AUTHOR	Chiara Morosinotto, Jon E. Brommer, Atte Lindqvist, Kari Ahola, Esa Aaltonen, Teuvo Karstinen, Patrik Karell
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Fledging mass is color morph specific and affects local recruitment in a wild bird

Running head title: Color morph specific early condition

Chiara Morosinotto[1,2], Jon E. Brommer[3], Atte Lindqvist[4,5], Kari Ahola[6], Esa Aaltonen[7], Teuvo Karstinen[8] and Patrik Karell[1,2]

[1]Novia University of Applied Sciences, Bioeconomy research team, Raseborgsvägen 9, FI-10600 Ekenäs, Finland

[2] Department of Biology, Lund University, Sölvegatan 39, SE-223 62 Lund, Sweden

[3]Department of Biology, Section of Ecology, University of Turku, FI-20014, Turku, Finland

[4] Environmental and Marine Biology, Department of Biosciences, Åbo Akademi University, Artillerigatan 6, FI-20520 Turku, Finland

[5] Current address: Sirkkalankatu 16A, FI-20500 Turku, Finland

[6] Tornihaukantie 8D 72, FI-02620 Espoo, Finland

[7] Vanhansahantie 13B 7, FI-08800 Lohja, Finland

[8]Juusinkuja 1, FI-02700 Kauniainen, Finland

Corresponding author: Chiara Morosinotto chiara.morosinotto@novia.fi

Abstract

Early life conditions may have long-lasting effects on life history. In color polymorphic species, morph-specific sensitivity to environmental conditions may lead to differential fitness. In tawny owl (*Strix aluco*) pheomelanin-based color polymorphism is expected to be maintained because the brown morph has higher adult fitness in warmer environments, while selection favors the grey morph under colder conditions. Here we investigate body mass at fledging and its consequences until adulthood in a population at the species' cold range margin. Using 40 years of data (1979-2017), we show that brown pairs, which mainly produce brown offspring consistent with a one-locus-two-alleles inheritance model, consistently raised heavier offspring than mixed pairs (grey-brown) and grey pairs. Offspring mass declined seasonally, except among offspring raised by brown pairs. Brown offspring could be heavier due to morph-specific parental care and/or offspring growth. Furthermore, mass at fledging is associated with fitness: the probability of local recruitment into the breeding population increased with higher mass at fledging, especially in mild winters and favorable food conditions, although recruitment is not morph-specific. Fledgling mass thus provides a fitness benefit in terms of recruitment probability that is modulated by environmental factors, which appear to level off any direct morph-specific recruitment benefits.

Keywords

Body mass, early-life condition, life history strategy, parent-offspring morph, plumage coloration, winter temperature.

Secondary language abstract (Swedish and Finnish):

Abstrakt

Förhållandena under en individs juvenilstadium kan ha långvariga effekter på individens livshistoria. Bland arter med färgpolymorfi kan morf-specifika anpassningar till olika miljöer driva olikheter i deras evolutiva duglighet. Hos kattugglan (Strix aluco) upprätthålls färgpolymorfin av att den rödbruna morfen klarar sig bättre i varma miljöer medan den gråa klarar sig bättre under kalla vinteromständigheter. Vi undersökte kroppsvikten hos flygga ungar och dess långvariga konsekvenser till vuxenstadiet i en population nära kattugglans nordliga utbredningsgräns. Vi analyserade 40 års data (1979-2017) och fann att rödbruna par, som i huvudsak producerar rödbruna ungar enligt mendelistisk nedärvning, konsekvent födde upp tyngre flygga ungar än blandpar (grå och rödbrun) eller gråa par. Ungarna vägde mindre ju senare i säsongen de var producerade hos både gråa par och hos blandpar, men inte hos rödbruna par. Rödbruna ungarnas större vikt kan bero på morf-specifik ungomvårdnad och / eller ungtillväxt. Tyngre flygga ungar hade större chans att återkomma som häckande individ i populationen, speciellt efter milda vintrar med goda födoförhållanden. Föräldraparets färg påverkade inte direkt rekryteringen. Kroppsvikten som flygg juvenil ger således en duglighetsfördel genom att påverka rekryteringssannolikheten som häckande individ. Rekryteringen regleras även av de rådande miljö-omständigheterna, vilket suddar ut potentiella morf-specifika rekryteringseffekter.

