

Tawny Owl females of intermediate colour morph reproduce better and increase in a local polymorphic population

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Individuals of the same population with differing melanin plumage colouration can respond differently through fitness to environmental stressors. In a local population of Tawny Owls (*Strix aluco*), we collected individual-based data on nesting attempts of this well-known colour polymorphic species between 1985 and 2014. We studied whether body size, condition, demographic parameters and habitat around occupied nest sites differ among grey, intermediate and brown coloured females. The proportions of females belonging to each of the three colour morphs in the local population changed during the study period, with intermediate individuals becoming more frequent in the last decade. Females were similar in body size and achieved similar body condition during breeding irrespective of plumage colouration. Although most of the analysed demographic parameters were not statistically significantly related to the colour morph, the intermediate owls raised more nestlings in a lifetime and tended to have higher recapture probability. We found little support for habitat and morph associations. In summary, we propose that the increase in intermediate Tawny Owl colour morphs in this local population is associated with their better reproductive performance compared to the other morphs.



1. Introduction

Colour polymorphism is the coexistence of two or more distinct and genetically determined colour forms in an interbreeding population (Roulin 2004). This is a phenomenon observed in many vertebrate taxa including birds, especially birds of prey and owls (Fowlie & Krüger 2003, Roulin 2004). Apostatic, disruptive and sexual selection are three major hypotheses proposed to explain the origin and maintenance of colour polymorphism

in birds (Fowlie & Krüger 2003, Galeotti *et al.* 2003). However, regardless of the mechanism that results in colour polymorphism in any particular species, this phenomenon is usually regarded as providing adaptive functions to local environmental conditions (Tate *et al.* 2016 and references therein). The ratio of different colour morphs within a local population of raptor species tends to vary spatially along geographical or environmental gradients (Galeotti *et al.* 2003, Amar *et al.* 2014, Roulin & Randin 2015, Tate *et al.* 2016).

The relationship between melanin-based plumage colouration and fitness in birds is species-dependent (Meunier *et al.* 2011). At temperate latitudes in Germany, individuals of the dominant intermediate morph of Common Buzzard (*Buteo buteo*) produced two times more nestlings than the individuals of the rare light and dark morph during their lifetime (Krüger & Lindström 2001). In the case of Tawny Owls (*Strix aluco*) breeding at northern latitudes in Finland, individuals of the grey colour morph survived better and produced more nestlings during their lifetime than brown individuals (Brommer *et al.* 2005). In a long-term study of Swainson's Hawk (*Buteo swainsoni*) in California, however, Briggs *et al.* (2011a) did not find any significant differences in survival and various reproductive parameters among individuals of three colour morphs. Similarly, brood size was independent of colour morph in the dimorphic Booted Eagle (*Aquila pennata*) population in south-eastern Spain (Martínez *et al.* 2016). Regardless of whether colour polymorphism influences fitness or not, the ratios of morphs usually remain stable over time within local populations of various raptor species (Brommer *et al.* 2005, Briggs *et al.* 2011a, Martínez *et al.* 2016). At the distribution range scale, however, temporal changes in plumage pigmentation may be region-specific (Roulin *et al.* 2011). The stable long-term ratio may be a result of different and temporally alternating performance strategies of the colour morphs at a fine scale (Roulin *et al.* 2003). Global warming, however, can selectively affect individuals in different ways in a given population (Roulin 2014). Karell *et al.* (2011b) demonstrated that changes in the climatic conditions resulted in an improvement in the fitness of brown-coloured individuals in Tawny Owls, leading to an increase in the number of individuals of this morph in the population.

In this study, we investigated fitness and habitat in the well-known polymorphic species Tawny Owl. Individuals of this generalist nocturnal predator vary from pale grey to reddish-brown, but two (i.e., grey and brown) or three (i.e., grey, intermediate and brown) distinct morphs are most frequently described with their proportions spatially distributed in Europe without a clear geographical cline (Galeotti & Cesaris 1996, Karell *et al.* 2011b). Melanin-based plumage colouration in

Tawny Owl is under strong genetic control, highly heritable and is not sensitive to environmental conditions (Brommer *et al.* 2005, Karell *et al.* 2011b, Emaresi *et al.* 2014). Tawny Owl individuals differing in plumage colouration show some behavioural (Da Silva *et al.* 2013), physiological (Galeotti & Sacchi 2003, Gasparini *et al.* 2009a, 2009b, Karell *et al.* 2013, Emaresi *et al.* 2016), morphological (Roulin *et al.* 2003) and fitness differences (Roulin *et al.* 2003, 2004, 2008, Brommer *et al.* 2005, Pault *et al.* 2009, Karell *et al.* 2011a, 2011b, Da Silva *et al.* 2013, Emaresi *et al.* 2014). Differently coloured Tawny Owls tend to be associated with specific regional environmental conditions (Galeotti & Cesaris 1996). This expectation, however, may be valid in a local population as well (Roulin *et al.* 2003) because environmental heterogeneity can promote the evolution of phenotypic plasticity with individuals matching their phenotypes with the environment (Roulin *et al.* 2008). Galeotti and Sacchi (2003) showed that differently coloured individuals are associated with varying habitats at a fine scale. Moreover, individuals of similar plumage colouration in distinct populations under different environmental conditions may even show opposite patterns of the same fitness trait (*cf.* Brommer *et al.* 2005, Emaresi *et al.* 2014) indicating that morphs are adapted to specific environmental conditions that vary geographically. Further, the effect of global warming may vary spatially and subsequently, distinct colour morphs may respond differently, in terms of fitness, to the same environmental stress (Roulin 2014). Karell *et al.* (2011b) demonstrated how environmental changes differently drive the fitness of the colour morphs of Tawny Owls in the same geographical area. Thus, former findings for any particular species in a specific geographical area, habitat and/or time period may not be a universal reflection of the fitness of a colour morph and its change over time within that species.

