

*Settlement, habitat preference,  
reproduction, and genetic diversity in  
recovering the white-tailed eagle *Haliaeetus  
albicilla* population*

**Ringaudas Treinys, Deivis  
Dementavičius, Saulius Rumbutis,  
Saulius Švažas, Dalius Butkauskas,  
Aniolas Sruoga & Mindaugas Dagys**

**Journal of Ornithology**

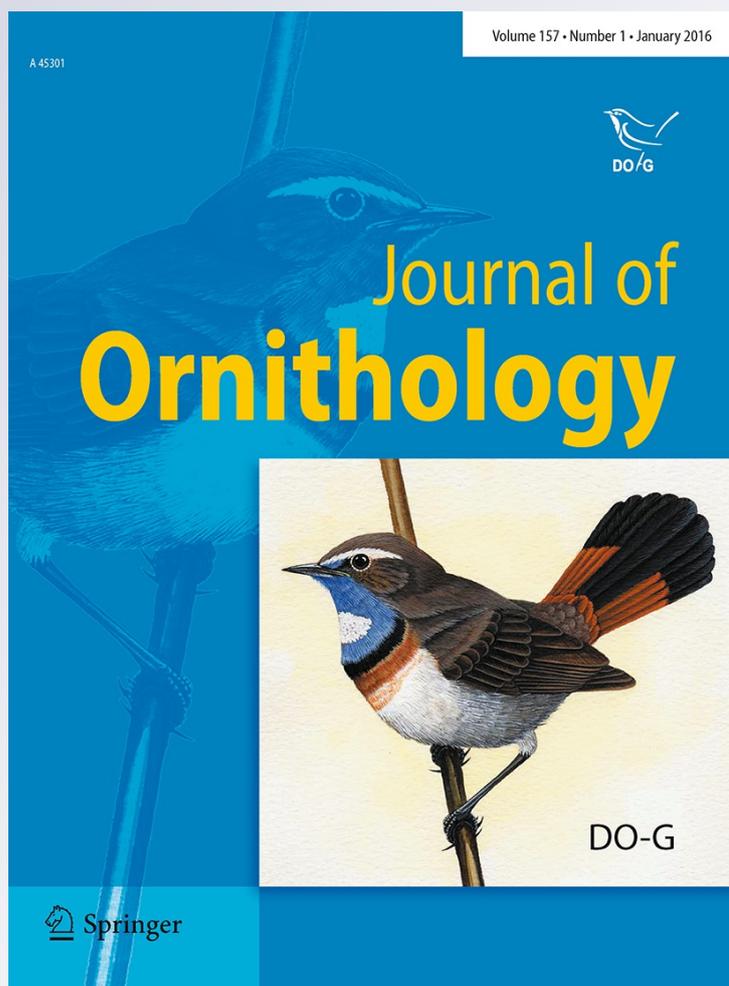
ISSN 2193-7192

Volume 157

Number 1

J Ornithol (2016) 157:311-323

DOI 10.1007/s10336-015-1280-8



**Your article is protected by copyright and all rights are held exclusively by Dt. Ornithologen-Gesellschaft e.V.. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at [link.springer.com](http://link.springer.com)".**

## Settlement, habitat preference, reproduction, and genetic diversity in recovering the white-tailed eagle *Haliaeetus albicilla* population

Rimgaudas Treinys<sup>1,2</sup> · Deivis Dementavičius<sup>2,3</sup> · Saulius Rumbutis<sup>2,3</sup> · Saulius Švažas<sup>1</sup> · Dalius Butkauskas<sup>1</sup> · Aniolas Sruoga<sup>1</sup> · Mindaugas Dagys<sup>1</sup>

Received: 18 February 2015 / Revised: 19 July 2015 / Accepted: 18 August 2015 / Published online: 4 September 2015  
 © Dt. Ornithologen-Gesellschaft e.V. 2015