Tiivistelmä

Nuoruusajan olosuhteilla voi olla pitkä-aikaisia vaikutuksia yksilön elinakaareen. Värimonimuotoisissa lajeissa värimuotojen evolutiivinen kelpoisuus voi usein riippua ympäristöolosuhteista. Lehtopöllön (Strix aluco) feomelaniiniin pohjautuvaa värimonimuotoisuutta ylläpitää punaruskean värimuodon korkeampi kelpoisuus lämpimässä ympäristössä ja harmaan värimuodon parempi selviytyminen kylmissä olosuhteissa. Me tutkimme lehtopöllöjen lentopoikaspainon vaihtelua ja sen pitkäaikaisvaikutuksia aikuisikään lehtopöllön levinneisyyden pohjoisrajan läheisyydessä Suomessa. Analysoimalla 40 vuoden aineistoa (1979-2017) pystyimme osoittamaan että punaruskeat emoparit, jotka pää-asiassa tuottavat punaruskeita poikasia mendelistisen perimän mukaisesti, johdonmukaisesti kasvattavat painavampia poikasia kuin sekaparit (harmaa ja punaruskea) tai harmaat parit. Lentopoikasten paino oli alhaisempi myöhäisissä poikueissa, mutta ei punaruskeiden emojen poikueissa. Punaruskeat lentopoikaset voivat olla painavampia koska emot ruokkivat niitä enemmän tai koska ne kasvavat nopeammin. Havaitsimme myös, että lentopoikasten paino vaikuttaa kelpoisuuteen: poikasten todennäköisyys palata takaisin pesimään tutkimuspopulaatioon oli korkeampi mitä painavampia ne olivat lentopoikasvaiheessa, ja mitä leudompi ja ravintorikkaampi ensimmäinen talvi oli. Emojen väri ei suoranaisesti vaikuttanut tähän todennäköisyyteen. Lentopoikaspaino näin ollen edesauttaa pitkäaikaisesti lehtopöllöyksilön kelpoisuutta, ja tämän lisäksi ympäristö-olosuhteet säätelevät tätä kelpoisuusvaikutusta ja tasoittavat mahdollisia värimuotokohtaisia kelpoisuusvaikutuksia.

Introduction

Condition during early life stages can have long-lasting fitness effects (Lindström 1999; Monaghan 2008; Millon et al. 2011; Monaghan 2014; Monaghan and Haussmann 2015) and even affect population dynamics (Beckerman et al. 2002; Lindström and Kokko 2002). Stressful early life conditions may lead to shorter adult life span (Metcalfe and Monaghan 2001) and altered metabolic rate (Criscuolo et al. 2008). These effects are largely dictated by parental effort and food availability (Naguib et al. 2006; Naguib and Nemitz 2007). However, in certain environmental conditions a morphological or physiological trait can be associated to both costs and benefits depending on the individual life stage. For example, some traits linked with higher survival as juveniles, could lead to lower reproductive success (Schluter and Smith 1986) or shorter life-span (Metcalfe and Monaghan 2001) as adults. The environmental conditions perceived through various life stages are expected to have differential effects according to individual genotype (Hoekstra 2006; Hubbard et al. 2010; Linnen and Hoekstra 2010; Saastamoinen et al. 2013; De Jong and Saastamoinen 2018) and thereby they are expected to impact evolutionary dynamics.

Melanin-based color polymorphic species are ideal systems to infer genetic variation from phenotypes, since color polymorphism is defined as heritable variation in coloration, independently of age and sex (Roulin 2004a). Color morphs are expected to evolve as adaptations to different environmental conditions (Galeotti et al. 2003; Roulin 2004a). On a genetic level color morphs have been linked to differential physiological profiles, which may be the true targets of selection under variable environmental conditions (reviewed in Hoekstra 2006; Ducrest et al. 2008; Linnen and Hoekstra 2010; Hubbard et al. 2010). Indeed, color morphs often exhibit strong differences in their behavioral and physiological responses to the environment (Krüger 2002; Brommer et al. 2005; Boerner and Krüger 2008; Chakarov et al. 2008; Karell et al. 2011a; Karell et al. 2017; Chakarov et al. 2017). Since selective forces can vary at different life stages, we can expect that selection upon the different color morphs might vary between juveniles and adults (Roulin et al. 2010; Récapet et al. 2013). For example, in urban environments, melanistic juveniles of feral pigeons (*Columba livia domestica*) have higher survival rate than paler individuals, but as adults morphs have similar survival (Récapet et al. 2013).

Our study species, the tawny owl (*Strix aluco*, Linnaeus 1758), is widespread in Europe and characterized by plumage color polymorphism consisting of a grey and a reddish-brown (hereafter "brown") morph. In tawny owls, plumage coloration is highly heritable and inheritance of coloration is consistent with a Mendelian one-locus-two allele pattern with brown dominance (Karell et al. 2011b). At the northern margin of the species range, males and females of the grey morph live longer than those of the brown morph and produce more offspring during their lifetime (Brommer et al. 2005). The converse is observed in the central part of the species' distribution (Emaresi et al. 2014), suggesting the brown morph outperforms the grey morph under warmer environmental conditions and vice versa under cold environmental conditions. This type of disruptive selection can maintain the color polymorphism over large spatial scales. Furthermore, similar environment-specific selection can operate within a population. For example, survival selection on adult owls is altered by variation in winter climate: the brown morph has lower survival than the grey in harsh winters with lots of snow, whereas in mild winters the morphs survive equally well (Karell et al. 2011b).

Apart from climate-driven selection in terms of adult survival, melanistic morphs appear to also gain differential reproductive fitness benefits. In a central European tawny owl population, nestlings of brown parents grow better, especially under ad lib food conditions compared to offspring of grey parents (Piault et al. 2009; Emaresi et al. 2014). Differential growth depending on parental color morph could be due to two non-mutually exclusive mechanisms: there could be intrinsic metabolic differences between morphs (Piault et al. 2009) or brown parents could provide higher quality parental care and could thus be able to raise larger offspring (Järvistö et al. 2015; Sumasgutner et al. 2016; Tate et al. 2017). Two aspects are unclear at present. (1) Are offspring of the melanistic (brown) tawny owl morph heavier in populations subsisting at the species' cold range margin, or do grey offspring enjoy a higher mass in these populations? (2) Does a good start in life in terms of higher offspring mass indeed result in increased fitness? (3) Is color morph itself associated to local recruitment probability?