Using data from breeding Tawny Owl females, captured over a period of 30 years in a temperate forest in Lithuania, Central Europe, we investigated whether body size, reproductive performance and habitat around nest sites is colour morph dependent. Additionally, we predict that: 1) proportions of morphs change over years; 2) reproduction and survival are morph dependent; 3) the relationship between mean winter tempera-

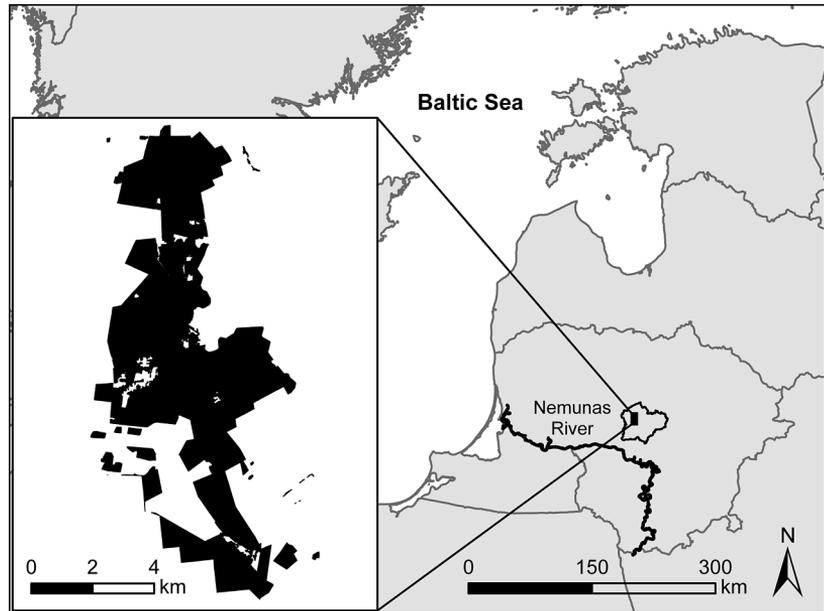


Fig. 1. Location of the study site (forest area = black fill) in Kėdainiai district (bold line), Lithuania.

tures, mean spring temperatures and reproductive parameters differs among morphs; and 4) habitat composition differs between nest sites occupied by females of the three colour morphs.

2. Material and methods

2.1. Data

Data for this study were collected between 1985 and 2014 in the Dotnuva forest (area: 39 km²), surrounded by agricultural fields in Kėdainiai district, Central Lithuania (55°23'27" N, 23°46'25" E) (Fig. 1). The terrain is flat and deciduous tree species dominate in the forest. All available nest boxes (nest boxes were first erected in 1977; from 30 to 55 nest boxes were available annually for occupation between 1985 and 2014) were checked by S. Rumbutis for occupation from February to March, depending on the winter weather conditions. On average, five pairs of Tawny Owls bred annually (S. Rumbutis, unpubl.). A nest box (hereafter nest site) was considered occupied if a clutch was found. Occupied nest sites were checked later in April–May to estimate breeding output, as well as to capture the females attending broods with a hand net.

The date of the start of breeding was estimated

using one of two methods, namely accounting for a) the age of nestlings; b) egg laying intervals (every second day) in cases of incomplete clutches were found during the early nest site checks. The age of the oldest nestling was estimated using a nestling age identification key compiled by S. Rumbutis (unpubl. data). The start of breeding then was determined by backdating calculation, accounting for the incubation duration (30 days; Southern 1970). For further analyses, we expressed the start of breeding in Julian days (wherein 1st January is day 1), also accounting for leap years. The length and maximum breadth of the eggs in full clutches were measured using a sliding calliper to the nearest 0.1 mm. Egg volume was calculated as $\pi \times \text{egg length} \times \text{breadth}^2 / 6000$ (Tatum's index; Hakkarainen & Korpimäki 1993). For further analyses, the mean volume of the eggs in the clutch and clutch size were used as response variables. Brood size was measured as the number of nestlings of at least two weeks of age.

