fox is inherited as a simple Mendelian trait determined by a single gene (MC1R), with the blue allele being dominant

over the white (Våge et al., 2005). Both colour morphs occur in most populations, but their proportion varies greatly among regions. The white colour morph is more common across the Alaskan Peninsula, on the Russian tundra and on High Arctic Islands (Braestrup, 1941; Chesemore, 1968). In the island populations of Iceland and Greenland, blue morph foxes are more common at coastal sites, whereas white morph foxes are more prevalent at inland sites (Hersteinsson & Macdonald, 1992; Pagh & Hersteinsson, 2008).

The camouflage benefit of fur colouration has been hypothesized to be the underlying cause of differences in the proportions of white and blue Arctic foxes at coastal and inland areas (Hersteinsson & Macdonald, 1992; Vibe, 1967). In Iceland, geographical variation in the frequency of white foxes was positively correlated with the duration of snow cover (Hersteinsson, 1989). Arctic foxes likely benefit from a camouflaged coat both for avoidance of predation risk from raptorial birds and larger carnivores (Braestrup, 1941; Meijer et al., 2011; Tannerfeldt et al., 2002) but also for successful hunting of small rodents and bird eggs (Angerbjörn et al., 1995; Hersteinsson & Macdonald, 1996). Regarding the thermal properties of the arctic fox fur, previous studies have compared summer versus winter pelage (Prestrud, 1991; Underwood & Reynolds, 1980), but no information is available on physiological or behavioural differences between the two colour morphs. Previous studies have not found thermal benefits for a darker pelt among other Arctic mammals, but we cannot a priori exclude a potential advantage of the blue arctic fox morph in colder temperatures. Indeed, evaluation of potential differences in fitness in relation to snow cover and winter temperature is needed to explore the relative importance of camouflage and thermoregulation as selective drivers of fur colouration in the Arctic fox. So far, no empirical study has addressed fitness of the two morphs under natural conditions, and the selection forces driving the observed variation in their spatial distribution remain unknown.

In Fennoscandia, the Arctic fox is considered critically endangered (Henriksen et al., 2015; Liukko et al., 2019) and large-scale conservation actions have been implemented in many subpopulations, including the release of captive-bred foxes (Angerbjörn et al., 2013; Hemphill et al., 2020; Ims et al., 2017; Landa et al., 2017). As a part of the Norwegian Arctic fox captive breeding and release programme (Landa et al., 2017), which aims to restore Arctic fox populations in mountain areas of Scandinavia, we studied the fate of released and wild-born foxes in south-central Norway over an 11-year period (2007–2017). We investigated three fitness components (survival, breeding propensity and litter size) for the two colour morphs in relation to annual and local variation in snow cover and winter temperature. The objectives of our study were to (a) investigate the proportions of the two colour morphs in the wild following the release of captive-bred Arctic foxes and (b) test whether camouflage or thermoregulation are important factors explaining fitness variation between the two colour morphs. The *camouflage hypothesis* predicts that the white morph should have higher fitness than the blue morph in areas with longer duration of snow cover, whereas the blue morph might have an advantage in areas with shorter duration of snow cover. The *thermoregulation hypothesis* predicts that the

blue morph should have higher fitness in colder winter temperatures compared to the white morph, due to differences in physiological properties and a potential thermal advantage among darker morphs.

2 | MATERIALS AND METHODS

2.1 | Study system

Our field study was conducted in two of the southernmost Arctic fox subpopulations in Norway, Snøhetta and Hardangervidda (Figure 1). The species had been previously extirpated from these areas (Eide et al., 2020) but was re-established by release of Arctic foxes during 2007–2013 and 2009–2016, respectively (Ulvund et al., 2020). The number of released arctic foxes differed between years and study areas (Appendix S9). Captive-bred Arctic foxes were born in May/June at the Sæterfjellet breeding station near Oppdal, Norway, and released during the following winter together with their siblings at historic den sites, or alternatively soft-released from the enclosure of the breeding station. In a few cases ($n = 15$), foxes escaped from the enclosure but were included as released, due to their contributions