Here, we investigate offspring fledgling mass in relation to morph in a tawny owl population living at the species' cold range margin, across 40 years of data. In line with hypotheses forwarded by previous work (Piault et al. 2009; Emaresi et al. 2014), we expect a link between melanistic (brown) morph and offspring mass; brown tawny owls parents are expected to produce larger offspring and brown offspring are expected to be larger. We further investigate whether higher tawny owl offspring mass indeed confers a fitness advantage in terms of increasing the probability to recruit as a breeding adult in the local population later in life. Although higher mass as a juvenile is typically favorable for performance in early life (e.g. Monaghan and Haussmann 2015), tawny owls in North Europe live in a highly variable environment, in terms of winter severity and prey (small mammal) abundance. These environmental conditions may override any positive effects of mass at fledging during the post-fledging period. Furthermore, grey offspring are expected to have advantages during the post-fledging period, possibly independently of their mass, because the grey morph has (at least as an adult) higher survival in cold climates (Karell et al. 2011b), likely linked to better insulating feather structure (Koskenpato et al. 2016) as well as their cryptic coloration in snowy conditions (Koskenpato et al. 2020). As a consequence, we expect pair crosses that predominantly produce grey offspring to produce more recruits.

Material and methods

The tawny owl population was studied between 1979 and 2017 in a study area of *ca.* 500 km^2 in western Uusimaa, Southern Finland (60˚15' N, 24˚ 15' E). The study area consists of two more or less equally sized subareas, one that was monitored from 1979 onwards and the other one from 1987 onwards. Both areas have approximately 100 tawny owl nest-boxes available for breeding. Nest boxes were checked in early April to detect breeding attempts, information on clutch size as well as hatching date and fledging success (i.e. the number of fledglings on the total clutch size) were recorded. Both parents were trapped at the nest box during the nestling period, aged, measured (wing length and mass) and ringed to allow individual identification (Karell et al. 2009). Plumage color was scored in adults using a semi-continuous score based on the level of pheomelanin in four body parts: facial disc, back, breast and general appearance. From this overall score we then categorized each individual as either grey or brown morph (Brommer et al. 2005). At *ca.* 25-28 days age, shortly prior to fledging, the offspring were ringed, weighed and measured. Local recruitment as breeding individuals within the study area was recorded when the adult owls were caught.

Between 1979-2017 we considered 845 breeding attempts where both parents were successfully trapped and color scored. Of these 20 nests failed, and thus we collected data on offspring mass on 825 successful breeding attempts, with overall 2698 offspring measured. All successful breeding attempts where both parents were trapped were classified according to pair morph: both parents grey (GxG, 355 pairs), grey female and brown male (GxB 202 pairs), brown female and grey male (BxG, 180 pairs) and both parents brown (BxB, 88 pairs). Pair morph combination was used as a proxy for offspring plumage (as suggested by Karell et al. 2011b). In addition, from 2006 onward, the plumage color of the fledglings was scored as either brown or grey by visual inspection of the plumage. Brown fledglings have clear development of reddish color in the facial disc, clearly reddish tertiaries and a more reddish-brown general appearance. In this subset we measured the proportion of brown offspring per pair morph as well as individual morph-specific fledgling mass (159 nests, 530 offspring: 292 grey and 238 brown fledglings, 2006-2017).

Overall 170 offspring recruited as breeder to the local population on the 2629 offspring ringed within 1981-2016. Probability of recruitment was considered not only according to offspring condition and pair morph combination, but also according to winter temperature and small mammal abundance during the post-fledging period. We collected annual winter temperature data from the Finnish Meteorological Institute (FMI), from Helsinki-Vantaa airport weather station, situated *ca.* 50 km east of the study area. We used data on annual winter mean temperature (1. December - 28. February) for each study year, which was then standardized with the long term average in years 1981-2010. This “winter temperature anomaly” (hereafter “winter temperature”) is a widely used index by the FMI. Small mammal abundance was estimated each year in autumn by snap trapping in two sites within the study area, each containing both field and forest habitats. Prey abundance was estimated as number of captures per 100 trap nights (Karell et al. 2009).

Statistical analyses

Analyses of generalized linear mixed models were implemented in MCMCglmm (Hadfield 2010) running in R (R Core Team 2019). Priors for fixed effects were uninformative following the standard settings of MCMCglmm. Prior specifications of random effects were as listed below and are in MCMCglmm inverse-Wishart distributed with the potential to range from vague, uninformative to parameter-expanded priors used primarily when inferred variances are boundary to zero. In deciding the number of iterations, burn-in and thinning of the chain, we used visual inspection of the posterior chain and posterior density, as well as autocorrelation statistics with the objective to obtain approximately 1000 posteriors with low autocorrelation. Uncertainty of parameters were based on the posteriors, and statistical significance of fixed effects were based on their pMCMC probability where probabilities below 5% were considered significant.

Offspring mass (standardized to the mean, 1979-2017) was analyzed using a linear mixed model with both brood ID and year as random effects. Brood ID is a unique numerical code identifying each brood in each year. Priors for brood ID and residual variance were uninformative (V=1, nu =0.002), and a parameter expanded prior for year was used (V=1, nu=1, alpha.mu= 0, alpha.V=1000). As fixed effects we included the pair morph combination (GxG, GxB, BxG, BxB morphs) and laying date (day of laying of the first egg per brood, standardized to mean=0 among all years). We assumed no differences in sex-ratio of the offspring (Kekkonen et al. 2008). Wing length (standardized to the mean) was included as a fixed-effect covariate in the analyses, thereby correcting for mass differences driven by size differences, including sexual size dimorphism (female offspring are bigger than males). For a subset of all offspring, we could test difference in offspring mass according to morph (2006-2017). As before, we included brood ID and year as a random effect (uninformative prior), and wing length as a fixed effect.