The wing and tail lengths of captured females were measured with a ruler, the individuals were weighed with a spring balance to the nearest five grams and, in the case of first time captures, the birds were ringed. Wing and tail lengths showed a statistically significant positive correlation, and hence we used scores of the first principal component as an index for individual body size. Larger

scores indicated larger individuals. To estimate body condition, we used the generalized linear model (GLM) where we related female weight (as a response variable) with body size and the day of capture (as explanatory variables) (following Blomberg *et al.* 2014). Female body weight tends to decline during the breeding period (Southern 1970), hence the day of capture was calculated as a difference between the Julian day of capture and the Julian day of the start of breeding. Additionally, we used standardized residuals of the above-mentioned GLM as an estimate of individual body condition in relation to body size and standardized to a common day of capture after the start of breeding. Assignment of females to colour morphs was always performed in the field at the time of capture and, in case of recaptures, without knowledge of their previous morph assignment. Furthermore, female captures and morph assignments were conducted by the same person – Saulius Rumbutis – during the entire 30 year period of the field work. Females were assigned to one of the three colour morphs based on the intensity to which the individual displayed brown or grey colours across the entire body plumage: grey – birds entirely lacked brown colour in the feathers, intermediate – both brown and grey colours were present in the plumage; brown – only brown feathers were present. Out of 57 females, 22 individuals were recaptured at least once. Only during two recaptures (5% out of 39 recaptures) females were assigned to different morphs. For these two females, we used the morph estimated during the first capture. Additionally, colour morphs of 69 dead female specimens, collected by the public from different localities in Lithuania between 1985 and 2014, were inspected in the skin collection of Kaunas T. Ivanauskas Zoological Museum. Using the same method as in the study population, S. Rumbutis assigned each of the specimens to one of the three morphs.

Spatial data on occupied nest sites throughout the study period were analysed in the GIS environment (ArcGIS 10.0 software). A habitat layer was created based on photo-interpretation of satellite images and orthophotographs at a scale 1:10,000 for non-forested land and State Forest Cadastre data derived from stand-wise inventories for forested land. Data sources for the year 2000 were used to represent the mid-period of the study. To

represent habitat around occupied nest sites, 0.4 km radius buffers were created (such a buffer covers the core area of the Tawny Owl home range; Sunde & Bølstad 2004). In the buffers, we measured proportions of 1) fields (intensively cultivated fields, pastures, grasslands), 2) openings within forests (clear cuts, small forest meadows, etc.), 3) deciduous forest (birch, aspen, black alder, grey alder, oak, ash, lime or maple dominating in the stands by volume proportion), and 4) coniferous forest (spruce or pine dominating in the stands by volume proportion). Thereafter, pairwise Pearson correlations between habitat variables were checked to reduce collinearity. If correlation between pair of variables is strong (i.e., $r > 0.6$), only the variable which was more relevant to the study species was retained (Sergio *et al.* 2006 and references therein). Only the proportions of fields and deciduous forest were strongly related ($r > 0.6$), hence for further analyses, we included all the above-mentioned habitat variables, except for the proportion of fields.

2.2. Data analysis

The proportions of individuals belonging to each of the three colour morphs over the three decades, i.e., 1985–1994, 1995–2004 and 2005–2014 were compared using the chi-square test. We assigned each individual to one of these decades according to the year of entering into the study population (i.e., year of the first capture of that individual). Altogether, 57 unique females were captured since 1985 for the first time at the study site.

For survival and recapture probabilities analysis, we included data on 57 females captured in total 96 times during the period 1985–2014. Survival and recapture probabilities of Tawny Owls, marked and recaptured during the nest site inspections, were estimated using the program MARK Version 7.1 (Cooch & White 2015), using Cormack-Jolly-Seber live mark-recapture models (Jolly 1965). Apparent survival probability (ϕ) accounts for both survival and permanent emigration of individuals from the studied population. Recapture probability (p) indicates the probability of recapturing a marked bird when it is still present in the study population. A number of models were examined with different assumptions regarding survival and recapture probabilities. Survival and

recapture probabilities were modelled as either constant (denoted $\phi(\cdot)$ and $p(\cdot)$) or morph dependent (i.e., denoted $\phi(\text{morph})$ and $p(\text{morph})$). Due to small sample size, models with time-dependent survival and/or recapture probabilities resulted in many inestimable parameters, therefore such models were not analysed. Akaike Information Criterion with a correction for small sample size (AICc) was used for model evaluation and selection of the most parsimonious model (Lebreton *et al.* 1992). Goodness of fit of the data was evaluated by running 1,000 bootstrap simulations of the global model ($\phi(\text{morph})$ $p(\text{morph})$). Overdispersion of the data was evaluated by calculating the \hat{c} (variance inflation factor) by dividing the deviance of the global model ($\phi(\text{morph})$ $p(\text{morph})$) by the mean deviance of the 1,000 simulations. In our case, \hat{c} of 1.0389 indicated some overdispersion in the data (lack of fit), therefore quasi-likelihood adjusted AICc (QAICc) was used for the final model selection (Cooch & White 2015). In order to account for the uncertainty in model selection and obtain the best estimates of survival and recapture probabilities, model averaging was applied (Cooch & White 2015) for the supported models (i.e., $\Delta\text{QAICc} < 2$).