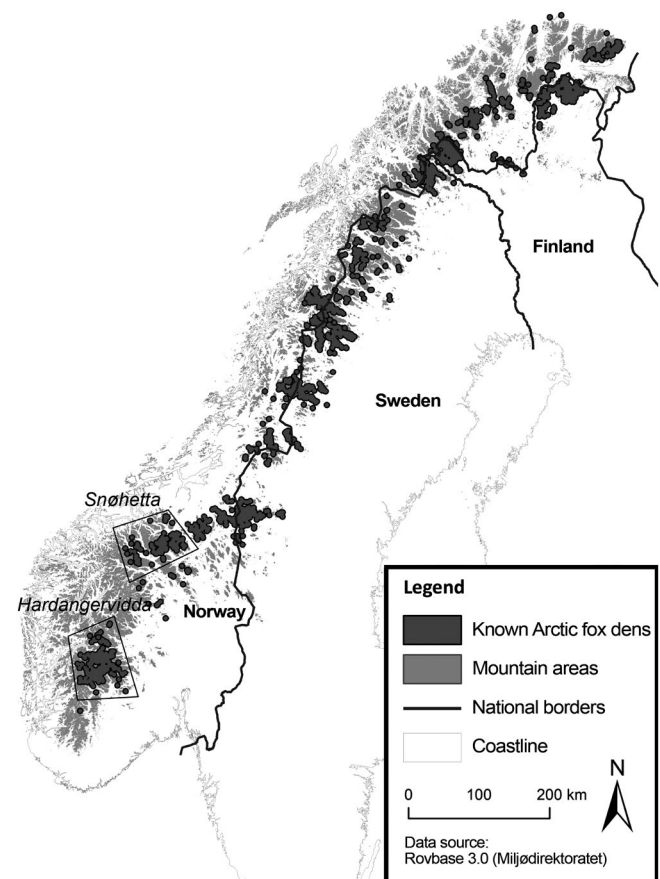


FIGURE 1 Map of the two Arctic fox study subpopulations (Snøhetta and Hardangervidda) in south-central Norway. The study area Snøhetta included Snøhetta and Knutshø, whereas Hardangervidda represented the mountain areas of Hardangervidda and Finse

to local wild populations. Pups, regardless of colour, were randomly distributed in the different mountain release sites. In release areas, supplementary food was provided at feeding stations designed to feed Arctic foxes exclusively. For further details regarding the captive breeding and release programme, see Landa et al. (2017). Before release, all captive-bred foxes were ear-tagged with a unique colour combination and marked with a passive integrated transponder (PIT)-tag. Wild-born pups descending from released individuals were trapped at the den sites during summer (July/August) and marked with PIT-tags only. During captures, we recorded colour morph, sex and body mass. Ear tissue and hair samples were taken for DNA identification. Our total study sample consisted of 798 Arctic foxes monitored between 2007 and 2017, including released foxes ($n = 252$) and wild-born descendants ($n = 546$). Live and dead encounters of individual foxes were obtained by seven different methods: (a) individual identification based on genotyping from faecal and hair samples collected during den controls in winter (Eide et al., 2020), (b) records of PIT-tags from readers set up at feeding stations based on Biomark (Biomark, Inc.) and Trovan systems (Trovan Ltd.; Landa et al., 2017; Thierry et al., 2020), identification of ear-tags from (c) wildlife camera traps or (d) opportunistic visual observations, (e) live captures of wild foxes, (f) recovery of carcasses of dead individuals and (g) parentage identification from tissue samples collected from offspring captured during summer marking on active dens (Table 1).

2.2 | Fitness traits

Four fitness traits were assessed for each monitored individual: juvenile apparent survival, adult apparent survival, breeding propensity and litter size. For all fitness trait measurements, 1st of July was used as a transition between biological years, corresponding to when the next cohort starts to emerge on the den sites. *Juvenile apparent survival* was estimated as the survival within the first 12 months of life from July to the following June. Captive-born foxes were exposed to the wild environment starting from the release event in January/February as 6-month olds, whereas wild-born foxes had a 12-month exposure period

in the wild, starting at birth. *Adult apparent survival* was the survival in the subsequent years after the age of 1 year. Age of the individuals was determined based on the marking event of juveniles, in the breeding station for the captive-born foxes, and during the summer den surveys for the wild-born foxes. We used the number of pups observed outside the den or trapped during the summer (July–August) den surveys each year to calculate (a) the *probability of breeding propensity* (binary, 0 if the fox did not breed, 1 if the fox produced young) and (b) *litter size* (number of pups seen at the same time, which must be considered as minimum litter size). Breeding propensity was assigned to each fox only for those years when the fox was detected at least once, excluding the first year of life.

2.3 | Environmental data

Three climate variables were included as explanatory covariates in our statistical analysis: (a) *duration of snow cover* was measured as the number of days with snow cover (when snow depth > 0), (b) *onset of snow season* referred to the first quartile over the Days of the Year (DOYs) with snow on the ground in winter after 1st September, which is used as fixed starting point in national monitoring programmes for the underlying snow models (Saloranta, 2014), (c) *average winter temperature* was calculated as the average of daily mean temperatures during the 3-month period from December to February (Appendix S1). We compiled climate data for individual foxes using a fixed distance buffer of 2.54 km at each den site where an individual was born, released or reproducing. The buffer radius was based on the average area of the annual home ranges of resident males and females (Landa et al., 1998). From 2007 to 2017, the average value of each climatic variable for each year of a given fox territory was then measured for the buffer areas calculated for each individual fox (Appendix S1).