Fledging success (1979-2017; considering 585 breeding attempts for which clutch was known) was scored for each egg as either producing a fledgling (1) or not (0) and analyzed using a Generalized Linear Mixed Model (GLMM) assuming a binomial response. Residual variance was fixed to 1, and female ID and year were included as random effects (both with uninformative priors; V = 1, nu = .002). As fixed effects we included the pair morph combination and laying date.

The probability for recapture a fledgling as breeding adult in the study population (termed "recruitment" from here on) was scored for each fledgling as either recruited (1) or not recruited (0). These data (1981-2016) were analyzed using two GLMMs with binomial response variable. Brood ID and year were included as random effects in both models (both with parameter expanded priors; V = 1, nu = 1, alpha.mu = 0, alpha.V = 1000). The first model (presented in Appendix, Table S1) included pair morph combination, winter temperature and prey abundance, as well as their interactions. The second model, presented among the results, included as fixed effects pair morph combination, standardized offspring mass, standardized offspring wing length, winter temperature and prey abundance, as well as three interactions: mass by winter temperature, mass by prey abundance, winter temperature by prey abundance. Thus, the first model investigated differences in recruitment probability according to pair morphs, while the second model investigated the role of offspring size (wing and mass), as well as pair morph; both models also accounted for environmental variables. Expected probability on the observed data derived from fixed and random effects in a non-Gaussian GLMM was calculated following de Villemereuil et al. (2016). We computed the expected probability for all posteriors across the observed range of covariates and computed the posterior mean and its 95% Credibility Interval.

Laying date (1979-2017; n=845 breeding attempts) and clutch size (1979-2017; n=585 breeding attempts) were analyzed using linear mixed models with year and female ID as random effects (presented in Appendix, Table S2). As fixed effect, pair morph combination was included.

We computed the expected frequencies of brown and grey morph offspring production for each pair assuming the population was at a single Hardy-Weinberg equilibrium and that morphs were determined by one locus with the allele for brown dominant over that for grey, following the procedure detailed in Karell et al. (2011b). A chi-square test with one degree of freedom was conducted for each cross. As the cross of putative homozygous recessive grey morphs is expected to only produce grey offspring, only the observed and expected values for grey offspring were used to compute the chi-square value. All the data used in these analyses are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.00000001s (Morosinotto et al. 2020).

Results

Tawny owl pair morph combinations did not vary in their laying date nor in clutch size (Table S2 in Appendix), although overall clutch size declined seasonally. The probability of within-nest survival, i.e. the proportional fledging success (N fledglings / N eggs), did not differ according to pair morph combinations nor laying date (Table S2 in Appendix).

Offspring mass and color morph inheritance

BxB pairs produced offspring with heavier mass than average, whereas the other pair morph combinations did not (Table 1A, Figure 1). Offspring mass overall decreased with advancing laying date (Table 1A), but this effect was absent in offspring raised by BxB pairs (Table 1A, Pair morph * laying date, Figure 2). From a subsample of data from 2006-17 with known offspring individual color morph (either grey or brown), we could confirm that BxB parents produce more brown offspring than GxG or mixed morph parents, as predicted from a one-locus-two alleles model (see also Karell et al. 2011b). In BxB parents, 85% of the offspring was brown (75/88; chi-sq = 0.92; P=0.34), while 95% of offspring of GxG pairs were grey (131/139; chi-sq=0.46, P=0.50). In mixed BxG pairs (grey males) 50% (60/121; chi-sq=2.50; P=0.11) and in GxB pairs (brown males) 52% (95/182; chi-sq=1.50; P=0.22) of offspring were brown (see Figure 3 for observed vs. expected values). Analysis of this subsample of data, where individual-based offspring color morph was known, confirmed that brown offspring were indeed heavier than the grey ones (Table 1B).

Probability of recruitment

In total, 6.5% (170/2629) of the fledglings produced during the years 1981-2016 recruited to the local population. Fledglings with higher mass had a higher probability to recruit to the local population (Table 2; Figure 4A). The probability of juveniles to recruit was also higher when winter temperatures were warmer than average in the first winter post-fledging (Table 2, Figure 4B) and when small mammal density was higher in autumn (Table 2, Figure 1S in Appendix). Pair morph combination did not affect offspring probability of recruitment (Table 2 and Table S1 in Appendix). A higher mass at fledging increased recruitment probability especially when winter temperatures were warmer (Table 2, Figure 4C).

Discussion

We here find that fledglings of brown morph parents (BxB) were consistently heavier than offspring of grey (GxG) or mixed pairs (GxB, BxG) across the 40 years of tawny owl data. Due to the simple putative Mendelian inheritance of tawny owl color morphs, the majority (approximately 85%) of the offspring of these brown morph crossings are brown morph fledglings. Indeed, we find that brown morph fledglings themselves are heavier than grey fledglings. Previous work demonstrating an association between tawny owl color and offspring mass was conducted in a population in central Europe (Piault et al. 2009; Emaresi et al. 2014). Because the ecological conditions are very different in our population living at the species' cold range margin, our findings imply that tawny owls show a genetically determined polymorphism associated with mass at fledging, which is in line with our expectations.