Linear mixed models (LMM) were used for analyses of continuous response variables (for body size, body condition, start of breeding, mean egg volume), while generalized linear (GLM) (for number of nesting attempts per female and total number of offspring per female) and generalized linear mixed models (GLMM) (for clutch size and brood size) were used for analysis of count variables and morph associations. LMM, GLM and GLMM models were fitted by the maximum likelihood method. Morph was entered as a fixed categorical variable. Female identity and year were included into LMM and GLMM models as random factors. Models with and without an explanatory variable of interest were compared with the likelihood ratio test.

The mean winter temperature before nesting attempts of the different colour morph females was analyzed through multinomial logistic regression (MLR), where morph was a response variable and mean winter temperature as the explanatory variable. Brown colour morph was used as a reference group. Models with and without the explanatory variable were compared using the likelihood ratio test. To estimate the significance of interac-

tion between colour morph and mean winter or spring temperature (T) (in models with response variables including body condition, timing of breeding, clutch size, mean egg volume in the clutch and brood size), we compared models (LMM, GLMM) with an additive effect of these explanatory variables (i.e., morph + winter T; morph + spring T) with the models where the same explanatory variables were included through interaction term (i.e., morph \times winter T; morph \times spring T) using the likelihood ratio test. Mean winter temperature was calculated from the mean monthly values of December, January and February, and mean spring temperature from the mean monthly values of March, April and May, respectively.

Habitats around the nest sites occupied by females of the three morphs were analyzed through a multinomial logistic regression. All possible combinations of the above mentioned three habitat variables were included in the models. Brown colour morph was used as a reference group in these models. Further, we used the information-theoretical approach for model selection and multi-model inference procedure (Burnham & Anderson 2002). Akaike Information Criterion with a correction for small sample size was used. The relative importance of each model was estimated through ranking the models by Eq. 1 (where AICc_{\min} is the best model in the model set).

$$\Delta\text{AICc} = \text{AICc}_i - \text{AICc}_{\min} \quad (1)$$

Model weight was estimated through the normalized Akaike weights, Eq. 2.

$$\frac{\exp(-0.5 \times \Delta\text{AICc})}{\sum_{r=1}^R \exp(-0.5 \times \Delta\text{AICc}_r)} \quad (2)$$

To separate good models from less supported models, the threshold $\Delta\text{AICc} \leq 2$ was used. Poisson error structure and log link function were used for all GLMs and GLMMs with the count variables as responses. Packages *lme4* (Bates *et al.* 2013), *nnet* (Venables & Ripley 2002) and *MuMIn* (Bartoń 2013), in the statistical environment R (R v.2.15.2; R Core Team 2012 and R v.3.3.2; The R Foundation for Statistical Computing), as well as Statistica 6.0, were used for analysis.

3. Results

During three decades of the study period, we captured 57 different breeding females with 42% of them being grey, 40% intermediate and 18% brown. Over the three decades, however, the proportion of grey-coloured females that entered the study population decreased, while intermediate breeding females increased and brown females fluctuated over time (Fig. 2). The proportion of the three plumage morphs was similar in the entering females in the first and second decades (i.e., 1985–2004) ($\chi^2_2 = 4.8$, $p < 0.09$), but significantly changed between the second and third decade (i.e., from 1995–2004 to 2005–2014) ($\chi^2_2 = 68.7$, $p < 0.0001$). During the first two decades, only 11% of 36 female specimens collected in Zoological Museum were of intermediate plumage colour, 47% of them being grey and 42% brown. The percentage of intermediate colour morph females found between 2005 and 2014 increased to 30% ($N = 33$), while the proportion of brown females remained similar (i.e., 40%) and grey decreased to 30%. These changes in the proportions of morphs were statistically significant ($\chi^2_2 = 21.8$, $p < 0.0001$).

Analysis of the survival of 57 marked female Tawny Owls revealed that the best model assumed constant survival, but different recapture probabilities between the colour morphs ($\phi(\cdot) p(\text{morph})$; Table 1). This model had 2 times more support than the next best (constant) model ($\phi(\cdot) p(\cdot)$) ($\Delta\text{QAICc} = 1.39$). Both models that included morph-dependent survival probability ($\phi(\text{morph}) p(\text{morph})$ and $\phi(\text{morph}) p(\cdot)$) were not supported by the data ($\Delta\text{QAICc} > 4$; evidence ratios > 8), indicating no difference in survival probability between the three colour morphs (Table 1). The recapture probability estimated after model averaging of the

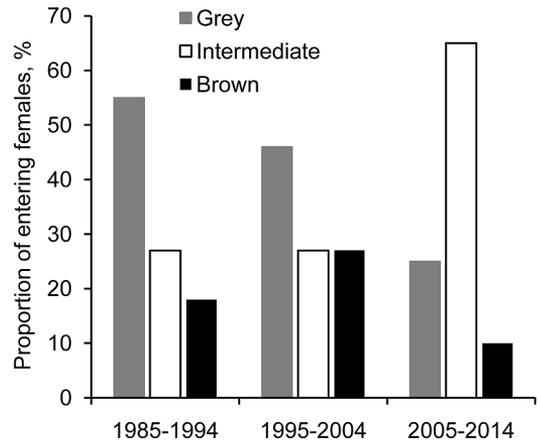


Fig. 2. Proportions of females belonging to each of the three colour morphs the first time they entered the study site in three decades: 1985–1994, 1995–2004 and 2005–2014. Sample sizes are 22, 15 and 20 females for each decade, respectively.

two supported models (i.e., $\Delta\text{QAICc} < 2$) was more than 1.6 times higher for the intermediate morph (0.46 ± 0.12 SE) compared to both grey and brown colour morphs (0.27 and 0.29 respectively; Fig. 3). The estimated survival probability of Tawny Owl females was 0.71 ± 0.05 SE.