**Abstract** The recovering population of white-tailed eagles *Haliaeetus albicilla* was studied in Lithuania, Central Europe. In the present study, we focused on (1) clarifying which theoretical distribution model better fits and describes the observed pattern of eagle settlement, (2) examining habitat preference at the level of nesting territory and its relationship with reproduction, (3) ascertaining the genetic diversity profile of the population using D-loop mtDNA. Between 1985 and 2011, the white-tailed eagle population recovered from 0 to 120 pairs and by the end of the period occupied a range of 34,000 km<sup>2</sup>. As indicated by a mean annual breeding success of 0.67, productivity 1.15, and brood size 1.73, the population reproduced well. The pattern of habitat settlement during the period of population expansion was not random as high-quality habitats were occupied first. Supporting the ideal free distribution model, reproduction was similar across nesting territories in three different habitat types, as well as between territories established in different years. The eagles preferred aquatic habitats, but these preferences were not adaptive in terms of breeding performance. Increased brood failures in later years possibly indicated the growing effect of density-dependent regulation. In total, six different haplotypes

were identified in the sample of 45 individual birds. Haplotype diversity was 0.711. Phylogenetically, the Lithuanian population is most closely related to the populations of Sweden, Poland, and Germany, while similarity with Lapland, Kola, and Estonian populations was evident too. These findings indicate possible source populations directly or indirectly participating in the process of recovery of the formerly extinct Lithuanian population. Haplotypes distribution across the three habitat types in Lithuania was uneven.

**Keywords** Ideal free distribution · Breeding success · mtDNA

### Zusammenfassung

**Besiedlung, Habitat-Präferenz, Fortpflanzung und genetische Vielfalt in einer sich wiederaufbauenden Seeadler-Population (*Haliaeetus albicilla*)**

Die hier untersuchte, sich wieder entwickelnde Population des Seeadlers (*Haliaeetus albicilla*) lag in Litauen, Zentraleuropa. Wir konzentrierten uns in der Untersuchung darauf, 1) welches theoretische Verbreitungs-Modell die beobachtete Besiedlung durch die Seeadler am besten beschreibt, 2) auf eine Prüfung möglicher Habitat-Präferenzen bei den Brutplätzen und eines Zusammenhangs mit der Fortpflanzung und 3) auf eine Bestimmung des Profils der genetischen Vielfalt in dieser Population mit Hilfe der D-loop mtDNS. Zwischen 1985 und 2011 erholte sich die Seeadler-Population von Null auf 120 Paare und besetzte gegen Ende der Beobachtungszeit ein 34.000 km<sup>2</sup> großes Gebiet. Wie der mittlere jährliche Bruterfolg von 0,67, eine Produktivität von 1,15 und eine Gelegegröße von 1,73 nahelegen, entwickelte sich die Population gut. Während

Communicated by M. Wink.

✉ Rimgaudas Treinys  
 rimga.t@gmail.com

<sup>1</sup> Nature Research Centre, Akademijos 2, 08412 Vilnius, Lithuania

<sup>2</sup> The Foundation for the Development of Nature Protection Projects, Savanorių pr. 173, 03150 Vilnius, Lithuania

<sup>3</sup> T. Ivanauskas Zoological Museum, Laisvės ave. 106, 44253 Kaunas, Lithuania

der Wachstumsphase der Population verlief die Besiedlung der Habitate nicht nach einem Zufallsmuster, sondern qualitativ hochwertige Habitate wurden als erste besetzt. In Unterstützung des Modells einer freien Verbreitung war die Fortpflanzung in drei unterschiedlichen Habitat-Typen sowie in Nist-Gebieten unterschiedlicher Jahre sehr ähnlich. Die Seeadler bevorzugten aquatische Lebensräume, diese Präferenz war hinsichtlich des Fortpflanzungserfolgs jedoch nicht adaptiv. Die Zunahme von Brut-Mißerfolgen in späteren Jahren wies möglicherweise auf den wachsenden Effekt eines dichteabhängigen Regelungsmechanismus hin. Insgesamt wurden in einer Stichprobe von 45 Vögeln sechs unterschiedliche Haplotypen festgestellt, die Haplotyp-Diversität lag bei 0,711. Phylogenetisch ist die litauische Population mit denen in Schweden, Polen und Deutschland am nächsten verwandt, wobei es auch klare Ähnlichkeiten mit Populationen in Lappland, Estland und auf der Kola-Halbinsel gab. Diese Ergebnisse legen den Schluss nahe, dass bei der Erholung der früher ausgestorbenen litauischen Population Quellen-Populationen direkt oder indirekt eine Rolle spielen. Die Haplotypen waren auf die drei Habitat-Typen in Litauen ungleich verteilt.