Reproduction and population dynamics of arctic foxes are strongly influenced by annual variation in abundance of small rodents (Angerbjörn et al., 1999; Elmhagen et al., 2000). Small rodents, typically four species of voles (*Myodes* and *Microtus* spp.) and lemmings (*Lemmus*

TABLE 1 Sources of data for live and dead encounters of Arctic foxes, number of detections and number of unique individuals identified with each method for foxes of different colour morphs (white, blue) and age-classes (juvenile, adult). For each data source, we considered one detection per day for each Arctic fox. The same individual can be detected with multiple methods and is included in both the juvenile and adult counts

Data source	No. detections	No. individuals	No. white juveniles	No. white adults	No. blue juveniles	No. blue adults
DNA samples	443	170	39	118	4	24
Biomark and Trovan PIT-tag	12,335	351	67	236	17	62
Wildlife camera trap	3,041	108	77	59	9	9
Visual observation	66	27	5	16	0	7
Wild capture	597	545	81	331	33	101
Retrieved dead individual	17	17	8	9	0	0
Parentage identification	145	89	NA	69	NA	20

lemmus), were surveyed with systematic snap-trapping close to the study sites (Framstad, 2017). We included annual estimates of rodent abundance for each mountain area as a covariate based on number of rodents trapped/100 trap-nights (Framstad, 2017). Rodent abundance was categorized into four phases, following Angerbjörn et al. (2013): (a) *low phase*, when rodents are at the lowest densities following a peak or decline; (b) *increase phase*, increasing rodent density over the summer between low and peak phase; (c) *peak phase*, highest abundance of small rodents and (d) *decline phase*, a drastic decline in density from spring to autumn, after a peak or increase phase. We used a categorical classification in the analyses rather than raw data on abundances because trapping of rodents occurs at a limited spatial scale. We also observed considerable variation in local densities of rodents and voles, but the different phases were synchronized at a larger regional scale.

2.4 | Statistical analysis

All statistical analyses were conducted in an R environment (R Version 3.6.0, www.r-project.org).

2.4.1 | Colour morph proportions

To investigate the proportions of the two colour morphs in the wild following the release of captive-bred Arctic foxes, the average proportions of white and blue released foxes were compared with the proportions of wild-born foxes during the period following the release. Analyses were conducted separately for the two different mountain areas in our study. A generalized linear model (GLM) with a binomial distribution was run with the proportion of blue foxes (out of the total number of blue and white foxes) as a response variable and the origin (wild-born or captive-born and released) as explanatory variable. We checked the dispersion parameter to test for evidence of overdispersion.

2.4.2 | Survival of juveniles and adults

We used capture–mark–recapture analyses (CMRs) for open populations to investigate the effect of fur colour on the survivorship of Arctic foxes in our study populations. Encounter histories were built with a 12-month time step. Our analysis was based on animals first marked and released as juveniles in our study areas, and we censored 24 foxes that did not meet this criteria, including any juveniles held for more than a year, foxes marked as adults and a few immigrants from Sweden. Our total sample comprised 774 Arctic foxes. We used Cormack–Jolly–Seber (CJS) models to estimate the probability of apparent survival (ϕ), corrected for the probability of encounter (p) using functions of the package R_{MARK} in R as an interface to program Mark. The complement of apparent survival can include losses to mortality or to permanent emigration. Here, intensive range-wide monitoring of arctic foxes was effective at detecting dispersing individuals, and most losses were likely due to mortality.

Our models for apparent survival included three groups of factors: colour morph and age of foxes, year and phase of rodent cycle as annual factors, and three climatic conditions at the territory as individual covariates for each fox. Our study is the first test for the effects of colour morph but the other factors are known to be important drivers of population dynamics for many alpine species. For age, we used two age-class models that separated juvenile apparent survival in the first year (ϕ^{juv}) from adult apparent survival in the subsequent years (ϕ^{adt}). Models with greater age-structure were not supported (Appendix S6). We tested alternative models with factors from 1 to 3 groups in main effect (additive) and interactive models (factorial). Specifically, we tested factorial models with age, colour morph in combination with duration of snow cover, onset of snow season or winter temperature, to evaluate whether apparent survival of the two colour morphs was differently affected by environmental conditions during the natal year (Appendix S6). We did not test models with multiple climate variables because higher-order interaction terms were difficult to interpret. Our alternative models for the probability of encounter included fur colour of foxes, year, as well as duration of snow cover, onset of snow season and winter temperature as individual covariates. We hypothesized that the factors might affect the detection process via effects on either animal behaviour or movements. We used a function of the R_{MARK} package based on programme Release to test for the goodness-of-fit (GOF) of the starting global model and estimated the variance inflation factor (\hat{c}) to control for overdispersion. The estimated variance inflation factor (\hat{c}) was relatively low at 1.243 and indicated that our global model was a good fit to the encounter histories. We proceeded to conduct the model selection on our set of hypothesis-driven models using quasi-AICc (QAICc) to correct for the low levels of overdispersion in our dataset.

