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NATURE RESEARCH CENTRE

GINTARĖ GRAŠYTĖ

TIMING OF BREEDING, DYNAMICS OF INDIVIDUAL AND POPULATION PARAMETERS, THEIR LONG-TERM CHANGES AND RELATIONSHIPS WITH HABITAT AND CLIMATE CHANGE IN TAWNY OWL *STRIX ALUCO*

Summary of doctoral dissertation
Biomedical sciences, ecology and environmental science (03 B)

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Scientific supervisor – Dr Rimgaudas Treinys (Nature Research Centre, biomedical sciences, ecology and environmental science – 03B).

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Chairman – Dr habil Mečislovas Žalakevičius (Nature Research Centre, biomedical sciences, ecology and environmental science – 03 B).

Members:
Prof. Dr Gediminas Brazaitis (Aleksandras Stulginskis University, biomedical sciences, ecology and environmental science – 03 B);
Prof. Dr Virginijus Sruoga (Lithuanian University of Educational Sciences, biomedical sciences, zoology – 05 B);
Dr Rimvydas Juškaitis (Nature Research Centre, biomedical sciences, ecology and environmental science – 03 B);
Dr Ramūnas Žydelis (DHI, Biomedical Sciences, ecology and environmental science – 03 B).

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Address: Akademijos Str. 2, LT–08412 Vilnius, Lithuania.

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GINTARĖ GRAŠYTĖ

NAMINĖS PELĖDOS *STRIX ALUCO* PERĖJIMO PRADŽIOS, INDIVIDO IR POPULIACIJOS DINAMIKOS RODIKLIAI, JŲ ILGALAIKĖ KAITA IR SAITAI SU BUVEINIŲ IR KLIMATO POKYČIAIS

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Disertacija ginama Ekologijos ir aplinkotyros mokslo krypties taryboje:

Pirmininkas – habil. dr. Mečislovas Žalakevičius (Gamtos tyrimų centras, biomedicinos mokslai, ekologija ir aplinkotyra – 03B).

Nariai:
Prof. dr. Gediminas Brazaitis (Aleksandro Stulginskio universitetas, biomedicinos mokslai, ekologija ir aplinkotyra – 03B);
Prof. dr. Virginijus Sruoga (Lietuvos edukologijos universitetas, biomedicinos mokslai, zoologija – 05B);
Dr. Rimvydas Juškaitis (Gamtos tyrimų centras, biomedicinos mokslai, ekologija ir aplinkotyra – 03B);
Dr. Ramūnas Žydelis (DHI, Danija, biomedicinos mokslai, ekologija ir aplinkotyra – 03B).

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INTRODUCTION

Relevance of the study. The environment is dynamic, with extremely rapid changes, related to intensive human impact on natural habitats and climate change recorded in recent decades (Newton 2013; Žalakevičius 2013; IPCC, 2014). Birds respond to the environmental changes in different ways, depending on pattern of changes, their intensity, as well as life-history of particular species (Newton 2013). Environmental changes may act upon birds at individual and population level and affect several parameters simultaneously.

Avian predators may be used as important, easy to track indicators to elucidate long-term changes in the environment due to their position in food chains (Helander *et al*. 2008; Lõhmus 2011). Multidirectional trends in raptor populations, their key vital rates could be expected in response to environmental changes (Carrete *et al*. 2006; Krüger *et al*. 2012), as, for example, improved breeding performance (Helander & Bignert 2013) and survival (Karell *et al*. 2011). Moreover, morphological changes of nesting individuals also may be observed (Yom-Tov & Yom-Tov 2006). Recent review of raptor monitoring in Europe revealed, however, that data on population dynamics of common diurnal raptor birds and various owl species are lacking (Vrezec *et al*. 2012). The lack of knowledge about climate change impact on predatory and sedentary bird species is also highlighted recently (Møller *et al.* 2004). As environment and(or) population parameters change, this may drive the change in bird – habitat relationship as well (Bai *et al*. 2009; Vaitkuvienė 2014). Impact of environmental changes on species of long-lived birds is best revealed through long-term studies (Newton 2013), which simultaneously test morphological individual parameters, and population dynamics features. Long-term Tawny Owl (*Strix aluco*) research provides an opportunity to evaluate the individual, as well as population level parameters dynamic, and their interactions and variations, with changing habitats and climate. It contributes to the scientific knowledge about sedentary raptor birds

and their relationships with environmental factors that are relevant in understanding species response to rapidly changing environmental conditions.

Study objective and tasks. To determine the size, body condition, colour morph, start of breeding, reproduction and survival parameters dynamics of Tawny Owl, their interrelationships with habitats and local climatic conditions. The following tasks were set to achieve this objective:

1. To determine Tawny Owl's start of breeding, reproduction, survival probability and long-term dynamics of these parameters.

2. To analyse long-term dynamics of individual's body size and condition, and its importance on Tawny Owl's reproduction.

3. To ascertain Tawny Owl's habitat selection, and its importance to reproduction.

4. To analyse the effect of climate conditions in autumn-spring seasons on the body condition and reproduction of individuals.

5. To determine Tawny Owl's colour morph frequency and its changes.

6. To analyse whether different colour morph individuals differ in body size and condition, in survival and reproduction, as well as habitat selection and response to local weather factors.

Defended statements:

1. According to population dynamics parameters Tawny Owls in Dotnuva forest are similar to the northern populations of this species.

2. Tawny Owl body condition rather than body size is an important individual fitness trait.

3. Tawny Owl habitat preferences are adaptive.

4. Tawny Owl's body condition during breeding season is related with the amount of precipitation during preceding autumn.

5. Different colour morph Tawny Owls do not differ in size and achieve similar body condition.

6. Intermediate colour morph Tawny Owl individuals are superior to grey and brown colour morph individuals in the research area.

Novelty of the study. It was found, that there are significant body size changes in the breeding Tawny Owl individuals during long-term living in the same area. Quantitatively analysed habitat selection and its relationship with reproduction revealed habitat selection adaptivity. The influence of autumn precipitation on Tawny Owl start of breeding and body condition of females during breeding season was supported. Frequency change of different Tawny Owl colour morphs was identified in temperate latitudes for the first time.

Scientific and practical significance. This work provides knowledge about changes in long-term population dynamics parameters and morphological features, their relations, as well as habitat and climate influence on highest trophic level sedentary bird species. This work established that long-term environmental changes affect populations of common, non-threatened species, and that species respond to these changes by population dynamics, morphology and behavioural traits. In the future, these changes can lead to changes in species abundance as well. Study results suggest that climatic conditions several months before reproduction affect individuals' body condition during the breeding season. Therefore, climate change can affect Tawny Owl's fitness in different manner.