## Introduction

Finding a suitable place to live and reproduce is one of the key attributes of individual fitness (Krüger 2002). Birds are mobile organisms capable of visiting many patches before settling, and this is especially true for individuals of long-lived resident species with delayed maturity. Habitat settlement pattern in avian populations is traditionally explained by ideal free distribution (IFD) (Fretwell and Lucas 1970) or derivative models such as ideal despotic distribution (IDD) (Fretwell 1972), ideal pre-emptive distribution (Pulliam and Danielson 1991), and site dependence (Rodenhouse et al. 1997). The IFD and IDD models are suitable for analysing population performance in coarse-scale habitat patches (Sergio et al. 2007). Both models assume that individuals recognize suitable habitats where their fitness is highest. The IFD model assumes that all individuals are free to enter any habitat within the habitat gradient (Fretwell and Lucas 1970). When population increases, new arriving individuals settle in high-quality habitats resulting in higher densities and competition. This results in a similar decrease in success rates of early and later arrivals. Densities between different habitats could differ, but success rates are similar. The IDD model accepts individual inequalities and assumes that dominant individuals occupy high-quality habitats, and defending resources relegate subdominant individuals to lower-quality habitats (Fretwell 1972). When population increases,

early settlers prevent territory compression so that high-quality habitats continuously provide better success rates of early settlers compared to success rates of later arrivals relegated to low-quality habitats. In studies of territorial bird populations, there is usually less evidence to support the IFD model than the IDD (Löhmus 2001; Tome 2003; Zimmerman et al. 2003; Wightman and Fuller 2006; Sergio et al. 2007), but some populations do not follow the IDD model (Pagán et al. 2009) or either theoretical model (e.g., Bai et al. 2009).

Individuals recognizing and occupying high-quality patches will benefit by a higher degree of fitness (Sergio and Newton 2003; Sergio et al. 2007). A positive relationship between avian fitness and habitat choice drive the evolution of habitat preferences (Clark and Shulter 1999). Adaptive habitat choice, however, could be constrained for various reasons. Habitat choice can be based on the distribution of food resources or habitat cues, whereas reproductive success in the selected site may be determined by predators (Kristan et al. 2007). Some individuals cannot assess habitat quality due to limited perception, large territory size, or fluctuations in their prey (Zimmerman et al. 2003). Human-altered environments may also generate a mismatch between the attractiveness and quality of habitat (Hollander et al. 2011). Additionally, free movement between sites and selection of best sites can be rarely realistic for territorial species (Krüger 2002; Sergio et al. 2007). However, in the case of the white-tailed eagle *Haliaeetus albicilla*, a top avian predator, it can be assumed that habitat choice, and its consequences for reproduction, might be least affected by non-habitat factors, such as interspecific competition and predation. Moreover, natural population recovery in this species following Europe-wide DDT suppression (Helander and Stjernberg 2003; Stjernberg et al. 2005) offer the possibility to assume the free movement of individuals between sites is less affected and individuals can choose habitat patches according to quality. In Lithuania, Central Europe, the white-tailed eagle was considered a common breeder in the mid-nineteenth century, but heavy reduction and subsequent extinction occurred in the mid-twentieth century (Dementavičius 2007).

Genetic diversity loss is one of the main direct genetic consequences of population crashes (Roques and Negro 2005). However, in some birds of prey (for example, the greater spotted eagle *Aquila clanga* and lesser spotted eagle *A. pomarina*), genetic diversity is not related to population size (Väli et al. 2004). A similar pattern of reduced genetic diversity is characteristic of some populations of white-tailed eagle, e.g. the largest European population living in Norway is genetically uniform for mtDNA, but their nuclear diversity level is similar to the other European populations (Hailer et al. 2006). Recent comprehensive