Mass at fledging itself is a trait widely associated with greater probability for recruitment in birds (e.g. Naef-Daenzer et al. 2001; Monrós et al. 2002). We here find that in our tawny owl population, heavier mass at fledging constitutes a major fitness benefit as it improves the probability to recruit as a breeding adult (cf. Monrós et al. 2002; Emaresi et al. 2014). Heavier fledgling mass is particularly important in our study population when a fledglings' first winter is warmer than average. We further expected that in this northern population recruitment of the grey morph (GxG cross) would exceed that of the brown morph (other pair crosses). Previous studies indeed suggest that brown melanistic morphs should have higher fitness living under warmer conditions (central European populations, Emaresi et al. 2014), while grey tawny owls should be advantaged when living at the species' cold range margin (Karell et al. 2011b). However, we found no evidence of differential recruitment probability between color morphs (morph crosses).

A higher mass at fledging in offspring produced when both parents are of the brown morph could be the results of several mechanisms. Firstly, different morphs could vary in their parental effort. If brown morph parents provide more food to their offspring, i.e. they allocate more resources and reproductive effort than grey morph parents, they will raise offspring in better condition. Indeed, experimental studies have found that tawny owl color morphs differ in their reproductive tactics. Brown tawny owl parents are more consistent in the resources allocated to their brood compared to grey parents, independently if the brood was enlarged or reduced (Emaresi et al. 2014). It is also possible that parents with different morphs vary in their hunting skills or foraging activity, as in other color polymorphic species (e.g. Roulin 2004b; Tate et al. 2016; Tate and Amar 2017, San-Jose et al. 2019). A second, non-mutually exclusive explanation for the better condition of offspring of brown pairs could be that the offspring themselves convert food to growth more efficiently. Piault et al. (2009) found that offspring of brown mothers gain more mass than offspring of grey mothers per equal amounts of food provided, although they also lose mass more quickly under restricted food conditions and after immune challenges. Thus, one possibility is that brown morphs have a faster metabolism. Consistent with this hypothesis is that adult brown tawny owls show faster telomere shortening rate (Karell et al. 2017) and shorter lifespan (Brommer et al. 2005). From our dataset it is not possible to clearly distinguish between these two possible mechanisms leading to higher mass in offspring of brown pairs. Future studies combining a cross-fostering experiment with detailed observations of parental provisioning and growth patterns of the offspring are needed to disentangle the mechanisms at play.

Our results confirm the previous findings (Karell et al. 2011b) suggesting that color inheritance in tawny owls is consistent with a one-locus-two-alleles model with brown dominance, where BxB pairs produce mostly brown offspring and mixed pairs (GxB, BxG pairs) produce approximately

50% of brown offspring. However, we found that 6% of the offspring of GxG are brown, whereas under Mendelian inheritance the grey morph is homozygous recessive and one would therefore expect all offspring of GxG to be grey. This non-significant discrepancy can be due to extra pair paternity, which albeit low is present in this species (Saladin et al. 2007), to errors in assigning morphs in fledglings and/or to a genetic architecture that apart from a major locus for color morph also includes minor alleles in determining tawny owl morphs.

Heavier tawny owl offspring at fledging have higher probability of recruitment to the local population in subsequent years, as found also in another population (Emaresi et al. 2014). Tawny owls fledge at an early developmental stage, when they cannot fly and are dependent on their parents for food. Smaller individuals at fledging have higher probability of mortality due to predation and starvation (Overskaug et al. 1999). In general, fledging mass is thought to be especially important to overcome mortality due to harsh environmental conditions (Jones et al. 2017) and can thus have carry-over effects in post-winter survival (Harrison et al. 2011). We here find that favorable conditions in terms of first-winter temperature and abundance of small mammals indeed strongly improve recruitment probability of offspring into the breeding population. However, while there is a positive selection on mass, we could not find clear benefits for neither the grey nor the brown color morph in terms of recruitment. The lack of morph-specific recruitment benefits is contrary to our predictions and could be due to few non-mutually exclusive reasons. This result could be due to morph-specific dispersal patterns. A previous study on barn owls (*Tyto alba*) showed that pheomelanic individuals disperse further from their natal territory than pale ones (van den Brink et al. 2012). If brown tawny owls are more likely to disperse out from the study area they would also be less likely to recruit within the natal population. Unfortunately, dispersal out from the study area cannot be tested in the current dataset. The current analyses may also have limited power to detect morph specific patterns since we can only analyse this pattern based on parental morph information and relying on the inheritance pattern, and not based on offspring own morph in the complete 40 years dataset. However, the lack of morph-specific recruitment could also result from a selective advantage of the grey morph during the post-fledging period, which could level off the body mass benefit of the brown morph at fledging. For example, previous studies of adult tawny owls in this study population have found that, as adults, the grey morph has higher survival in cold and snow-rich winters than the brown one (Karell et al. 2011b). Grey morph tawny owls likely benefit in winter from a better insulation of their feathers (Koskenpato et al. 2016), as well as their more cryptic plumage under snowy conditions (Koskenpato et al. 2020). These morph-specific benefits, respectively for fledging condition (for brown) and capacity to deal with winter conditions (for grey), could lead to neither morphs being advantaged more than the other in terms of post-fledging survival and ultimately recruitment.