Approbation of results and publications. Based on the results of this work 3 scientific articles were prepared; 2 of them were published in peer-reviewed scientific journals. On the basis of this doctoral dissertation 6 reports were presented in Lithuanian and international conferences: Lithuanian Academy of Science conference for young scientists "Biofuture: natural and life sciences perspectives" (Lithuania, 2014), 10th National Scientific

Conference "Biodiversity in Lithuania: status, structure, protection" (Lithuania, 2015), 11th international life and natural sciences conference "The Coins'16" (Lithuania, 2016), 4th international symposium "Research and Protection of Birds of Prey & Black Stork in the Baltic region (Latvia, 2016). The dissertation was four times presented and approved at annual reporting seminars at the Nature Research Centre (Vilnius, Lithuania, 2013, 2014, 2015, 2016).

Scope and structure of dissertation. The dissertation consists of the following chapters: *Introduction, Literature Review, Materials and Methods, Results* (the chapter consists of 4 subsections), *Discussion, Conclusions, References, List of the Author's Publications, Annexes* (9). The list of references includes 247 sources. The dissertation is presented in 155 pages. The text contains 28 figures and 17 tables. The dissertation is in Lithuanian with a summary in English.

LITERATURE REVIEW

This part of the dissertation discusses the ecological group of birds of prey and presents its study object – Tawny Owl (*Strix aluco*). An overview is given about bird population dynamics, reproduction, phenology, habitat selection, and climate impact on birds. Also bird individual trait geographic variation and colour polymorphism is discussed. The chapter *Literature Review* consists of five subsections.

MATERIALS AND METHODS

Field data collection. Data were collected in 1978–2014 in Kėdainiai district, Central Lithuania (55° 23' 27" N, 23° 46' 25" E). In 1977, S. Rumbutis erected nest boxes and checked them annually from 1978 onwards. The number of nest boxes available for owls varied over the study period (mean 41, range 30–55, n = 37) due to both forest logging and the need of replacing old nest boxes with new ones. All available nest boxes were checked for occupancy in February–March, depending on spring weather conditions, with the timing based on the established Tawny Owl nesting phenology relationship with weather conditions (Southern 1970). A nest box was considered occupied if a clutch was found. Occupied nest boxes were again checked from March till May for breeding output, number of offspring, prey items and/or prey remains. Females attending their offspring were captured using hand nets and ringed at first capture. 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 their feathers, intermediate – both brown and grey colours were present in the plumage; brown – only brown feathers were present. The length of the wing and tail was measured, also the owls were weighed with a spring balance to the nearest five grams.

Start of breeding, demography parameters, body size and condition estimation. The date of the start of breeding was estimated using one of the two methods, either accounting for a) the age of nestlings; or b) egg laying intervals (every second day) in cases where 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 was then determined by backdating calculations, accounting for the incubation duration (30 days; Southern 1970). For further analysis, the start of breeding was expressed in Julian days (wherein 1st of January is day 1), also accounting for leap years. The length and maximum breadth of the eggs in full clutches was measured using a sliding calliper to the nearest 0.1 mm. Egg volume was calculated as $\pi \times$ egg length $\times$ breadth^2/6000 (Tatum's index; Hakkarainen & Korpimäki 1993). Brood size was measured as the number of nestlings of at least two weeks of age.

Wing and tail lengths showed a statistically significant positive correlation, and thus, scores of the first principal component as an index for individual body size was used. Larger scores indicated larger individuals. To estimate body condition, the generalized linear model (GLM) was used where female weight was related with body size and the day of capture (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. For further analysis, standardized residuals of the above-mentioned GLM were used as an estimate for individual body condition in relation to body size and standardized to a common day of capture after the start of breeding.

Tawny Owl body size and body condition importance to the start of breeding and reproduction was analysed using linear mixed model (LMM) and generalized linear mixed model (GLMM). The start of breeding, reproduction, individual body size and body condition changes in the study area in 1978–2014 were estimated using the generalized additive model (GAM).

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. Recapture probability in owls' studies is considered a breeding probability or breeding frequency (Saurola, Francis 2004). Data from ringed females captured since 1980 was used (n = 61 unique females). In the analysis it was assumed that the probability of survival and the breeding frequency shift during the study period remained stable (denoted φ (.) and p (.)) or was characterized as a trend. In our case, $\hat{c}$ 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).

Habitat selection analysis. Spatial data on occupied nest boxes throughout the study period were analysed in GIS environment (*ArcGIS 10.0* software). A habitat layer was created following the standard CORINE Land Cover methodology (Heymann *et al.* 1994; Bossard *et al.* 2000; European Environment Agency 2007) based on photo-interpretation of orthophotographs at a scale 1:10000 for non-forested land, while State Forest Cadastre data, derived from stand-wise inventories, was used for forested land. Data sources for years 2000 and 2010 were used to represent the mid-periods of the two decades of the study, i.e. 1995–2004 and 2005–2014. Buffers with a radius of 0.4 km were created around the occupied nest boxes to describe habitats within the most important part of the Tawny Owl home-range (ca. 50 ha; Sunde & Bølstad 2004). Proportions of 1) intensively cultivated fields (mainly for crop growing); 2) extensive fields (pastures, grasslands), 3) openings within forests (recently (i.e. < 10 years) felled areas, small forest meadows, etc.), 4) young forest and 5) mature forest were calculated in each buffer. Young and mature

forest was classified according to the age of stands, considering the dominant tree species by volume proportion. Forest was considered young if a) dominant oak, maple, lime and ash stands were up to 60 years old; b) dominant birch, black and grey alder, aspen stands were up to 40 years old; and c) dominant coniferous (mainly spruce) stands were up to 50 years old. Older stands of the corresponding dominant tree species were considered as mature forest. Proportion of intensive fields and mature forests strongly correlated ($r = -0.5$), thus these two variables were considered redundant and for further analysis only the proportion of mature forest was retained as a more relevant one for the ecology of the study species (see Treinys $et\ al.$ 2011 and references therein).

To evaluate whether habitat composition around nest boxes was important for occupancy, data from 724 nest box checks was used and the proportions of the above mentioned habitat variables around occupied and unoccupied nest boxes was assessed through GLMM. To estimate habitat composition effect under different resource availability conditions, occupied nest boxes during good years (68 cases of occupation) and poor years (20 cases of occupation) were compared. The median number of nesting pairs during the period 1995–2014 was used as a threshold value for classifying years as good ($\geq$ 5 nesting pairs; 11 years) or poor (< 5 nesting pairs; 9 years). To assess the effect of habitat composition on the breeding success (88 cases established) GLMMs were used.

GLM was used to analyse temporal changes in the habitat composition around the nest boxes in 1995–2004 and 2005–2014. First, habitats around available nest boxes in different periods (sample size was 65 and 66 unique nest boxes for each period, respectively) were compared. Second, habitats around occupied nest boxes were compared (sample size was 31 and 24 occupied nest boxes for each period, respectively).

During nest box visits from 1978 to 2014, all discovered prey items (n = 623) were assigned to 5 prey groups ($Microtus$ voles, bank vole, murids, thrush and other birds). GLMs were applied to analyse long-term changes in the detection probability of each prey group.