investigations into the genetic diversity of white-tailed eagles in Europe confirmed that the present population size poorly explains patterns of genetic diversity detected in different countries (Langguth et al. 2013). Despite the fact that birds have good ability to cover large distances, populations of white-tailed eagle are not spatially homogenous, contrary to species with lower dispersal potential as, for example, House Sparrow *Passer domesticus* (Kekkonen et al. 2011). Even geographically neighbouring populations of White-tailed Eagle show, in some cases, significant genetic differences (Hailer et al. 2007; Langguth et al. 2013; Ponnikas et al. 2013). In Eurasia, western A and eastern B mitochondrial lineages found in the white-tailed eagle (Hailer et al. 2007) are distributed unequally with a more pronounced gene flow from west to east (Langguth et al. 2013). Thus, the formation of genetic profiles in recently recovered populations is complicated and can actually be different from previously studied neighbouring populations. An investigation into the genetic structure of the recently recovered white-tailed eagle population in Lithuania, following many decades of extinction, is important from theoretical and practical points of view. Moreover, the process of the formation of the genetic structure in the recovering population in Lithuania could be revealed in the context of available data of well-studied populations in northern and central–western Europe. We studied population dynamics, reproduction, settlement, habitat use, and genetic structure in the recovered white-tailed eagle population in Lithuania, Central Europe. We especially focussed on (1) clarifying which theoretical distribution model better fits to describe eagle settlement, (2) examining habitat preferences at the nesting territory level and their relationship with reproduction, (3) ascertaining the genetic diversity profile using mtDNA. We made several predictions: (1) if prey-abundant habitat types are occupied earlier and the breeding performance of eagles is similar between different habitats and sites occupied at early and later years, the studied population conforms with the IFD model. The IDD fits better if prey-abundant habitat types are occupied earlier, but the breeding performance of eagles differs between habitats and eagles better reproduce in earlier occupied sites. (2) The white-tailed eagle mainly prey on aquatic species. Hence, we suggest preferences for aquatic habitats and a positive relationship between the abundance of these habitats within the nesting territory and occupation year and reproduction success. (3) We also expect genetic population structure with high haplotype diversity, similar to neighbouring northern and central–western populations as well as no differences in haplotype distribution among different habitat types taking into consideration their distribution in the landscape and relatively small geographical study scale.

## Materials and methods

### Population data

We searched for occupied white-tailed eagle nesting territories (term according to Oehme 2003) in the period 1995–2011 in Lithuania (65,200 km<sup>2</sup>, central coordinate 55°10'N, 23°39'E). White-tailed eagles prey mainly on fish and waterfowl (Cramp and Simmons 1980), thus surveys were conducted in areas supporting different types of water bodies and wetlands using methods described in detail elsewhere (Dementavičius 2007). Search efforts were similar regardless of the many differing types of water bodies and wetlands. White-tailed eagle nesting territories found by other researchers in Lithuania prior to 1995 were also monitored by us during the period mentioned above. When nesting territories were found, we visited them one or several times a year and checked for activity of pairs. In each nesting territory, known nests were checked to determine occupancy (term according to Oehme 2003) and reproductive output. An occupied nest was considered successful if at least one nestling with well-developed plumage (at least 3 weeks of age) was recorded. Data on number of nestlings were collected annually by climbing except in cases where nestlings were close to fledging and could be reliably observed and counted from the ground. If known nests within a nesting territory were unoccupied, we searched for a new alternative nest. When pairs were present in their nesting territories without occupying nests, or at least we were not able find them, we excluded these years from our reproductive output analysis to avoid erroneous estimations. The mean for control years with collected data on reproductive output per nesting territory was  $6 \pm 3$  SD (range 1–14 years,  $n = 89$ ). The reproductive output of the white-tailed eagle in results was presented as breeding success (the proportion of nests containing at least one nestling of at least 3 weeks of age, out of all occupied nests), productivity (the mean number of nestlings of at least 3 weeks of age, out of all occupied nests), and brood size (the mean number of nestlings of at least 3 weeks of age in nests containing young) (Helander et al. 2013).

The establishment year of the nesting territory was determined using a set of complementary criteria: (1) age of mated eagles, estimated according to plumage (for details see Forsman 1999) or the reading of rings where possible, (2) nest appearance and decay of material, (3) occupancy of artificial nests in previously empty areas (a total of 92 artificial nests were built in the country near potential feeding habitats during the study period), (4) information supplied by local foresters, ecologists of protected areas, or birdwatchers. For each nesting territory, the

establishment year was back-dated accordingly. To minimize bias in nesting territory establishment, each nesting territory was attributed to one of the four settlement phases: first 1985–1995, second 1996–2000, third 2001–2005, and fourth 2006–2010. Each nesting territory was attributed to the one of three habitat types: (1) coastal (the area in western Lithuania, specifically in the Nemunas River delta and areas less than 10 km from the Baltic Sea coast and the Curonian Lagoon), (2) inland fishpond, and (3) inland natural. Fishpond and natural habitats were described as areas outside coastal habitats containing or not fishponds, respectively. Final distinction between fishpond and natural was based on the presence/absence of fishponds within a 6-km radius from the nests; observed hunting flights and prey remains at nests (i.e. fish species used in aquaculture differ from species available in natural water bodies) also supported such distinction too. Fishponds and other types of water bodies in inland areas differ markedly in the density of the main prey for white-tailed eagles, thus are potentially ecologically unequal in terms of habitat quality. Coastal and fishpond habitats contain ample supplies of key prey for white-tailed eagles, thus these habitats were treated as high-quality habitats.