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Authors' contribution:

Data collection: KA, TK, EA, PK. Original idea: PK. Data preparation: AL, CM. Preliminary analyses: AL, PK. Final analyses and modelling: JEB, CM. Manuscript preparation: CM, PK, JEB. All authors have read and approved the final version of the manuscript.

Data accessibility:

All the data are deposited in Dryad Data Repository, https://doi.org/10.5061/dryad.00000001s.

Ethical statement

All applicable international, national and institutional guidelines for the care and use of animals were followed. All the birds were captured, handled and ringed with an appropriate ringing license.

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Table 1 Estimates of the linear mixed model on offspring mass according to pair morph combination (long term dataset 1979-2017; A) and according to offspring individual morph (subset 2006-2017; B).

		Posterior mean	95 % Credibility interval	pMCMC
A. Offspring mass (long term dataset)				
Fixed effects	GxG	0.10	-3.56 – 4.10	0.96
	GxB	-3.16	-8.25 – 1.57	0.21
	BxG	2.38	-2.61 – 7.49	0.37
	BxB	9.23	1.98 – 15.86	**0.006**
	Wing	1.63	1.57 – 1.69	**<.001**
	Laying Date	-0.45	-0.73 – -0.17	**<.001**
	Pair morph * Laying Date			
	GxB*laying	0.14	-0.25 – 0.60	0.53
	BxG*laying	-0.36	-0.87 – 0.07	0.15
	BxB*laying	0.66	0.03 – 1.30	**0.040**
Random effects	Brood ID	757.5	664.4 – 881.1	
	Year	41.02	0.01 – 87.01	
B. Offspring mass (subset 2006-017)				
Fixed effects	Grey morph	1.92	-6.10 – 9.80	0.60
	Brown morph	6.69	-0.10 – 13.38	**0.04**
	Wing	1.54	1.39 – 1.66	**<.001**
Random effects	BroodID	709.9	477.0 – 954.9	
	Year	109.2	<.000 – 372.9	

Response variable is standardized mass, both wing and laying date are standardized. Values of pMCMC <0.05 are in bold and indicate the probability the parameter is zero. For both models iterations 13000 and thinning interval 10.

Table 2 Estimates of MCMCglmm for offspring recruitment probability according to pair morph, offspring mass at fledgling and both winter condition ("winter temperature") and prey availability ("mammal density") in the first autumn post-fledging.

		Posterior mean	95 % Credibility interval	pMCMC
Recruitment				
Fixed effects	Intercept	-3.63	-4.17 – -3.13	**<.001**
	Pair morph			
	GxB	-0.18	-0.70 – 0.36	0.50
	BxG	-0.17	-0.67 – 0.39	0.54
	BxB	-0.08	-0.73 – 0.58	0.86
	Mass	0.008	0.002 – 0.01	**0.003**
	Wing	0.0009	-0.01 – 0.01	0.88
	Winter temperature	0.21	0.07 – 0.37	**0.005**
	Mammal density	0.06	0.02 – 0.10	**0.002**
	Mass*winter	0.001	-0.0005 – 0.003	0.13
	Mass*mammal	-0.000003	-0.0004 – 0.0005	0.96
	Winter*mammal	-0.006	-0.027 – 0.01	0.52
Random effects	BroodID	0.77	<.001 – 1.68	
	Year	0.56	0.09 – 1.11	

Mass, wing and mammal density were standardized to the mean, winter temperature is calculated as weather anomaly (see methods). GxG is used as reference level for pair morph combination. Values of pMCMC <0.05 are in bold. Iterations 250000 thinning interval 200.

Figure 1

Standardized mass according to the four pair morph combination. Coefficients of the GLMM with 95% CRI

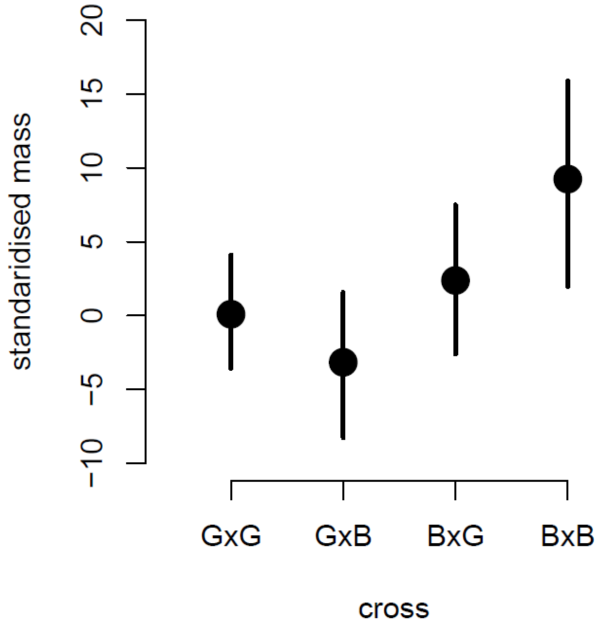


Figure 2

Standardized mass according to the four pair morph combination by laying date (Pair morph*laying date interaction in Table 1A). Coefficients of the GLMM with 95% CRI