Climate conditions' analysis. From 1984 till 2014, autumn (September to November), winter (December to February), and spring (March to April) average temperatures and precipitation changes were analysed using GAM. We tried to ascertain if weather parameters before the owl breeding period affect the body size and body condition of nesting owls. LMMs were used for this analysis. Weather condition's impact on start of breeding, clutch and brood size were analysed using LMM and GLMM.

Colour polymorphism 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 (χ^2) test. Each individual was assigned 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.

LMMs were used for analysis of continuous response variables (body size, body condition, start of breeding, mean egg volume) and morph associations, while GLMs – for total number of offspring per female dependence on morph associations, and GLMMs for clutch size and brood size dependence on morph associations. Survival and breeding frequency of different colour morph owl's was analysed using MARK program.

Habitats around the nest sites occupied by females of the three morphs were analysed through a multinomial logistic regression (MLR). The proportions were measured for 1) fields (intensively cultivated fields, pastures, grasslands), 2) openings within forests, 3) deciduous forest (birch, aspen, black alder, grey alder, oak, ash, lime or maple dominating in the stands by volume proportion), 4) coniferous forest (spruce or pine dominating in the stands by volume proportion). Only the proportions of fields and deciduous forest were strongly related ($r > 0.6$), hence for further analysis, all of the above-mentioned habitat variables were included, except the proportion of fields. 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.

The mean winter temperature before the nesting attempts of the different colour morph females was analysed through MLR. Brown colour morph was used as a reference group. To estimate the significance of interaction between colour morph and mean winter or spring temperature to response variables (i.e., body condition, start of breeding, clutch size, mean egg volume in the clutch and brood size), models with an additive effect of these explanatory variables (i.e., morph + winter T; morph + spring T) were compared with the models, where the same explanatory variables were included through interaction term (i.e., morph × winter T; morph × spring T) using LMMs and GLMMs.

Statistical analysis. Variable significance in models was determined using the likelihood ratio test or according to the model parameters. Akaike information criterion corrected for small samples (AICc) (Burnham, Anderson 2002) was used for the selection of the supported models. To separate good models from less supported models, the threshold of ΔAICc ≤ 2 was used. Models were arranged according to formula ΔAICc = AICc$_i$–AICc$_{min}$ (where AICc$_{min}$ is the best model in the set). Model weight was calculated using formula $\dfrac{\exp(-0.5 \times \Delta AICc)}{\sum_{r=1}^{R} \exp(-0.5 \times \Delta AICc_r)}$. In case of model uncertainty, relative importance of variables (RIV) was calculated from the supported set of models.

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.

RESULTS

Start of breeding, demography, body size and condition. During the 37-year period in the study area, 0 to 10 (mean 5.0) pairs of Tawny Owls nested annually. During the research years Tawny Owls started breeding on average on the 83.5±11.6 SD Julian day, i.e. March 24th on non-leap years (n = 150). The mean clutch size was 3.9 ± 0.9 SD (n = 153). The average Tawny Owl's egg volume was 38.1 ml ± 2.3 SD (n = 126 clutches). 68 % of established nesting attempts of Tawny Owl were successful (n = 184). Average brood size was 3.1 ± 1,1 SD, nestlings (n = 125). The average breeding Tawny Owl female wing length in the research area was 293.7 mm ± 6.4 (SD), tail length – 196.5 mm ± 9.7 (SD) (n = 93). Average weight of the females (n = 93) was 596.0 g ± 46.8 (SD).

In the period from 1978 to 2014, the Tawny Owl tended to start breeding earlier (GAM: F = 3.55, p = 0.06). Breeding Tawny Owl pair number was not constant and varied statistically significantly during the research period (GAM: χ^2 = 13,07, p = 0,04) (Fig. 1), also the breeding success (GAM: χ^2 = 9.1, p = 0.02) (Fig. 2). The clutch size (GAM: χ^2 = 0.16, p = 0.7), average egg volume (GAM: F = 0.35, p = 0.57), and brood size (GAM: χ^2 = 1.74, p = 0.19) did not change.
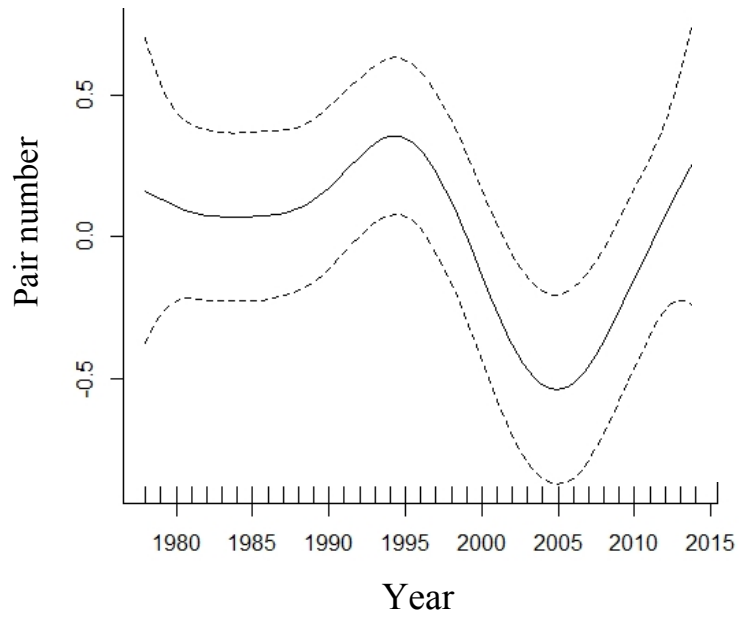
Fig. 1. Tawny Owl breeding pair number from 1978 to 2014. The dotted line represents 95% confidence intervals.
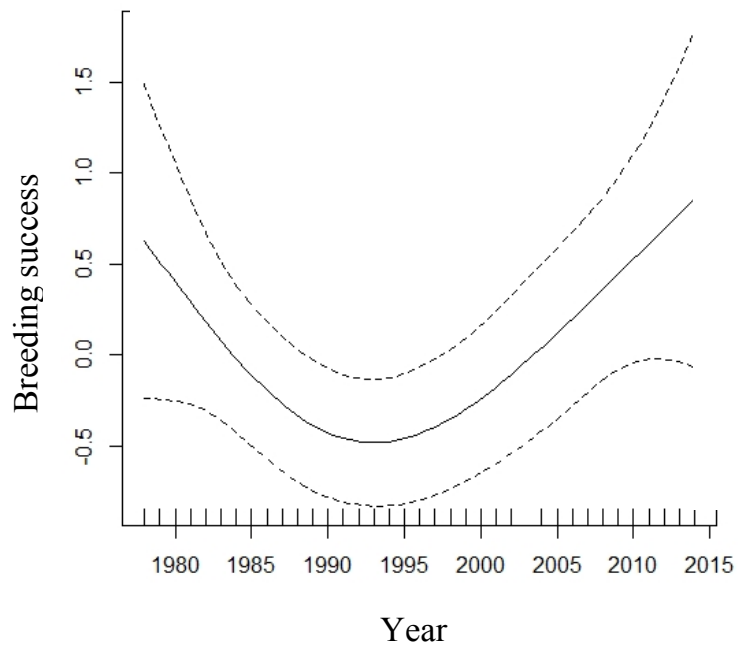

Fig. 2. Tawny Owl breeding success change from 1978 to 2014. The dotted line represents 95% confidence intervals.