### Range dynamics

Data on 94 nesting territories (89 monitored by us and an additional five by other ornithologists) were used to analyse range dynamic. The Range Tool for Article 12 (Birds Directive) and Article 17 (Habitats Directive), provided by the European Topic Centre on Biological Diversity (Mac Sharry 2012) was employed to assess quantitatively the expansion of the white-tailed eagle range in Lithuania over the study period. White-tailed eagle nest distribution data in the Pan-European ETRS89 LAEA5210 grid with 10-km resolution (available from the European Environment Agency) were prepared, representing four points in time at 5-year intervals: 1995, 2000, 2005, and 2010. In the Range Tool, the gap distance of five grid cells was used as recommended by the European Environment Agency, i.e. it was considered a gap in the white-tailed eagle range only if the distance between the known occupied grid cells exceeded 50 km.

### Habitat characteristics

Territorial pairs of white-tailed eagles are resident and highly faithful, generally occupying the same nesting territories for life (Helander and Stjernberg 2003). A radius of 6 km around the nest was selected to represent the most important landscape level habitat characteristics for year-round and lifetime occupied nesting territories. Such a circular area covers most of the home-range estimates

(references in Krone et al. 2009) and foraging flights (Struwe-Juhl 2000; author's observations), despite being too large for pairs nesting in optimal habitats (Krone et al. 2013). The white-tailed eagle pair typically uses several nests within the nesting territory (Fischer 1959). The central point of the nest cluster was used in nesting territories with two or more nests (Bakaloudis et al. 2005). The CORINE Land Cover 2000 database (Vaitkus and Juzefaitė 2004) was used to describe habitat within each nesting territory. A database based on satellite images made in 1999–2000 was selected to represent land cover, this being approximately in the middle of population recovery period. The total proportion of the following land cover types were used: (1) artificial surfaces (CORINE Land Cover code 1xx), (2) agriculture areas (code 2xx), (3) deciduous forest (code 311), (4) coniferous forest (code 312), (5) mixed forest (code 313), (6) semi-open areas (codes 321, 322, 324, 331, 333, 334), (7) wetlands (codes 41x), (8) streams (code 511), (9) water bodies (code 5121), (10) fishponds (code 5122), and (11) lagoon and sea (code 52x). Data from the National Association of Aquaculture and Fish Products Producers were used to classify further the CORINE class of standing water (512) into water bodies (5121) and fishponds (5122), as these two types greatly differ in terms of the main prey for white-tailed eagle (see above). Random points to represent the available landscape of Lithuania were used. Random points were generated in forested areas only, represented by CORINE Land Cover classes 311, 312, and 313 and patches of class 324 (transitional woodland and shrub) that shared a border with one of the aforementioned forest classes. Country-wide stratification of random points was applied by generating one random point in each of 654 10 × 10 km grid cells that had their centroids on the territory of Lithuania and contained at least some forested area. Out of these, a further 200 points were selected at random through a random number generator according to the point ID number. The same 6-km radius was used around the random points to extract habitat characteristics from the CORINE Land Cover database. All the GIS procedures and data management in this study were implemented in ESRI Arc Map 10 software.

### Statistical analysis

Proportions were arcsine-square-root transformed. We checked correlations between pairs of habitat variables to reduce collinearity (Sergio et al. 2006 and references therein). When variables were strongly correlated ( $r > 0.6$ ), only the variable more relevant in terms of white-tailed eagle ecology was retained. We omitted only the proportion of agriculture areas from the set of initial variables. We performed a series of stepwise discriminant