2.4.3 | Non-random mating

We investigated pairing behaviour and reproductive performance among Arctic foxes that survived their natal year. We tested the occurrence of non-random mating between the two colour morphs, being a potential force acting on the colour morph proportions in the wild: a Fisher's exact test (two-sided) was conducted on the Arctic fox pairs detected breeding during the study period. The expected values under the null hypothesis of random mating were compared with the observed numbers of breeding pairs with different combinations of the colour morphs.

2.4.4 | Reproductive performance

Breeding propensity and litter size were compared between white and blue Arctic foxes. Moreover, we investigated whether the reproductive performance of the two colour morphs was differentially affected by duration of snow cover, onset of snow season and temperature of the winter preceding the breeding event. Five individuals that emigrated from the study area were excluded from the analysis ($n = 3$ white and 2 blue). Our analysis of litter size was restricted to

individuals that were detected breeding. We built generalized additive models (GAMs) with a binomial distribution for the breeding propensity and generalized additive mixed models (GAMMs) with Poisson distribution for the litter size. We used GAMs since these models allowed us to flexibly model the effect of fox age as a smooth term that controlled for a nonlinear relationship between age and the reproductive biology of Arctic foxes (Landa et al., 2017, unpubl. data). GAMs are often used for environmental data analyses and are a useful approach for modelling nonlinear relationships (Moro et al., 2019).

We first compared a series of models to establish which main effects should be included (rodent phase, origin, colour morph, sex). Then, we developed a set of models that varied in climatic variable (duration of snow cover, onset of snow season, average winter temperature) and the interaction between the climatic variable and colour morph to test our main hypotheses of interest. We also tested the interaction colour \times sex because of some evidence of sex-specific colour morph differences in semen characteristics (Stasiak et al., 2019), and the interaction colour \times rodent phase, to investigate potential different responses of the two colour morphs to their main source of food. In the model for litter size, the breeding event (den site ID concatenated with year of breeding) was included as a random effect to group together paired males and females. Prior to model fitting, we examined the association between all pairs of explanatory variables to examine whether there might be multicollinearity problems (Appendix S2). We

then conducted a model selection using AICc (Table 2, see full lists of models in Appendices S7 and S8). We used the `GGEFFECTS` and `EMMEANS` packages to look at the predicted probabilities for each variable, controlling for the mean values of the other covariates (Lüdecke, 2018; Russell, 2020). We focus on the parameter estimates from the top model (i.e. model with lowest AICc) unless otherwise stated.

3 | RESULTS

3.1 | Colour morph proportions

During the 11-year study period (2007–2017), 252 captive-bred Arctic foxes were released by the captive-breeding and release programme in the target study areas. Of these foxes, 89% were white (131 males, 94 females) and 11% were blue (14 males, 13 females). Following the releases, a total of 546 wild-born pups were recorded from litters where at least one parent originated from the captive breeding programme. Of the wild-born foxes, 75% were of the white colour morph and 25% blue. The average proportion of the blue morph was more than twice as high among wild-born compared to the captive-born pups released in the wild (odds ratio = 2.65, 95% CI = 1.71–4.12, Fisher's exact test, $p < 0.001$), and the difference was similar in both study sites; $S_{\text{north}}: 0.11 \pm 0.03$ to 0.25 ± 0.02

TABLE 2 List of top models ranked based on model selection for (a) CJS models for juvenile and adult apparent survival, (b) GAM models for breeding propensity and (c) GAMM models for litter size of Arctic foxes. Survival models included effects of two age-classes (2ac, juvenile, adult), rodent phase (4 levels) and three climatic variables measured at the natal or release den site (duration.snow.cover, onset.snow.season and av.winter.temp). For the reproductive performance models (breeding propensity and litter size), rodent was the rodent phase of the same year as the Arctic fox breeding event, the climatic variables refer to the year preceding the breeding, and s(age) was a smooth effect for age at breeding. We ranked models by QAICc for survival and AICc for the reproductive performance. We report the subset of models that ranked highly in the different analyses ($\Delta\text{AICc} < 4$); see Supporting Information for the full list of models. The minimum-(Q)AICc model ($\Delta\text{AICc} = 0$) for survival, breeding propensity and litter size had a value of 1,511.6, 457.6 and 128.8, respectively

	Model	npar	Deviance	Delta AICc	Weight
Apparent survival	Phi(~2ac * average.winter.temp) p(~time)	14	1,846.0	0.000	0.604
	Phi(~2ac * colour * average.winter.temp) p(~time)	18	1,838.3	2.058	0.216
	Phi(~2ac * rodent) p(~time)	18	1,839.5	3.039	0.132
Breeding propensity	s(age) + rodent + colour + onset.snow.season	8	441.9	0.000	0.240
	s(age) + rodent + colour	7	444.7	0.780	0.163
	s(age) + rodent + colour + onset.snow.season + origin	9	441.1	1.230	0.130
	s(age) + rodent + onset.snow.season	7	446.1	1.870	0.094
	s(age) + rodent + colour + average.winter.temp	8	444.3	2.500	0.069
	s(age) + rodent + colour + duration.snow.cover	8	444.7	2.820	0.059
	s(age) + rodent + colour + sex + colour * sex + onset.snow.season	10	440.5	2.840	0.058
	s(age) + rodent + colour + onset.snow.season + colour * onset.snow.season + origin + sex	11	439.6	3.920	0.034
Litter size	s(age) + rodent + onset.snow.season	8	111.7	0.000	0.329
	s(age) + rodent + av.winter.temp	8	113.3	1.570	0.150
	s(age) + rodent + colour	8	113.7	1.960	0.123
	s(age) + rodent + duration.snow.cover	8	113.9	2.190	0.110
	s(age) + rodent + colour + onset.snow.season + origin	10	111.1	3.980	0.045