Statistically significant changes of the nesting females body size were evident from 1985 to 2014 (GAM: F = 8.5, $p < 0.001$) (Fig. 3). Breeding Tawny Owl female body condition did not change during the same period (GAM: F = 0.5, $p = 0.65$).
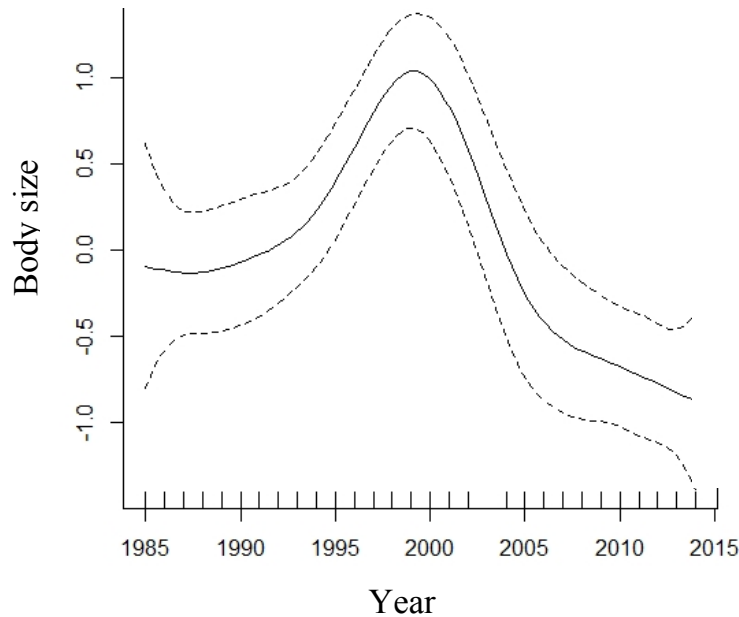

Fig 3. Breeding Tawny Owl female body size changes in the research area in 1985–2014. The dotted line represents 95% confidence intervals.

Better body condition females in the research area started breeding earlier (LMM: $\chi^2 = 5.21$, $p = 0.02$) and raised larger broods (GLMM: $\chi^2 = 4.49$, $p = 0,03$). Body condition tended to explain clutch size (GLMM: $\chi^2 = 2.85$, $p = 0.09$) as well as mean volume of eggs in the clutch (LMM: $\chi^2 = 3.23$, $p = 0.07$). Female body size did not explain the variations in start of breeding, clutch size, average egg volume or brood size (all $p \geq 0.70$).

Analysis of survival of 61 marked Tawny Owl females revealed that the best-supported model was constant model (i.e. $\varphi(.)\, p(.)$), where neither survival nor recapture probabilities varied over the study period (Table 1). Survival and recapture probabilities estimated in this best supported model are 0.70 ± 0.04 SE and 0.32 ± 0.06 SE, respectively. The second data best-supported model shows tendency of increase in breeding frequency during the research period.

Table 1. Models describing Tawny Owl's survival and breeding frequency in the research area in 1980–2013.

Model	ΔQAICc	Model weight
φ (.) p (.)	0,00	0,49
φ (.) p (Tr)	1,46	0,23
φ (Tr) p (.)	2,05	0,17
φ (Tr) p (Tr)	3,02	0,11

Habitat selection. The subset of best models, explaining the effect of habitat variables in a 0.4 km radius on the occupancy probability of nest boxes, included three models. Most supported (model weight = 0.5) was the model which included all four habitat variables. Based on the evidence ratio, this model was ca. 2 times more likely than the other two models with fewer habitat variables. Similar model weights, however, indicate model selection uncertainty. Occupancy probability increased with the increase in the proportions of extensive fields, openings within forest and mature forest stands, and with the decrease in young forest stands in the surroundings of the nest boxes. Moreover, proportions of two hunting habitats – extensive fields and openings within forests, were more influential (both RIV = 1.00) than mature (RIV = 0.77) and young (RIV = 0.73) forest stands.

The analysis of habitat composition and probability that a nest box will be occupied by owls during good but not during poor years resulted in four supported models. Models weights (0.4–0.15) indicated model selection uncertainty. Moreover, the intercept-only model received most support, while the three remaining models had 1.5–2.6 times lower support compared to the best model. Low support for habitat composition importance for the occupation probability of nest boxes during poor and good years emerged.

The probability of successful nesting proved to be associated with habitat composition around the occupied nest boxes. Two models were supported by

the data. The first model received strong support (model weight = 0.73) and included two fixed effects – the proportions of openings within forest and young forest stands. The next model had only one fixed effect – the proportion of openings within forest. The probability of successful nesting of Tawny Owl increased with more openings within forest and fewer young forest stands.

Five models were supported by the data when analysing the differences in habitat composition around available nest boxes between two decades. Again, similarity in model weights indicated high model selection uncertainty. The best (intercept-only) model had 2–2.7 times more support compared to the remaining models in the subset. Together with low RIV values this indicates only marginal changes in the availability of analysed habitats between 1995–2004 and 2005–2014.

Analysis of changes in habitat composition around nest boxes occupied by the Tawny Owl between 1995–2004 and 2005–2014 resulted in two models supported by the data. The best model (weight = 0.69) included only the proportion of openings within forest as a fixed effect. It was 2.2 times more supported than the next best model in the set (ΔAICc = 1.6, weight = 0.31), which included proportions of openings within forest and mature forest stands as fixed effects. According to RIV values, the proportion of openings within forest is ca. 3 times more important than the proportion of mature forest stands in differentiating occupied nest boxes during the two decades. Openings within forest in a 0.4 km radius around occupied nest boxes increased during the last decade.

Prey items, found during nest box checks in 1978–2014, were analysed. *Microtus* voles, detected during brood rearing period, decreased in 1978–2014 (GLM: $z = -5.0$, $p < 0.001$), thrush detection increased (GLM: $z = -3.74$, $p < 0.001$) together with other birds (GLM: $z = 3.96$, $p < 0.001$). Bank vole detection in the nest boxes did not change during the time of the study (GLM: $z = 0.2$, $p = 0.84$), and neither did murids (GLM: $z = 0.58$, $p = 0.57$).