function analyses to explore (1) habitat preferences of white-tailed eagle and (2) habitat preferences during the four settlement phases. The mean productivity of nesting territories during the controlled years and its relationship with habitat type, settlement phase, and interaction of these variables was tested using two-way ANOVA. To test settlement relationship with reproduction, two periods were used (i.e. 1985–2000 and 2001–2011) due to limited sample for each 5-year period. The relationship between mean productivity and habitat variables was analysed in generalized linear models (GLM) with normal error distribution and identity link function. As the productivity of eagles fluctuated from year to year, the response variable was standardized prior to analysis against annual mean and standard deviation for each year. The average per each nesting territory was then calculated and further termed as relative productivity. Generalized linear models were built with all possible combinations of key feeding habitats (namely water, stream, fishpond, lagoon, and sea) proportion within a 6-km radius around nest sites as explanatory variables. The best models were selected based on Akaike information criterion with a correction for small sample size (AICc). The relative importance of each model was estimated through ranking the models by  $\Delta\text{AICc} = \text{AICc}_i - \text{AICc}_{\min}$  (where  $\text{AICc}_{\min}$  is the best model in the model subset). Model weight was estimated through the normalized Akaike weights,  $\exp(-0.5 \times \Delta\text{AICc}) / \sum_{r=1}^R \exp(-0.5 \times \Delta\text{AICc}_r)$ . The threshold separating good models from less supported models was  $\Delta\text{AICc} \leq 2$ .

### Population genetic analysis

The population genetic structure of breeding white-tailed eagles in Lithuania was investigated using a mtDNA control region marker previously applied in studies of genetic structure and phylogeography of white-tailed eagles in Europe (Hailer et al. 2007; Honnen et al. 2010; Langguth et al. 2013; Ponnikas et al. 2013). In order to fill the gap in the dataset regarding variation in sequences of control region and haplotype diversity in the naturally recovered population of white-tailed eagles in Lithuania, blood samples were collected from nestlings in nests. Sampling of only one offspring per breeding pair avoided the inclusion of close relatives and ensured representation of local breeders. Sampling was organized proportionally from nests distributed in the three different habitat types.

DNA was extracted from EDTA preserved blood samples using a previously described method after digestion with proteinase K (Aljanabi and Martinez 1997). DNA fragments of the mtDNA control region were amplified using primers

*Hal-HVRIF* 5'-CCCCCCTATGTATTATTGT-3' and *Hal-HVRIR* 5'-TCTCAGTGAAGAGCGAGAGA-3' (Hailer et al. 2007). A 544-bp DNA fragment containing most of the control-region variability were amplified in the 25- $\mu\text{l}$  PCR volume for each sample consisting of 1 $\times$  PCR buffer (with 50 mM KCl), 0.2 mM dNTP, 0.2  $\mu\text{M}$  of each primer, 2.5 mM  $\text{MgCl}_2$ , 0.75 U Taq DNA polymerase LC (MBI Fermentas), and 0.04–0.06  $\mu\text{g}$  template DNA.

Amplification started with an initial denaturation step for 5 min at 95 °C, followed by 35 cycles of denaturation for 45 s at 95 °C, annealing for 45 s at 56 °C, and elongation for 1 min at 72 °C, and ended with a final elongation step for 10 min at 72 °C. Purified PCR products and the same primers *Hal-HVRIF* and *Hal-HVRIR* were used for DNA sequencing at the Sequencing Centre of the Institute of Biotechnology of Vilnius University (Lithuania) using Big-Dye<sup>®</sup> Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, USA) and 3130xl Genetic Analyzer (Applied Biosystems, USA).

A total of 45 newly established sequences whose length was 499 bp were used for the sequence analysis of mtDNA control region in order to establish the dataset representing the white-tailed eagle population breeding in Lithuania. Studied birds were attributed to three groups occupying the three different habitat types. An additional 419 sequences of control region deposited in the GenBank by previous researchers (Langguth et al. 2013) were included into the analysis of phylogenetic relationships between different European populations of white-tailed eagle. All sequences were aligned using ClustalW algorithm (Thompson et al. 1994) implemented in MEGA6 program (Tamura et al. 2013). DNASP 4.10 (Rozas et al. 2003) was used to determine the number of haplotypes  $h$  and haplotype diversity parameters  $H_d$ , indicating the divergence between groups of sequences as measured by the uncorrected average number of nucleotide substitutions per site between populations. Actual numbers of all identified haplotypes distributed in different sampling locations were plotted on the maximum likelihood (ML) phylogenetic tree with bootstrapping values computed using MEGA 6.

The evolutionary history was inferred by using the maximum likelihood method based on the Tamura 3-parameter model (Tamura 1992). A discrete Gamma distribution was used to model evolutionary rate differences among sites [five categories (+G, parameter = 0.1000)]. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 36 nucleotide sequences. All positions containing gaps and missing data were eliminated. There were a total of 464 positions in the final dataset.