($\beta = 1.01$; $z = 2.87$; $p < 0.01$), Hardangervidda: 0.11 ± 0.02 to 0.29 ± 0.05 ($\beta = 1.21$; $z = 3.39$; $p < 0.001$).

3.2 | Survival estimates

Out of the 774 wild- and captive-born foxes in our survival analysis, 21% were blue (134 wild-born, 27 captive-born) and 79% were white (394 wild-born, 219 captive-born). The model with the minimum QAICc value included an interaction between age-class and average winter temperature, and had 2.8 times more support than the second-best fit model (Table 2). To examine the effect of colour morph on apparent survival in relation to climatic variables, we used the second-best fit model, which also included an interaction with colour morph, for parameter estimation. The parameter estimates indicated that juvenile apparent survival decreased with increasing average winter temperature for both colour morphs (Figure 2). However, the slope was steeper for blue foxes, indicating a possible greater sensitivity of the blue morph to changes in winter temperature, compared with the white morph (Figure 2). Adult apparent survival did not vary much with average winter temperature but showed a tendency for general higher apparent survival among blue morph adults ($\phi = 0.84$, 95% CI = 0.80–0.88) compared with the white morph ($\phi = 0.72$, 95% CI = 0.71–0.73; Figure 2). Models that included an interaction term for colour morph \times duration of snow cover, or colour morph \times onset of snow season had lower support, suggesting that both snow cover variables were relatively unimportant for colour morph differences in survival ($w \leq 0.005$, Appendix S6). Parameter estimates from a time-dependent model showed that the detection probability (p) varied among years from 0.31 to 0.86, with an average detection probability of 0.69. The lowest p (0.31) belongs

to the last occasion of the encounter history, which had lower effort because it was based on a half year of sampling instead of a full year. Alternative models for the detection process, where the probability of encounter was modelled as a constant rate or as a function of fur colour or climatic conditions, received essentially no support ($w_i < 0.001$).

3.3 | Non-random mating

We found no evidence of assortative or disassortative mating according to colour morph among the Arctic foxes. Out of 52 unique pairs in which the colour morph of both partners was known, 26 pairs were white/white, 15 pairs were a white male/blue female, 9 pairs were a blue male/white female and 2 pairs were blue/blue, with no detectable difference with the expected values under the null hypothesis of random pairing (Fisher's exact test, $p = 0.304$).

3.4 | Reproductive performance

A total of 89 individuals (69 white, 20 blue) were detected breeding in the 8-year period from 2010 to 2017. For breeding propensity, the three top models ($\Delta\text{AICc} < 2$) all included an effect of colour morph (Table 2), with a higher probability of breeding for blue compared to white foxes (the top model predicted breeding probability of 0.18 (95% CI = 0.14–0.24) for white morphs and 0.28 (95% CI = 0.19–0.39) for the blue morph, Figure 3, Appendix S3). For litter size, only one of the three top models ($\Delta\text{AICc} < 2$) included colour morph (Table 2), and parameter estimates suggested that any difference was relatively small. The model including colour morph predicted