The body size (LMM: $\chi^2_2 = 0.08$, $p = 0.96$) as well as body condition of the females (LMM: $\chi^2_2 = 0.58$, $p = 0.75$) did not differ between the colour morphs (the original measurements for body weight, wing and tail length are presented in Table 2). Similarly, timing of breeding, number of nesting attempts, mean egg volume, clutch and brood size were also independent of the female colour morph (see Table 2). On the other hand, total number of nestlings produced in all observed nesting attempts recorded during the entire study period was significantly different between the morphs

Table 1. Survival and recapture probability model selection, based on quasi-likelihood adjusted AICc (QAICc). ϕ – survival probability, p – recapture probability, (\cdot) – parameter is constant, (morph) – parameter varies over the three morphs (i.e., grey, intermediate and brown).

Model	QAICc	ΔQAICc	Weight	Model likelihood	Number of parameters	QDeviance
$\phi(\cdot) p(\text{morph})$	211.2	0.00	0.58	1.00	4	171.31
$\phi(\cdot) p(\cdot)$	212.5	1.39	0.29	0.50	2	177.04
$\phi(\text{morph}) p(\text{morph})$	215.4	4.25	0.07	0.12	6	171.01
$\phi(\text{morph}) p(\cdot)$	215.8	4.68	0.06	0.10	4	175.99

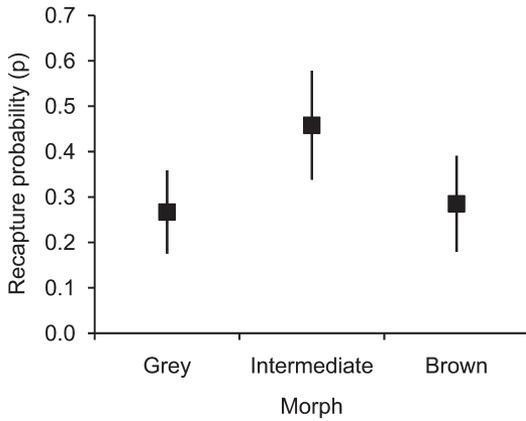


Fig. 3. Recapture probabilities (\pm SEs) for the three colour morphs, estimated through model averaging of the supported models (Δ QAICc < 2).

(Table 2, Fig. 4). According to estimates of the GLM, intermediate females raised 0.57 nestlings (\pm 0.14 SE, $p < 0.0001$) more than grey females and 0.43 nestlings (\pm 0.18 SE, $p = 0.014$) more than brown females.

The change in the mean winter temperature before the nesting season was not associated with the change in the log-odds of capturing different colour females (MLR: $\chi^2_1 = 0.1, p = 0.95$). Furthermore, the interaction between mean winter temperature and colour morph was not significant for Tawny Owl body condition (LMM: $\chi^2_2 = 2.24, p = 0.33$), timing of breeding (LMM: $\chi^2_2 = 2.13, p = 0.34$), clutch size (GLMM: $\chi^2_2 = 1.22, p = 0.54$) or mean egg volume (LMM: $\chi^2_2 = 4.33, p = 0.11$).

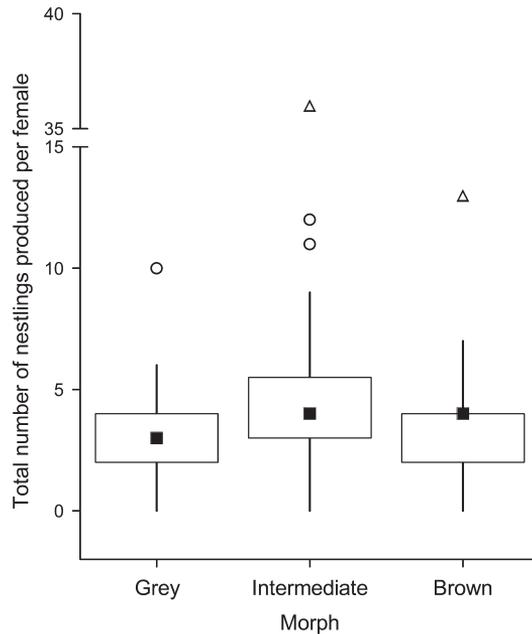


Fig. 4. The total number of nestlings raised by the females of brown, intermediate and grey colour morph. Filled squares represents medians, boxes represent inter-quartile ranges, lines represent non outlier range, hollow circles represent outliers and hollow triangles represent extremes.