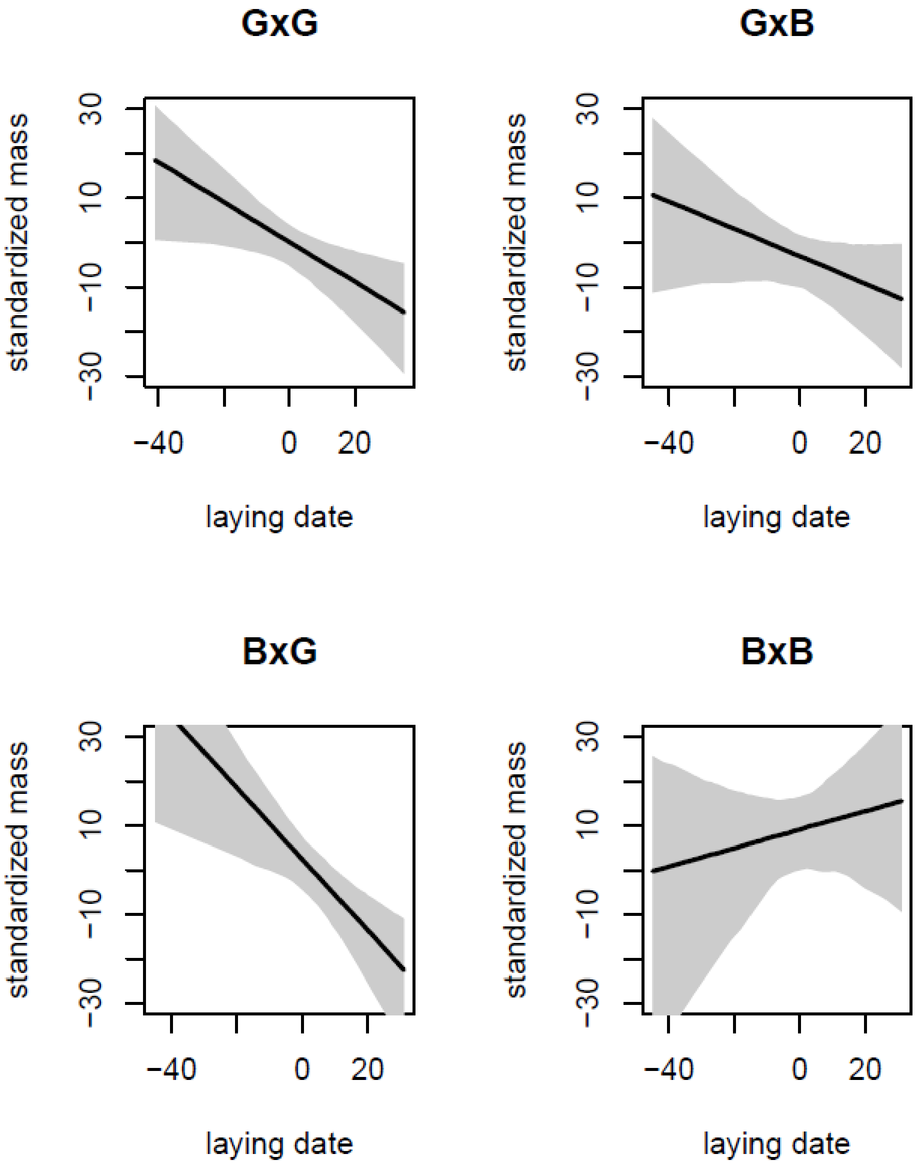


Figure 3

Observed (respectively in dark grey and dark brown column) vs expected (respectively in light grey and light brown column) number of offspring according to pair morph combination (GxG, GxB, BxG, BxB parents), following the one locus two allele model. The observed and expected numbers are also indicated with “O” and “E” at the bottom of each column respectively.