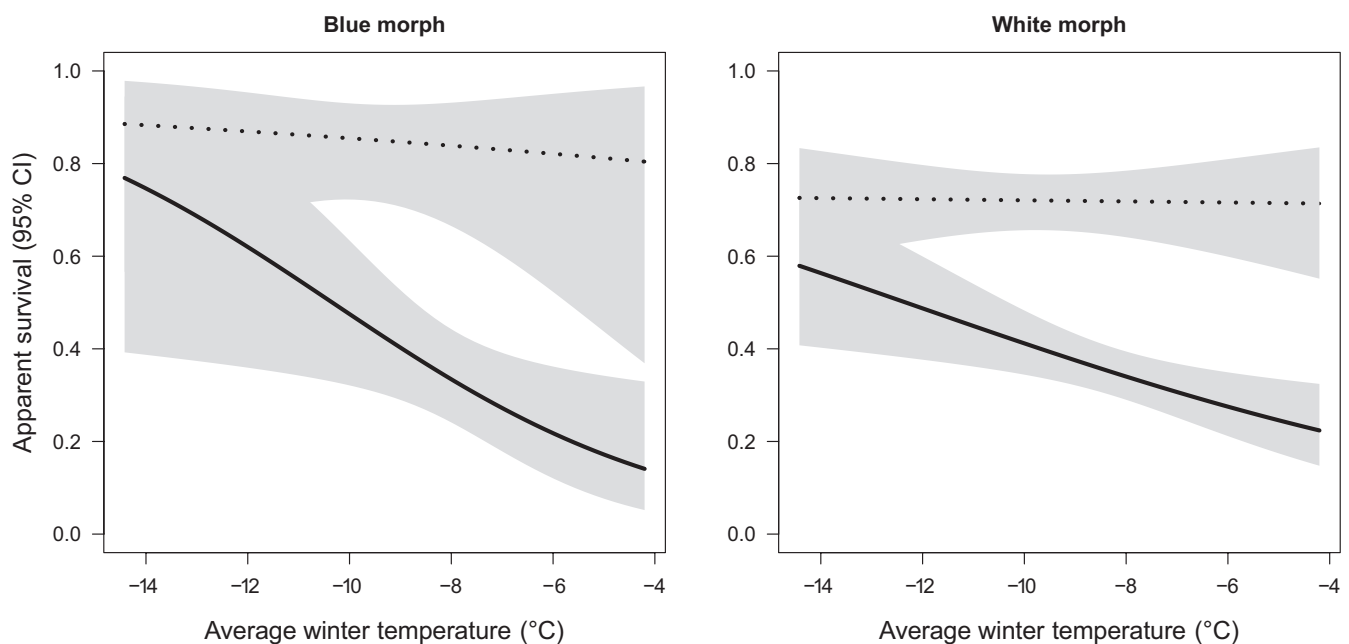


FIGURE 2 Estimates of apparent survival (with 95% CI) for juveniles (solid line) and adults (dotted line) for blue (left plot) and white morph Arctic foxes (right plot) in relation to average winter temperature (°C) at fox territories in south-central Norway, 2007–2017

litter size of 6.35 (95% CI = 5.65–7.14) for white morphs and 6.08 (95% CI = 5.23–7.08) for blue morph foxes. None of the climatic variables differently affected the breeding propensity or the litter size of blue and white foxes. In fact, all models with colour morph

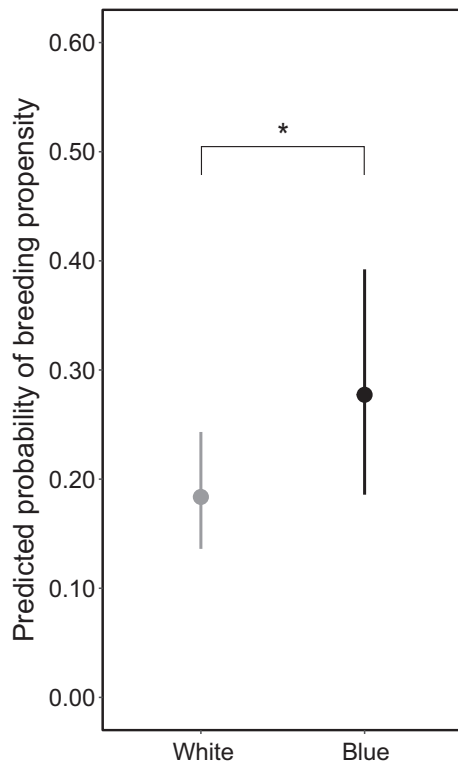


FIGURE 3 Predicted probability of breeding propensity of white and blue Arctic foxes from the best general additive model (GAM), controlling for the other variables

interacting with the climatic variables were low ranked and not within any of the top models (Appendices S7 and S8).

For both colour morphs, probability of breeding was lowest during the low rodent phase and higher under increase, peak and decline rodent phases (Appendix S3 and S5). In addition, the onset of snow season of the year preceding the breeding showed a tendency of negative effect, with lower breeding propensity with later onset of the snow season (Figure 4a; Appendix S3). Breeding propensity also varied with fox age, with increasing success for older individuals, but with evidence of senescent declines among the oldest individuals (Figure 4b; Appendix S3). Litter size was also significantly higher during peak and decline rodent abundance compared to other phases (Appendices S4 and S5), and increased with age at breeding (Appendix S4 and S5).