Influence of climate conditions. The average autumn temperature has significantly increased during the research period (GAM F = 5.8, *p* = 0.01), the average winter temperature fluctuated significantly (GAM F = 3.3, *p* = 0.01) with coldest winters in the begining of the study, while spring temperature did not change (GAM F = 1.6, *p* = 0.2). Precipitation remained similar during all seasons through three decades (autumn, GAM F = 0.47, *p* = 0.5; winter, GAM F = 0.4, *p* = 0.53; spring GAM F = 2.3, *p* = 0.14).

A set of 4 models was derived after the analysis of Tawny Owl breeding start dependency on climate parameters (taking into account the individual body size). The strongest identified model comprised of two variables – precipitation in autumn and average temperature in winter (model weight – 0.41). This model was 1.8 times more supported than the second model, which included only one of the variables – average winter temperature. The remaining two models were 2.2–2.6 times less supported than the strongest model. Taking into consideration RIV values, it was found that Tawny Owls started breeding earlier when winter average temperature was higher (RIV – 1.00), and when previous autumn precipitation was lower (RIV – 0.77).

When analysing the influence of weather parameters on Tawny Owl's clutch size, 2 models were obtained. The strongest was a model with a single variable – autumn precipitation level (model ΔAICc = 0.00, weight 0.62). This model was 1.6 times more supported than the second intercept-only model (ΔAICc = 0.98, weight 0.38). The results show that Tawny Owl clutch size tends to be higher when previous autumn precipitation is lower.

The analysis of Tawny Owl brood size dependence on the spring temperature and precipitation (with regard to the female body condition), showed that these climate parameters do not explain the number of owlets in brood. Models with climate variables were less supported (ΔAICc > 2), compared to the model, where the independent variable was the female body condition (ΔAICc = 0.00, weight 1.00; Tawny Owl's brood size was higher when female body condition during the breeding period was better).

A set of 3 models was obtained for the analysis of breeding owl body size dependence on the previous seasons' weather conditions. The strongest was the intercept-only model (model weight 0.53). This model was more than twice better, supported than the other two models. These models had a single variable, either winter precipitation level, or average autumn temperature. The RIV values of these variables were low. Furthermore, the analytical results show that neither the autumn and winter temperature, nor precipitation levels explain the size of the females breeding in the research area.

The analysis of Tawny Owl's body condition during the breeding season dependence on climate parameters (taking into account the body size) revealed a set of 5 models. The strongest was a model with a single variable – autumn precipitation level (model weight 0.31). Similarly supported was the second model (weight 0.30) with two variables – autumn precipitation and average winter temperature. The remaining three models were 2.4 times less supported than the strongest model. The results show that the Tawny Owl female body condition is best explained by autumn precipitation, e.g. breeding owls tend to be in better condition when previous autumn precipitation is lower.

Colour polymorphism. During three decades of the study 57 different breeding females were captured, 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. 4). 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) ($\chi^2_2 = 68.7$, $p < 0.0001$).
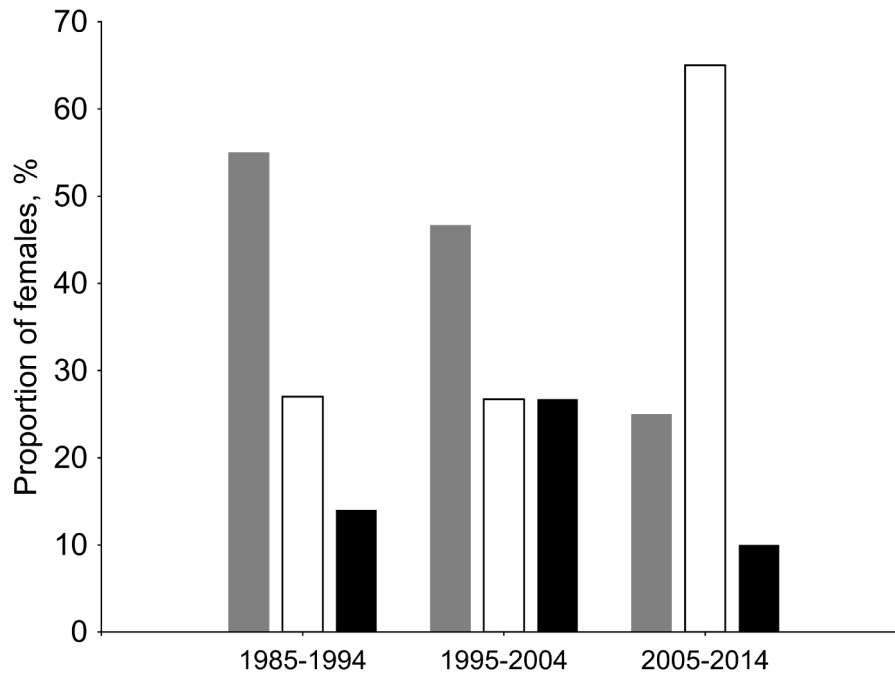
Fig 4. Tawny Owl female morph frequency during three decades of research (1985–1994 n = 22, 1995–2004 n = 15, 2005–2014 n = 20). Brown morph is represented in black, intermediate – in white, and grey – in grey.

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. Similarly, start of breeding (LMM: $\chi^2 = 0,62$, $p = 0,73$), mean egg volume (LMM: $\chi^2 = 3,59$, $p = 0,17$), clutch (GLMM: $\chi^2_2 = 0,29$, $p = 0,86$) and brood size (GLMM: $\chi^2 = 3,52$, $p = 0,17$) were also independent of the female colour morph. 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 (GLM: $\chi^2 = 18,4$, $p < 0,0001$); intermediate colour morph females raised more offspring than other morphs.

Analysis of the survival of 57 marked female Tawny Owls revealed that the best model premised constant survival but different recapture probabilities between the colour morphs (φ (.) p (morph)). This model had 2 times more support than the next best (constant) model (φ(.)p(.)) (ΔQAICc = 1.39). Both models that included morph-dependent survival probability (φ (morph) p (morph) and φ (morph) p (.)) were not supported by the data (ΔQAICc > 4; evidence ratios > 8), indicating no difference in survival probability between the three

colour morphs. The recapture probability estimated after model averaging of the two supported models (i.e. ΔQAICc < 2) was more than 1.6 time higher for the intermediate morph (0.46 ± 0.12 SE) compared to both grey and brown colour morphs (0.27 and 0.29 respectively).

Habitat composition varied around nest sites occupied by females of the three colour morphs. Although the intercept-only model received most support (ΔAICc = 0.00), similar AICc weights of MLR models (i.e., 0.281–0.031) indicated model selection uncertainty. The null model had only 1.2 times more support compared to the next best model (ΔAICc = 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 decreased the log-odds of occupation of a nest site by intermediate females compared to brown females (–5.45 ± 2.97 SE, $p = 0.096$). 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, $p = 0.2$). The other supported model (ΔAICc = 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 compared to brown females (5.53 ± 3.32 SE, $p = 0.07$), but not grey females compared to brown females (4.46 ± 3.45 SE, $p = 0.44$). The last supported model (ΔAICc = 1.39, evidence ration 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 (ΔAICc > 2; evidence ratios 3.8–9).