## Results

### Population dynamics

There were no records of breeding white-tailed eagles in Lithuania between the middle of the twentieth century and 1985. Following the first breeding pairs found in 1985, the population increased sharply and reached 30 pairs in 1995 with a range covering 2800 km<sup>2</sup> (Fig. 1). During the second settlement phase (i.e. 1996–2000), the population increased by 100 % to 60 pairs, and the range expanded massively by 325 % to 11,900 km<sup>2</sup>. During 2001–2005, the population and range grew much slower than before (50–139 %, respectively), reaching 90 breeding pairs in a range of 28,400 km<sup>2</sup> in 2005. By 2010, the end of the last phase, the population increased a further 33 % to 120 pairs, while the range expanded only by 20 % to 34,000 km<sup>2</sup>.

### Reproduction

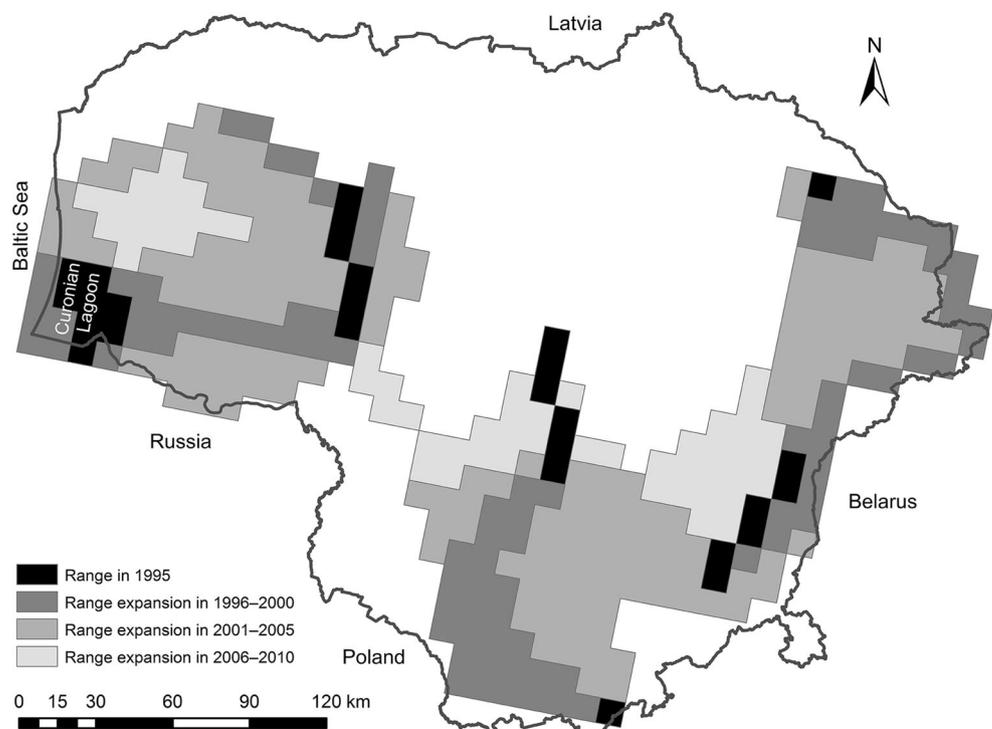
During 1995–2011, we observed 531 breeding attempts, 66.3 % of which were successful. The white-tailed eagle productivity was  $1.13 \pm 0.95$  SD ( $n = 531$ ) and brood size  $1.70 \pm 0.61$  SD ( $n = 352$ ). The mean breeding success per white-tailed eagle nesting territory was  $0.64 \pm 0.26$  SD ( $n = 89$ ) and productivity  $1.06 \pm 0.48$  SD ( $n = 89$ ). During the last 12-year period (i.e. 2000–2011), the mean annual breeding success was  $0.67 \pm 0.12$  SD, the mean