4 | DISCUSSION

Our 11-year field study of Arctic foxes in two re-established sub-populations in south-central Norway showed that the white and blue colour morphs of Arctic foxes differed in their demographic performance under natural conditions. Following population re-establishment in the two study areas, a higher average proportion of individuals of the blue colour morph was observed among wild-born Arctic foxes (25%–29%) compared to released foxes (11%). Moreover, the blue morph had a higher breeding propensity compared to the white morph. The two colour morphs were not differently affected by any of the climatic variables that we tested, except for juvenile survival. Blue juveniles showed a tendency for higher apparent survival under colder winter temperatures and lower survival under warmer temperatures as compared to white juveniles. Apparent survival of adults was unaffected by winter temperatures

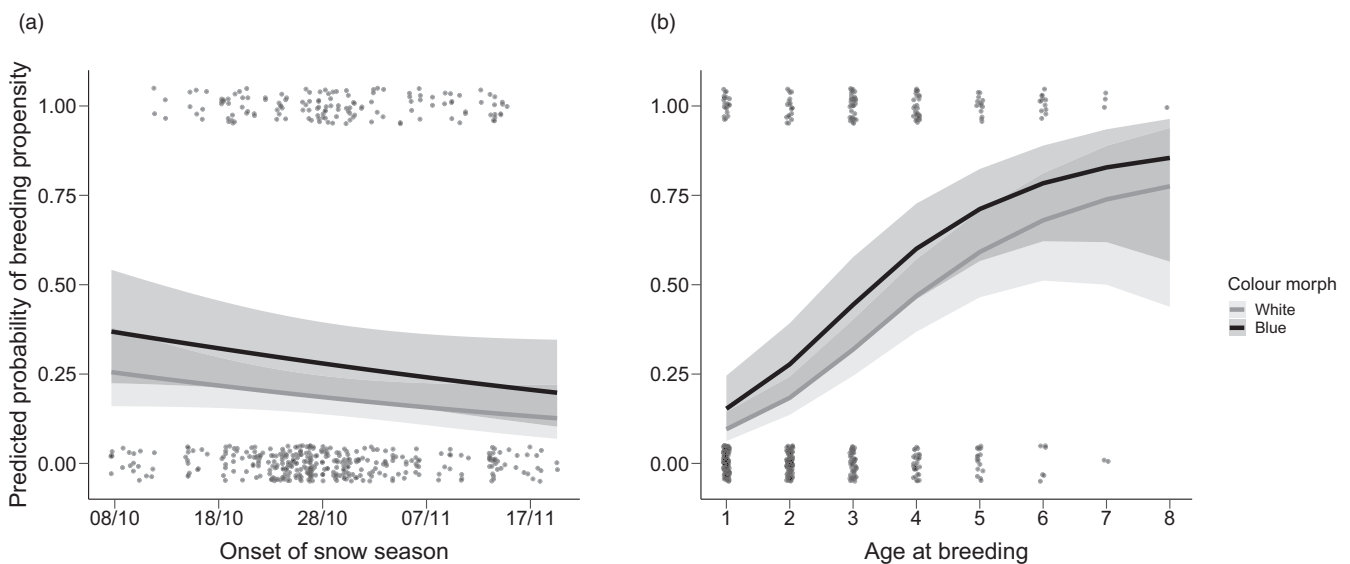


FIGURE 4 Predicted probability of breeding propensity of Arctic foxes from the best general additive model (GAM) in relation to (a) onset of snow season and (b) age at breeding, controlling for the other variables, separately for blue and white Arctic foxes in south-central Norway, 2007–2017

but blue morphs had consistently higher annual survival than white morphs. Overall, our findings do not provide strong support for either the *camouflage* or the *thermoregulation hypotheses*.

The observed changes in proportion of the two colour morphs could be driven by several non-exclusive mechanisms. We explored the occurrence of non-random mating among wild foxes, but we found no support for assortative or disassortative mating. Considering the small population size of Arctic fox subpopulations in Fennoscandia (Ulvund et al., 2020), genetic drift could also explain the increased proportion of the blue morph, caused by random change of the allele frequencies from one generation to the next (Lanfear et al., 2014). Moreover, the documented fitness differences between the two colour morphs could play a role in the colour frequency changes.

Juvenile and adult Arctic foxes are known to be vulnerable to predation by red foxes *Vulpes vulpes*, wolverines *Gulo gulo* and golden eagles *Aquila chrysaetos* (Meijer et al., 2011; Tannerfeldt et al., 2002). Nevertheless, when testing the *camouflage hypothesis*, both juvenile and adult white foxes appeared to have no advantage in more snow-covered territories, nor the blue morph in less snow-covered territories. Our results might reflect the low numerical densities of apex predators or low predation pressure in our study areas (Bischof et al., 2020; Gomo et al., 2020; Mattisson et al., 2020; Rød-Eriksen et al., 2020). Hence, predation might not represent a strong selective pressure for the Arctic fox in our study populations, weakening the adaptive value of fur colouration as camouflage. However, we found evidence for a steeper reduction in juvenile survival with increasing winter temperature for blue foxes that may be indirectly linked to predation risk. It has been reported that red foxes take over former Arctic fox den sites at lower elevations, where temperatures are milder and ecosystem productivity higher (see e.g. Frafjord, 2003; Killengreen et al., 2007). If predation pressure from red foxes is higher on Arctic foxes living in habitats with milder winter temperatures, blue juveniles with less camouflage against a snowy background could potentially be more vulnerable to predation. However, we lack direct data on the numerical or functional response of predators in our study areas. Extending our study to Arctic fox subpopulations in low arctic regions of northern Norway where densities of red foxes are higher could give more insight into the role of predation risk (Ims et al., 2017).