Similarly, the interaction between spring temperature and plumage colouration was not significant in the model where brood size was included as a covariate (GLMM: $\chi^2_2 = 2.09, p = 0.35$). These results indicate that differently coloured females re-

Table 2. The mean, standard deviation and sample size (in brackets) of Tawny Owl female body measurements and reproductive variables. χ^2 and p represent results of the likelihood ratio tests between intercept models and corresponding models with the colour morph as the fixed variable. LMM – linear mixed, GLMM – generalized linear mixed and GLM – generalized linear model.

Variable	Colour morph			Model	χ^2	p
	Grey	Intermediate	Brown			
Wing length (mm)	293 \pm 6 (32)	294 \pm 6 (45)	293 \pm 9 (16)			
Tail length (mm)	197 \pm 9 (32)	195 \pm 10 (45)	198 \pm 11 (16)			
Weight (g)	593 \pm 50 (32)	598 \pm 48 (45)	596 \pm 38 (16)			
Start or breeding (Julian day)	86 \pm 9 (32)	82 \pm 12 (45)	83 \pm 12 (16)	LMM	0.6	0.73
Mean egg volume (cm ³)	37.1 \pm 2.1 (20)	39.1 \pm 2.9 (34)	38.5 \pm 1.9 (12)	LMM	3.6	0.17
Clutch size	3.7 \pm 0.9 (32)	3.8 \pm 0.9 (45)	3.5 \pm 1 (15)	GLMM	0.3	0.86
Brood size	2.4 \pm 1.5 (32)	3.1 \pm 1.3 (45)	2.6 \pm 1.5 (16)	GLMM	3.5	0.17
Nesting attempts per female	1.4 \pm 0.6 (23)	1.9 \pm 2.1 (24)	1.5 \pm 0.7 (11)	GLM	1.9	0.39
Number of nestlings produced per female	3.3 \pm 2.2 (23)	5.9 \pm 7.0 (24)	3.8 \pm 3.7 (11)	GLM	18.4	<0.0001

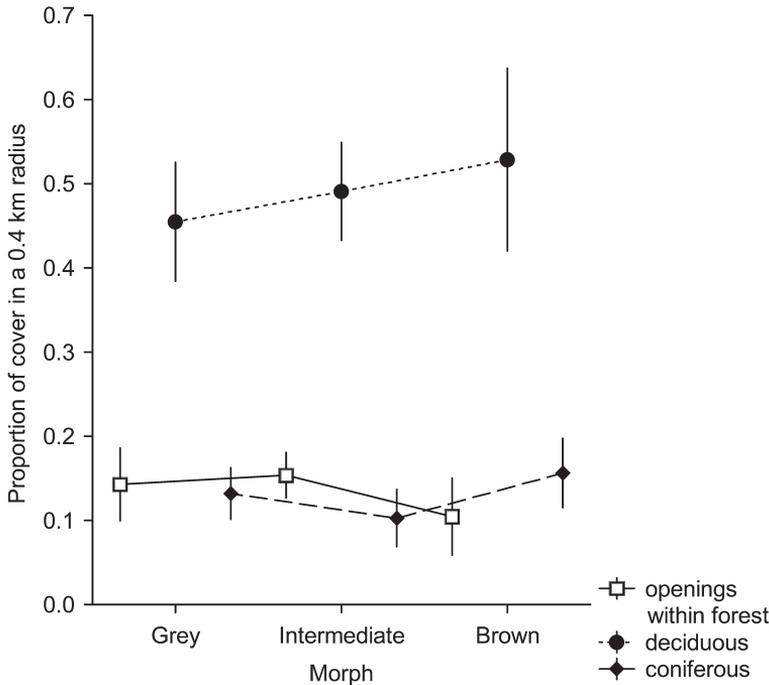


Fig. 5. Mean (\pm 95% CI) of the proportion of the openings within forest, deciduous forest and coniferous forest in a 0.4-km radius around occupied nest sites by grey, intermediate and brown colour morph females.

sponded similarly to the mean winter and spring temperatures during the reproductive season.

Habitat composition varied around nest sites occupied by females of the three colour morphs (Fig. 5). Although the intercept-only model received most support ($\Delta\text{AICc} = 0.00$), similar AICc weights of MLR models (i.e., 0.281–0.031) indicated model selection uncertainty (Table 3). The null model had only 1.2 times more support compared to the next best model ($\Delta\text{AICc} = 0.39$, weight = 0.23), which included the share of coniferous forests at the nest site surroundings as an explanatory variable. It suggested that an increase in the proportion of coniferous forest decrease the log-odds of occupation of a nest site by intermediate females compared to brown females (-5.45 ± 2.97 SE). An increase in the proportion of coniferous forest, however, did not influence the log-odds of occupation of a nest site by grey females compared to brown females (-2.31 ± 2.98 SE). The other supported model ($\Delta\text{AICc} = 1.25$), which included the proportion of forest openings as an explanatory variable, was 1.9 times less likely than the best null model. Results show that the increase in the proportion of forest openings tended to increase the log-odds of occupation of a nest site by intermediate females (5.53 ± 3.32 SE) and grey fe-

males (4.46 ± 3.45 SE) compared to brown females. The last supported model ($\Delta\text{AICc} = 1.39$, evidence ratio 2.0), with the proportion of coniferous forest and forest openings as explanatory variables, indicated similar relationships between habitat and morphs as described above. Other models were poorly supported by the data ($\Delta\text{AICc} > 2$; evidence ratios 3.8–9).