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's body condition (LMM: $\chi^2_2 = 2.24$, $p = 0.33$), start 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: $\chi^2_2 = 4.33$, $p = 0.11$). 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 responded similarly to the mean winter and spring temperatures during the reproductive season.

DISCUSSION

Start of breeding, demography, individual body size and condition. A trend in earlier breeding start was established in the research area. For comparison, in Finland the Tawny Owl breeding start did not change (Lehikoinen *et al.* 2011). It is noted that long-term phenological research for raptor birds is very scarce (Møller *et al.* 2004). In other, mostly passerine species, earlier breeding phenology trends are identified and associated with a warming climate (Brown *et al.* 1999; Crick *et al.* 1997; Dunn & Winkler 1999; research review Møller *et al.* 2004). A tendency for better body condition owls to begin breeding earlier was established during research in Finland (Solonen 2013). The adequate accumulation of resources is considered one of the driving factors for earlier breeding start in birds (Daan 1980). A trend was found in many species of birds that earlier clutches are more successful, thus the birds are experiencing environmental pressure to lay their eggs as soon as conditions allow (Møller *et al.* 2004). The best quality individuals are the first to breed (Verhulst & Nilsson 2008).

This study found that the Tawny Owl reproductive variables are closer to those found in northern Europe (Mikkola 1983; Sasvári & Hegyi 2002; Baudvin & Jouaire 2003; Solonen 2005; Marchesi *et al.* 2006, Kekkonen *et al.* 2008; Chausson *et al.* 2014; Emaresi *et al.* 2014). This is consistent with trends observed for Tawny Owl and other raptor birds, where clutch size increases geographically from south to north (Newton 1977; Mikkola 1983). Mikkola (1983) points out that a similar trend in clutch size for Tawny Owl can be

observed from west to east.

The trends in the research area show that better body condition females have higher reproductive parameters, however, they do not depend on female body size. Furthermore, clutch size dependence of the female body condition is determined for various bird species (Daan 1980).

The number of breeding pairs and reproduction success changed significantly in the research area between 1978 and 2014, while other reproduction parameters did not change significantly. Reproductive success of the Tawny Owl was lowest around the time when largest number of breeding pairs was observed in the research area, and began to increase with the decrease in pair numbers. According to the habitat heterogeneity hypothesis (Krüger *et al*. 2012; Newton 2013), reduction of number of pairs in a given area allows the remaining pairs to occupy the best quality areas that hold sufficient resources for high reproductive results. And vice versa, increased density of individuals drives more pairs to occupy sites of poorer quality where bird reproductive parameters decrease (Sergio & Newton 2003). Such density dependent population regulation is characteristic to raptor populations (Carrete *et al*. 2006; Newton 2013).

The survival of the Tawny Owl females estimated in the present study is similar to one described in various other studies (Francis & Saurola 2002; Roulin *et al*. 2003; Pavon-Jordan *et al*. 2013; Emaresi *et al*. 2014). Breeding frequency (i.e. recapture probability) was close to established in Finnish Tawny Owl population (Francis & Saurola 2002; 2004). And in addition, Tawny Owl breeding frequency upward trend was also determined in Finland in 1981–1998 (Francis & Saurola 2004) as in the present study.

The long-term significant change in the body size of breeding females over study years in the research area was found, yet such data from other populations of this species is not available. In Denmark, a long-term decline in the size of the goshawk individuals of both sexes was found (Yom-Tov & Yom-Tov 2006), and in Finland the size of this species individuals differed: females increased while the males decreased (Tornberg *et al*. 1999). The

authors linked these changes to dietary change. When discussing changes in the size of individuals in different groups of organisms (including birds, mainly passerine) Gardner *et al.* (2011) attribute them to climate change.

Habitat selection. In the research area Tawny Owls occupying nest boxes preferred forest openings, extensive fields and mature forests while avoiding young forests. Tawny Owl habitat research in other countries showed that the owl preferred forest habitats (Redpath 1995; Sunde *et al.* 2001), and they were more intensively used (Sunde *et al.* 2006) compared to open habitats. Redpath (1995) found that the optimal Tawny Owl habitat is fragmented, medium sized (4–10 ha) forest. This assessment was carried out taking into account prey (small mammals) abundance, which decreased with increasing forest area, and increased owl energy loss in open habitats (greater flight distances). Preference for high quality and / or typical feeding habitats has been frequently demonstrated in raptor studies (Väli *et al.* 2004, Sergio *et al.* 2006, Ortego 2007, Bai *et al.* 2009, Treinys *et al.* 2009). Tawny Owl habitat preference and avoidance established in present study also may be associated with prey resources. It was found that felling sites support abundant populations of small mammals (Petty, 1999; Čepukienė & Jasiulionis 2012) while small mammal density is low in intensive farming, monoculture fields and / or young forests (Alejūnas & Stirkė 2010; Panzacchi *et al.* 2010).

In the research area, the probability of successful nesting for Tawny Owls increased with higher abundance of openings within the forest and fewer young forest stands. This coincided with the owl's habitat preferences and avoidances. These findings indicate that the owl tends to select high quality sites. Such behaviour corresponds to theoretical 'ideal' habitat selection model (Sergio *et al.*, 2007). The ability to select optimal habitats is identified for Tawny Owl (Sasvári & Hegyi 2011) and other species of raptor birds (Forero *et al.* 1999; Lõhmus 2001; Sergio *et al.* 2007), though it was not confirmed for the Spotted Owl (*Strix occidentalis*) (Zimmerman *et al.* 2003). In the course of evolution habitat preferences evolved due to the positive consequences of

habitat selection to species' fitness (Clark & Shutler 1999).

In spite of increasing deforestation (National Forest Service 2014) and agricultural changes (EPA 2008), the nesting environment of Tawny Owl did not change significantly between 1995–2004 and 2005–2014 in the study area. However, owls in 2005–2014, compared to the previous period, chose nest boxes which were surrounded by more forest openings. Preferences for forest openings was associated with higher breeding success, so this habitat selection change had a positive effect on Tawny Owl reproduction. Habitat preference adaptivity was also found in other studies, e.g. the Eagle Owl (*Bubo bubo*) raised better quality offspring in preferred habitats (Ortego 2007).