Juvenile survival was lower compared to adult survival in both colour morphs, consistent with previous studies where 75% of the total mortality usually occurs during the first 6 months (Meijer et al., 2008, 2013). Winter temperature had a strong effect on juvenile survival, with lower apparent survival in warmer winters for both colour morphs. A possible explanation is that milder winters could be related to 'rain-on-snow' events and icing. Under wet conditions that affect the subnivean environment, densities of rodents can be dramatically reduced, leading to population crashes (Ims et al., 2011; Kausrud et al., 2008), which, in turn, would strongly affect the survival of juvenile foxes.

Under colder temperatures, we found an indication of higher survival for blue juveniles than for white juveniles, which is consistent with a potential thermal advantage of the darker morph, providing some support for the *thermoregulation hypothesis*. However, the

difference was small and hence any support rather weak. Moreover, no information is available on the insulative and thermal properties of the pelage of the two Arctic fox colour morphs. Future comparative studies are needed to investigate the physiological mechanisms of the possible advantage of the blue morph.

Our field study provides the first evidence for an effect of colour morph on the reproductive performance of Arctic foxes, with a higher breeding propensity of the blue morph compared to the white morph. The difference in reproductive performance of the two morphs was not clearly related to any of the climatic variables that we tested, with little support for predictions from the *camouflage* or the *thermoregulation hypotheses*. Both colour morphs were similarly affected by the different phases of small rodent cycles, suggesting no crypsis benefits on foraging success. The higher breeding propensity for blue foxes might rather be explained by other physiological traits associated with fur colour, such as higher sperm concentrations in the ejaculates of male blue arctic foxes (Stasiak et al., 2019), or higher rates of sexual receptivity among females with darker fur (Ducrest et al., 2008). Other covarying physiological traits such as stress response, immune function or energy homeostasis could also improve the body condition of blue foxes during harsher winters and increase the breeding propensity.

Our results add to the growing evidence that colour polymorphisms and a suite of associated traits can influence fitness in a wide range of vertebrate species (Brommer et al., 2005; Emaresi et al., 2014; Forsman et al., 2008; Morosinotto et al., 2020; Roulin et al., 2004). With limited support for our two hypotheses, the fitness difference among arctic fox colour morphs is more likely explained by some other linked physiological and behavioural traits, and probably influenced by the melanocortin system that have been shown to covary with melanin-based colouration (Ducrest et al., 2008; McKinnon & Pierotti, 2010; San-Jose & Roulin, 2017; Van Den Brink et al., 2012). Wild vertebrates of the darker morph can score higher in traits such as sexual activity, aggressiveness, stress response, immune functions and energy homeostasis compared with the lighter morph (Ducrest et al., 2008; Ibanez et al., 2016; Roulin et al., 2001). Other functional traits with the potential to influence animal fitness can also directly result from the physiochemical properties of melanin pigments, such as antibiotic activity, resistance to solar radiation and oxidative stress (Slominski et al., 2004).

5 | CONCLUSIONS

At our study sites in mountain areas of south-central Norway, blue morph Arctic foxes had a higher breeding propensity and a tendency of higher apparent survival than white foxes. While the higher apparent survival of blue juveniles in colder temperatures could suggest a thermal advantage of the blue morph, the difference in reproductive performance was not related to any of the explored climatic variables. Thus, our findings provide little to no support for the predictions of the *camouflage* and *thermoregulation hypotheses*. Low population numbers of apex predators and hence low predation risk

may have reduced the selection for camouflage among foxes in our study populations. The high success of the blue morph but relatively low support for thermoregulatory effects suggest that other physiological or behavioural advantages may be important for blue morph foxes, which could be linked to the genetic basis for fur colouration. Future research on colouration in wild vertebrates should include a long-term perspective, as species with winter colour polymorphisms represent model systems to test whether adaptive responses are sufficiently fast for evolutionary rescue from climate change (Mills et al., 2018).

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AUTHORS' CONTRIBUTIONS

C.D.B., A.L. and A.-M.T. conceived and designed the study on colour morphs; A.L., N.E.E. and Ø.F. coordinate the long-term national programmes for captive-breeding and monitoring of Arctic fox in Norway; C.D.B., A.-M.T., A.L., N.E.E. and L.T. collected the field data through these programmes, with the help of numerous mountain rangers and field personnel; C.D.B. and B.K.S. analysed the data with additional statistical help from D.E.B., A.-M.T. and L.R.-E.; S.B. extracted the climatic data used in this manuscript; C.D.B. wrote the manuscript and all authors contributed critically to the drafts.

DATA AVAILABILITY STATEMENT

Compiled encounter histories and R scripts available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.wdbrv15nk> (Di Bernardi et al., 2021). Arctic foxes are species of conservation concern in Norway so sensitive data on den locations will not be released. For further information related to the data, contact Nina E. Eide: nina.eide@nina.no.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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