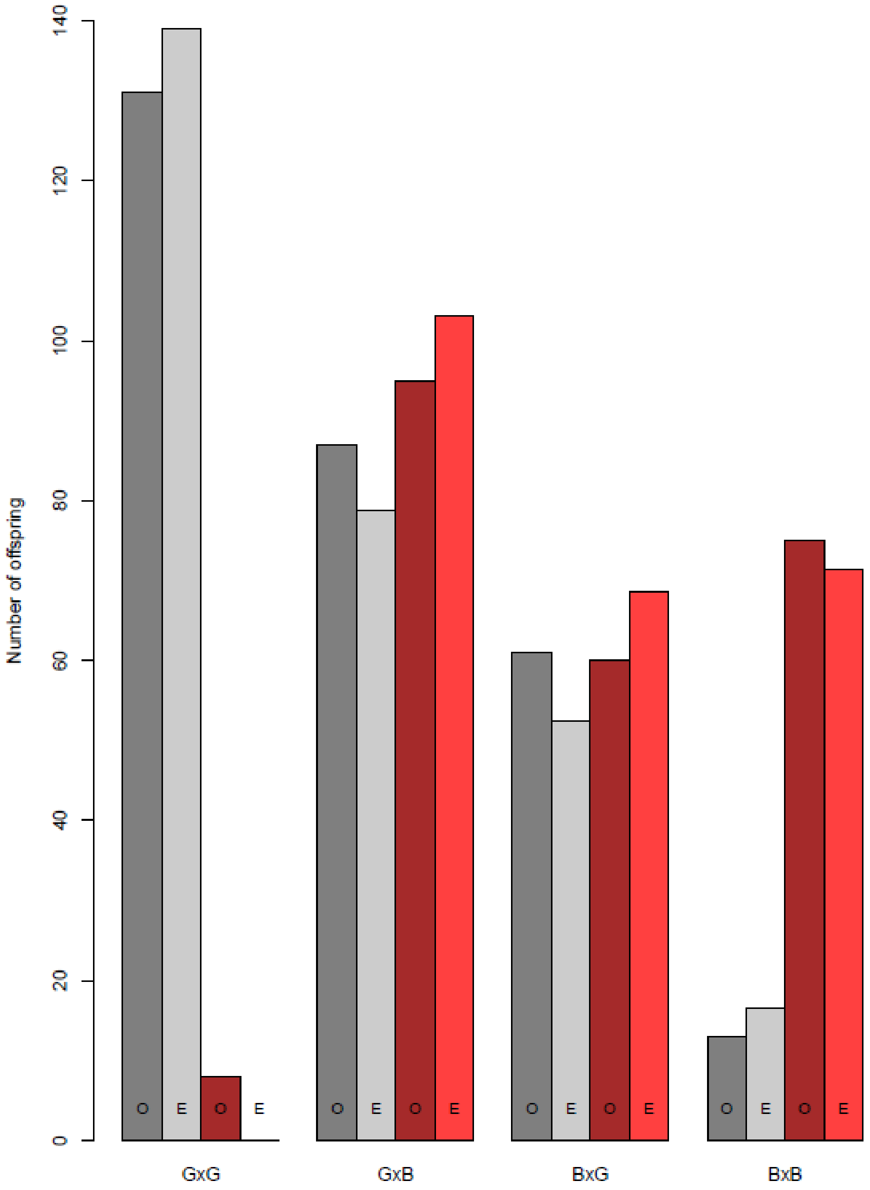
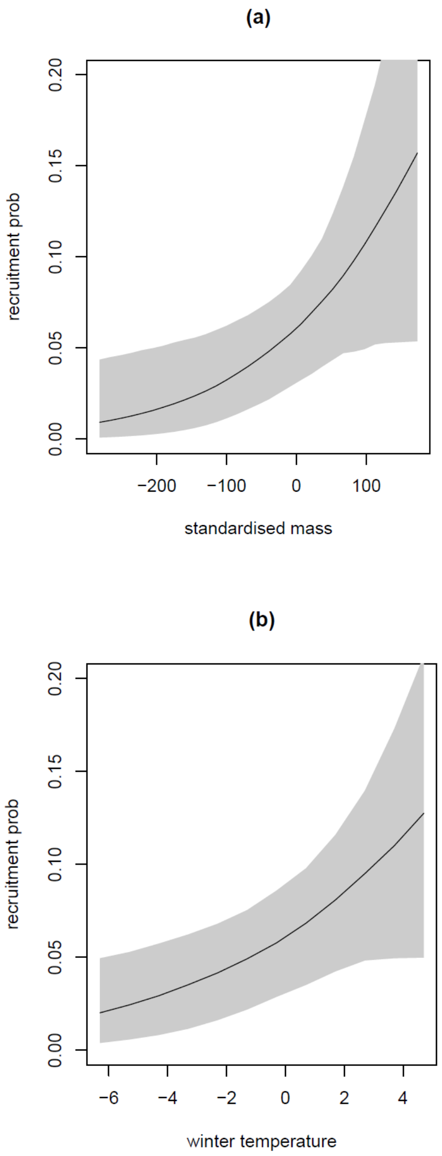
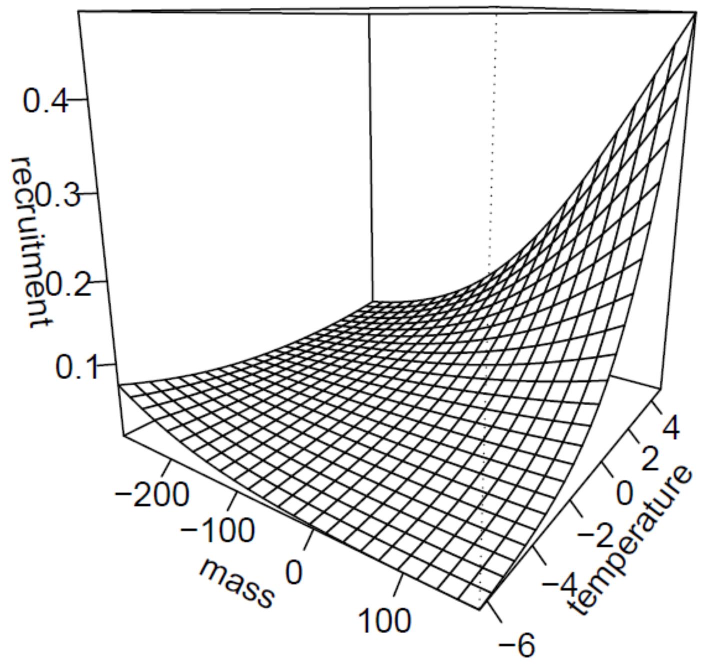


Figure 4

Recruitment probability according to standardized mass at fledging (in g, panel A), winter temperature (in degrees C°, panel B), and their interaction (C). Expected values are computed on the basis of the statistics reported in Table 2, where all other fixed-effect covariates apart from the ones plotted are assumed to be at their mean value (i.e. 0). Graph C is plotted across the observed range of winter temperature and standardized mass.



(c)


0.4
0.3
0.2
0.1
recruitment
−200
−100
0
100
mass
−6
−4
−2
0
2
4
temperature