During checking of owl nest boxes in the study area in 1978–2014, it was found that detection probability of *Microtus* voles as prey decreased, while thrush and other birds' increased, and bank vole and murids' detection probability remained stable. Although the approach and collected data insufficiently reflect the owl diet during whole breeding season, it is likely that Tawny Owl prey has changed in the study area. Long-term changes in the Tawny Owl's prey (voles and amphibians decrease, birds increase) were determined in the middle of the 20th Century in Germany (Wendland 1984). In Great Britain the prevailing small rodent species changed in a 19 year period (Petty 1999). Vole decrease trend in Tawny Owl's prey was identified by Solonen & Karhunen (2002). Same vole decrease in prey was also reported for Tengmalm's Owl (Korpimäki 1988). Long-term decrease in vole abundance and changes in their cycles was observed in the Nordic countries (Solonen & Karhunen 2002; Hörnfeldt 2004; Sundell *et al.* 2004). Balčiauskienė *et al.* (2008) found that Tawny Owls prey was mostly comprised of *Microtus* vole when the nest box environment contained more open habitats. Tawny Owl habitat selection changed in the study area, with greater significance of forest habitats (forest openings) after 2005; however, the change in prey trends started from the 1990s.

Influence of climate conditions. Climatic conditions in the research area changed differently throughout the seasons. Even though global warming is worldwide, different locations and/or different seasons variate in their changes (IPCC 2014). Cyclical winter temperature fluctuations observed in the research area confirm previous studies stating that winter temperature varies depending on the NAO in Lithuania (Bartkevičienė 2004; Mickevičius & Bukantis 2013). Due to climate change, global precipitation levels record an upward trend, though these changes are also uneven between regions and over time (IPCC 2014).

The data on the influence of autumn weather conditions on the Tawny Owl reproduction from other studies is not present, however, the brood size of the same genus Spotted Owls was found to be associated with previous year's precipitation amount (Glenn *et al.* 2011). Tawny Owl reproduction cycle begins in autumn: territorial behaviour is demonstrated, new territories are occupied and new limits for old ones are established (Southern 1970). In autumn, the weight of individuals' increases and preparation for the breeding season begins – the ovaries start growing, depending on the weight of the female body (Hirons *et al*. 1984). Southern (1970) indicates that heavy rain adversely affects the search for prey. It was found that during autumn and winter seasons the Tawny Owl mainly feeds on small rodents (Petty 1999; Capizzi 2000; Romanowski & Żmihorski 2009). In autumn, voles and mice reach the annual abundance peak (Pucek *et al.* 1993; Solonen 2006). Their abundance in autumn determines the Tawny Owl's breeding start in spring (Lehikoinen *et al*. 2011; Solonen 2013; 2014) and reproduction (Solonen 2014, but not found by Lehikoinen *et al*. 2011). Extensive precipitation in autumn might have a negative impact on the condition of an owl through thermoregulation, circumstances for prey search and/or prey abundance, thus, the owl may not achieve good body condition.

Colour polymorphism. The most commonly used morph in different studies is the brown morph, which is described using similar criteria by most authors. Morph colour frequency differs in Europe, brown morph prevails mostly in its western part (France, Great Britain) (Galeotti & Cesaris 1996). Brown morph frequency determined in Dotnuva study area (18%) was close to rates in Germany, Czech Republic, Switzerland (10–33%; Galeotti & Cesaris 1996), yet in the central part of Poland grey and brown morph owls were almost equal (Gryz & Krauze-Gryz 2013). According to Gloger rule (Millien *et al.* 2006), in the direction of south-north, dark morph individuals should decrease and light morph should increase. Italy is dominated by grey morph owls (Galeotti & Cesaris 1996) and in Finland brown morph accounted for about one-third, and recently – more than 40% of owls (Karell *et al.* 2011). So clear latitudinal morph gradient according to Gloger rule may not exist; however, colour morph frequency dependence on climate conditions is identified and discussed below.

During the period of 1985–2014 colour morph frequency of the Tawny Owl changed: grey colour morph decreased and intermediate owls increased. Such intermediate morph increase and grey decrease was observed not only in the area of research, but also on a larger scale (analysis of museum data from all over Lithuania; Grašytė *et al.* 2017). The stability of colour morph ratios over time for the Tawny Owl was found during research in Finland (Brommer *et al.* 2005). Such long-term morph frequency stability is also characteristic to other polymorphic raptor bird species (Briggs *et al.* 2011; Martínez *et al.* 2016). However, Karell *et al.* (2011) showed rapid Tawny Owl's brown morph growth from around 1990 in the northern part of the distribution range, as well as in whole Finnish population. In Italy, long-term Screech Owl (*Otus scops*) colour morph changes were determined as well (Galeotti *et al.* 2009). Hence, increase of darker individuals (i.e. with a higher pheomelanin concentration in feathers) in polymorphic populations may be interpreted as an adaptation to climate warming (see Roulin 2014).

Different colour morph owls in Dotnuva research area did not differ significantly in body size, condition, start of breeding, survival probability, clutch size, average egg volume or brood size. However, the intermediate morph females bred more often than other morphs and raised more offspring during all registered breeding events. Roulin *et al.* (2003) in Switzerland also found no differences between morph wing length and weight, but greyer females had shorter tarsus there. Different colour morph body measurements and body condition did not differ in Italy (Galeotti & Sacchi, 2003). According to Roulin *et al.* (2003) study in Switzerland, different colour morph survival rate was the same, though Emaresi *et al.* (2014) determined that in the western part of Switzerland individuals with more pheomelanin in feathers had better survival probability. However, in Finland, survival for such individuals was poorer than for individuals who had little or no pheomelanin in feathers (Karell *et al.* 2011). Brommer *et al.* (2005) also found that brown morph owls live shorter than grey morphs in Finland. In Switzerland, breeding frequency varied depending on the ambient temperature, but the highest was characteristic to brown morphs, and the lowest to grey morphs (Roulin *et al.* 2003). Different morph owls in Finland bred in similar frequency, raised similar size broods; however, grey morph owls lived longer, resulting in higher lifetime reproductive success (Brommer *et al.* 2005). In Switzerland, Tawny Owl colour morphs had no difference in brood size nor in the total number of offspring, but owls with less pheomelanin in their feathers raised better condition offspring (Roulin *et al.* 2003). In the research of other raptor birds, various different colour morph reproduction trends emerge (Boerner & Krüger 2009; Briggs *et al.* 2011; Martínez *et al.* 2016). Overall, there is great diversity among bird species related to reproduction and survival of individuals depending on colour polymorphism (Meunier *et al.* 2010). Different Tawny Owl colour morph regional reproduction and/or survival differences discussed herein indicate that under diverse environmental conditions different colour morphs can have superiority over one another.

Different colour morphs are associated with adaptation to different habitats, when darker individuals are better adapted to the dark, closed environments, and lighter individuals to more open/bright conditions (Galeotti *et al*. 2003). In Italian parks, brown owls were found in denser forest habitats compared to grey ones (Galeotti & Sacchi, 2003). Although, different colour morph owl habitat selection differed little in Dotnuva forest, yet the general trend was similar to an expected one. Namely, brown morph owls were associated with the sites characterized by the largest coniferous forest area and lowest open forest area around nest boxes. Tawny Owls stay in the same area for the whole year (Sunde *et al*. 2003), thus, coniferous forests may be important for the brown owl when avoiding predators during winter.