4. Discussion

The proportions of females belonging to the three colour morphs entering the study area changed during the 30-year study period, with intermediate individuals becoming more frequent since the mid-2000s. The three colour morphs of Tawny Owls were similar in body size and achieved similar body condition during breeding. We did not find any support that the influence of the winter and spring weather on the performance of the owls was colour morph dependent. Most of the analysed demographic parameters of the differently coloured females did not differ, but intermediate birds tended to be recaptured more frequently and produced a higher number of nestlings during all nesting attempts in comparison to grey as well as

Table 3. AICc, Δ AICc and weight of multinomial models for association between colour morph (response variable) and habitat variables (proportions of coniferous, deciduous forests and openings within forests in a 0.4-km radius around each nest site).

Model No.	Explanatory variables	AICc	Δ AICc	Weight
null		194.10	0.00	0.281
3	coniferous	194.50	0.39	0.231
1	openings within forest	195.30	1.25	0.151
5	openings within forest + coniferous	195.50	1.39	0.140
2	deciduous	196.80	2.69	0.073
4	coniferous + deciduous	197.20	3.14	0.058
6	deciduous + openings within forest	198.20	4.18	0.035
7	deciduous + coniferous + openings within forest	198.50	4.40	0.031

brown females. Although there were no clear habitat differences between morphs, we found some indication that brown females might occupy nest sites with more coniferous stands compared to intermediate, and less fragmented forest cover in surroundings compared to intermediate and grey morphs. In summary, we suggest that Tawny Owl females of intermediate colour morph reproduced better and this may be the key reason for the spread of this morph since the mid-2000s.

Proportions of females of each of the three colour morphs entering the study site were similar between 1985–1994 and 1995–2004, but changed significantly during the decade since 2005. The increase in the intermediate morph in both our study area and the museum skin collection suggests a recent spread of intermediate-coloured individuals at a wider spatial scale than our study site. The stability of colour morph ratios over time was repeatedly found in other studies on different raptor species (Brommer *et al.* 2005, Briggs *et al.* 2011a, Martínez *et al.* 2016), but a rapid spread of brown coloured breeding Tawny Owls has been observed since the 2000s in the population at the northern part of the distribution range (Karell *et al.* 2011b). Although the assignment of Tawny Owl individuals to the different morphs varies from study to study (e.g., Roulin *et al.* 2003, Karell *et al.* 2011b), it might be supposed that an increase of darker individuals in Tawny Owl populations is a recent, widespread process acting not only at higher latitudes.

An increase in darker coloured individuals in the population of a polymorphic species is likely to be an adaptation to global climatic warming as more intense plumage pigmentation may be an im-

portant trait of organism's resilience to this environmental stress (Roulin 2014). We did not find support that mean winter temperatures were associated with the nesting attempts of differently coloured females or differently affected their performance. Roulin *et al.* (2003) found that the number of breeding grey females in a population in western Switzerland was negatively related to the spring and summer temperatures, but was not related to the winter temperatures. The mortality of grey individuals was higher during warm years in Italy (Galeotti & Cesis 1996). At our study site, spring, summer and autumn temperatures significantly increased over the last three decades, but not the mean winter temperature (Grašytė *et al.* in prep.). Although Galeotti and Cesis (1996) suggested that the intermediate phenotype of the Tawny Owl was disadvantageous under all climate regimes, we speculate that the increase in the proportion of intermediate but not brown females observed at our study site might be a consequence of the seasonally contrasting local climate trends (see above) favouring the intermediate but not pure phenotypes.

What performance component may explain the increase of intermediate-coloured individuals? First, females assigned to the three morphs were similar in size and, at least those birds that bred, achieved similar body condition. Roulin *et al.* (2003) suggested that grey females skip reproduction in poor years, hence we cannot reject the hypothesis that females of the three colour morphs achieve different body condition under varying food supply. However, Roulin *et al.* (2003) did not find differences in wing length and body mass, just as Galeotti and Sacchi (2003) did not find differ-

ences in body condition and morphology of differently coloured Tawny Owls. Roulin *et al.* (2003) and Brommer *et al.* (2005) found random mating with respect to plumage colouration in Tawny Owl. Hence, body size is not likely to influence competition among differently coloured females and thus facilitate the recent spread of intermediate females.

Second, although based on a limited sample size, our results support no differences in survival among the owls of three morphs at our study site. Emaresi *et al.* (2014) found that dark coloured individuals of Tawny Owl survived better compared to light coloured individuals in western Switzerland. Karell *et al.* (2011b) found, however, that the survival of brown Tawny Owls was lower than that of grey females in the Finnish population, likely due to poorer plumage insulation (Koskenpato *et al.* 2016), but had improved in recent years as a consequence of decreased winter severity. Taking into consideration that the mean winter temperature has not increased over the 30-year study period and that the survival of females belonging to the three colour morphs was similar, viability is not likely to be the reason for the observed changes in morph composition at our study site.

Third, although we have found that most reproductive variables were independent of morphs, the sum of all the offspring produced during all the nesting attempts of established individuals was higher and the recapture probability (which may be approximated to the breeding frequency; Hakkarainen *et al.* 2002) tended to be higher for intermediate birds compared to other colour morphs. Brommer *et al.* (2005) found similar recapture probabilities and similar brood sizes per nesting attempt for brown and grey Tawny Owls, but they differed significantly over the lifespan of the individual owls, resulting in higher number of offspring in grey females. Tawny Owl plumage colouration was not associated with hatching date, brood size or total number of offspring produced per female in Switzerland, but greyer females produced heavier nestlings (Roulin *et al.* 2003). In other species, lifetime reproductive success was highest for intermediate individuals in Common Buzzard, but similar between light and dark females (Boerner & Krüger 2009). Briggs *et al.* (2011a) did not find significant fitness differences

among individuals of three colour morphs in Swainson's Hawk. Likewise, brood size was independent of colour morph in Booted Eagle (Martínez *et al.* 2016). Across bird species the sign and magnitude of the relationship between plumage colouration and fitness is species dependent (Meunier *et al.* 2011). In parallel, within species, or at least in Tawny Owl, associations of fitness components and plumage colouration are likely dependent on environmental conditions and lack spatially and/or temporally consistent pattern at a range scale. Furthermore, as plumage colouration in Tawny Owl is a highly heritable trait (Karell *et al.* 2011b) and individual reproduction has been found to positively correlate with subsequent recruitment (Wiens & Reynolds 2005, Briggs *et al.* 2011b), fecundity but not the viability component is likely to be responsible for the increase in the intermediate morph in the Lithuanian population.

We failed to show straightforward morph dependent habitat occupation pattern. Brown females, however, might occupy nest sites with greater forest cover in the surroundings. It is usually considered that darker individuals benefit from close/dark habitats, while light individuals – from open/bright habitats due to crypsis to predators, prey, conspecifics and heterospecifics under varying light conditions (Galeotti *et al.* 2003). Roulin *et al.* (2003) did not find different distributions of morphs in respect to altitude in a local population. In a study of Tawny Owls in urban parks, Galeotti and Sacchi (2003) found darker rufous owls in more wooded habitat compared to grey owls.

Our findings tended to resemble this general colour morph – environmental gradient pattern because: a) the brown morph females were found breeding in nest sites with more abundant coniferous stands, but with fewer forest openings compared to nest sites occupied by intermediate females; and b) the openings within a forest around nest sites occupied by brown females tended to be less abundant compared to the nest sites of grey females. Moreover, coniferous forest may be more important for brown females for crypsis during the leaf-less months within the deciduous dominant forest, because females stay within breeding territories year-round (Sunde & Bølstad 2004, S. Rumbutis unpubl. data from study site). Of note, the size of the study site and its habitat heterogene-

ity may be too small to reflect morph preferences for specific habitat types. Amar *et al.* (2014) found an approximately 5% decrease of dark morph birds for every 100 km along a cline in Black Sparrowhawk (*Accipiter melanoleucus*). In the relatively homogenous habitat, exposure to light may be rather uniform in contrast to a large-scale latitudinal gradient, which favours dark or light coloured birds under different light conditions (Galeotti *et al.* 2003).

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Väriykseltään välimuotoisten lehtopöllöjen parempi pesimämenestys selittää niiden kasvavaa osuutta väripolymorfisessa populaatioissa

Ympäristökijät voivat vaikuttaa höyhenpeitteen melaniiniväriykseltään erilaisten yksilöiden kel-poisuuteen eri tavalla. Lehtopöllö (*Strix aluco*) on tunnettu väripolymorfioistaan. Keräsimme yksilöllistä aineistoa lehtopöllön pesinnästä vuosina 1985–2014 ja tutkimme, eroavatko harmaat, ruskeat ja väriykseltään välimuotoiset pöllönaaraat koon, kunnan, pesimäparametrien tai pesäpaikko-ja ympäröivän habitaatin suhteen.

Tutkimusjakson aikana populaation naaraiden värimuotojen jakauma muuttui: välimuotoiset värimuodot tulivat yleisemmäksi viimeisenä vuosikymmenenä. Eriväriset naaraat olivat samankokoisia ja -kuntoisia. Suurimmassa osassa analysoituista pesimäparametreista ei löytynyt eroa eriväristen naaraiden välillä. Värikseltään välimuotoiset naaraat kuitenkin kasvattivat elinaikanaan eniten lentopoikasia, ja niillä oli suurempi uudeleupesinnän todennäköisyys. Värimuotojen ja habitaattien välillä ei löydetty yhteyttä.

Yhteenvedon voidaan todeta, että väriykseltään välimuotoisten lehtopöllönaaraiden lisääntyminen populaatioissa liittyy todennäköisesti niiden parempaan lisääntymismenestykseen.

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