Breeding success of the different Tawny Owl colour morphs in the study area was not related to the weather conditions before breeding season. In Switzerland, greyer morph owls would breed when spring and previous summer were cooler (Roulin *et al*. 2003). Increased grey morph owl mortality was recorded in Italy during warmer years (Galeotti & Cesaris 1996). Rapid brown morph individual spread in Finnish population was due to improved survival of this morph's individuals in warmer winters (Karell *et al*. 2011). Different morph adaptation to different climatic conditions is confirmed by further study: grey colour morph owl plumage is typically denser than brown morph plumage (Koskenpato *et al*. 2016). Birds with more pheomelanin in their feathers are more resistant to UV radiation and have better thermoregulation – features that are important during climate warming (Roulin 2014). Temperature changes in Dotnuva research area during different seasons were diverse: while autumns were warmer, the average winter temperature during the study period did not change. Therefore, intermediate morph individuals might be better adapted to survive and reproduce in differently changing seasons.

CONCLUSIONS

1. Tawny Owl's breeding start date in the research area was 24th of March, on average; breeding success was 68%, average clutch size – 3.9 eggs, average brood size – 3.1 juveniles. Owl survival probability – 0.70, breeding frequency – 0.32.

2. Breeding Tawny Owl pair number was not constant in the research area during nearly four decades. Tawny Owl breeding success differed significantly during the study period, poorest performance was in the middle of the study. Tendency for the earlier breeding start and increase in breeding frequency were observed. Clutch size, brood size and survival probability was stable during study period.

3. During thirty years, breeding individuals have changed in size, smallest breeding females were recorded in the last decade of research. Body condition of breeding individuals has not changed. Better body condition females bred earlier and achieved higher reproductive parameters. Reproduction parameters did not depend on individual body size.

4. Tawny Owl's breed earlier when average winter temperature is higher and precipitation amount during preceding autumn is lower. Tawny Owl's body condition is better during breeding season, when lesser amount of precipitation is during preceding autumn. Brood size was not associated with weather parameters during spring.

5. Tawny Owl preferred forest openings, extensive fields and mature forests, and avoided young forests when occupying nest boxes. Such habitat selection was adaptive, because larger proportion of open forest areas and smaller proportion of young forest areas around nest boxes was associated with better breeding success probability. Preferences for forest openings increased during the last decade of research.

6. Tawny Owl exhibited polymorphism in the research area: 42% of breeding females were grey, 40% – intermediate, 18% – brown colour morph. Grey owls dominated in 1985–2004, but decreased in 2005–2014, while the intermediate morph owls increased in frequency.

7. Different colour morph owls do not differ in breeding start, clutch and brood size, survival probability, body size and body condition; however, the intermediate morph females breed more often and raise more offspring during all breeding events.

8. Climate parameters' and colour morph interactions did not explain reproduction and body condition of Tawny Owl females.

9. Some support was found, that brown morph owls tend to occupy nest boxes with the larger proportion of coniferous forests and lower proportion of forest openings in surroundings, compared to the intermediate morph owls.

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LIST OF PUBLICATIONS ON THE DISSERTATION TOPIC

1. **Gintarė Grašytė**, Saulius Rumbutis, Mindaugas Dagys, Rimgaudas Treinys. 2016. Breeding performance, apparent survival, nesting location and diet in a local population of the Tawny Owl *Strix aluco* in Central Lithuania over long-term. *Acta Ornithologica* 51 (2), 163–174.

2. **Gintarė Grašytė**, Saulius Rumbutis, Mindaugas Dagys, Daiva Vaitkuvienė, Rimgaudas Treinys. 2017. Tawny Owl females of intermediate colour morph reproduce better and increase in a local polymorphic population. *Ornis Fennica* 94, 33–44.

3. Saulius Rumbutis, Daiva Vaitkuvienė, **Gintarė Grašytė**, Mindaugas Dagys, Deivis Dementavičius, Rimgaudas Treinys. Adaptive habitat preferences in a local population of Tawny Owl *Strix aluco*. (Submitted to *Bird Study*).

Abstracts of scientific conferences:

G. Grašytė. Long-term dynamics of predator and prey interaction in a Tawny Owl (*Strix aluco* L.) example. Presentation summaries in Young Scientists Conference "Biofuture: natural and life sciences perspectives. 2014. (In Lithuanian).

G. Grašytė. Linking individual traits and demography with the avian colour polymorphism. Abstract book of 11th international conference of natural life sciences "The Coins'16". 2016 m.

Naminės pelėdos *Strix aluco* perėjimo pradžios, individo ir populiacijos dinamikos rodikliai, jų ilgalaikė kaita ir saitai su buveinių ir klimato pokyčiais

Santrauka. Vykstant aplinkos pokyčiams, kurie daugiausiai susiję su žmogaus poveikiu natūralioms buveinėms ir klimato kaita, ypač paveikiamos sėslios, aukščiausios mitybinės grandies rūšys. Tačiau iki šiol nedaug žinoma apie tokių rūšių reakciją į vykstančius pokyčius. Šio darbo tikslas – nustatyti sėslios plėšrių paukščių rūšies, naminės pelėdos *Strix aluco,* individų dydžio, kūno būklės, spalvinių morfų, veisimosi ir išgyvenamumo rodiklių dinamiką, jų tarpusavio ryšius ir saitus su buveinių bei klimato pokyčiais. Darbe analizuojami 1978–2014 m. surinkti duomenys apie 186 pelėdos perėjimo atvejus, 61 ženklintos patelės individualias savybes, rudens–pavasario klimato sąlygas ir buveines 0,4 km spinduliu aplink inkilus. Taikant regresines analizes nustatyta, kad tyrimų metu patikimai kito perinčių porų skaičius, pelėdų veisimosi sėkmingumas bei perinčių individų dydis. Be to, nustatytos perėjimo pradžios ankstyvėjimo ir perėjimo dažnumo didėjimo tendencijos. Geresnės kūno būklės patelės perėjo anksčiau ir pasiekdavo geresnius veisimosi rodiklius. Tyrimų plote naminės pelėdos rinkosi buveines su didesniu miško laukymių, brandžių miškų ir pievų plotu, vengė jaunų miškų. Nustatytas buveinių pasirinkimo ir veisimosi sėkmingumo ryšys rodo, kad pelėdos buveinių pasirinkimas yra adaptyvus. Naminės pelėdos perėjimo pradžia buvo susijusi su rudens ir žiemos orų sąlygomis, be to, rudens kritulių kiekis turėjo įtakos pelėdos kūno būklei perėjimo metu. Pilkos, rudos ir tarpinės spalvinės morfos pelėdos nesiskyrė kūno dydžiu ir būkle, tačiau tarpinės morfos individai perėdavo dažniau ir išaugindavo daugiau jauniklių.