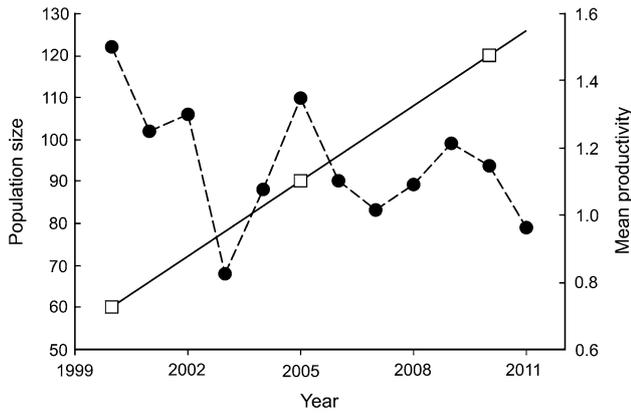
annual productivity  $1.15 \pm 0.08$  SD, and mean annual brood size  $1.73 \pm 0.14$  SD. The white-tailed eagle mean annual productivity fluctuated with a slightly declining trend ( $r = -0.45$ ,  $P = 0.14$ ) (Fig. 2). Mean productivity was significantly inversely related with skewness ( $r = -0.92$ ,  $P = 0.00003$ ,  $n = 12$ ). The brood size distribution differed significantly between two periods, representing low (2000–2002) and high (2009–2011) density periods ( $\chi^2_3 = 15.3$ ,  $P = 0.002$ ). The brood size shifted from a right-skewed distribution at low density to a left-skewed one in the last years indicating an increase in breeding failures (Fig. 3).

### Settlement, habitat use, and relationship with reproduction

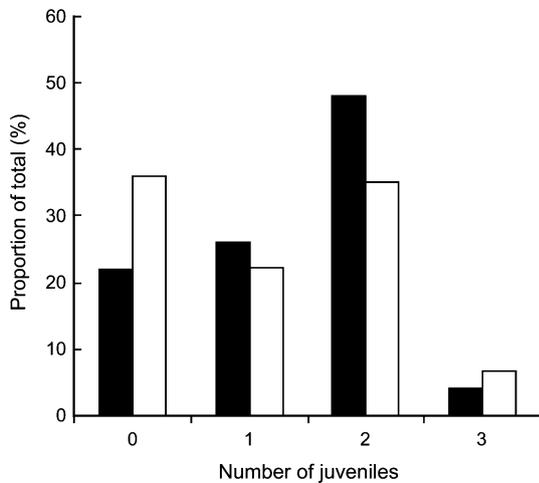
The first white-tailed eagle pairs in the country settled in coastal and inland fishpond habitats approximately at the same time, i.e. in 1985, while in inland natural habitats the first pair settled only 10 years later in 1995. Although not significantly, frequencies of eagle settlement in the three habitat types during the four phases deviated considerably from equal frequencies ( $\chi^2_6 = 11.6$ ,  $P = 0.07$ ) (Fig. 4), indicating uneven settlement. Nowadays, however, white-tailed eagle nesting territories are distributed across the three habitat types similarly: 36 % ( $n = 89$ ) in inland fish pond, 35 % in inland natural, and 29 % in coastal habitats ( $\chi^2_2 = 0.7$ ,  $P = 0.71$ ). Seven variables were chosen as

**Fig. 1** Range expansion of the white-tailed eagle at 5-year intervals. Prepared using Range Tool (see methods for details) and  $10 \times 10$  km grid in ETRS89 LAEA 5210 projection. Here, the map is presented in the Lithuanian coordinate system LKS-94



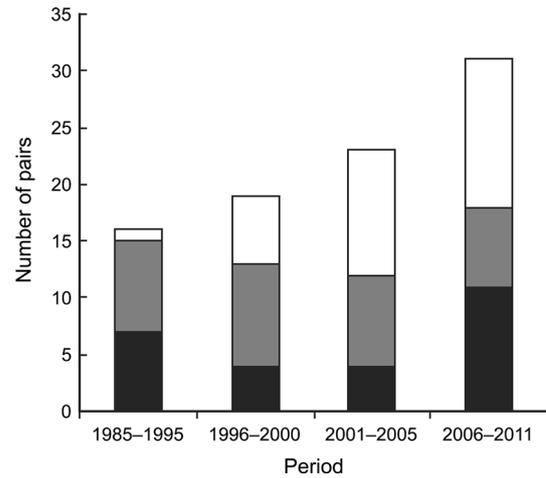


**Fig. 2** Changes in white-tailed eagle population size (open squares, solid line) and mean productivity (black circles, broken line) in Lithuania during 2000–2011



**Fig. 3** Frequency distribution of the white-tailed eagle nestlings in Lithuania in years with relatively low density (2000–2002) (black bars) and relatively high density (2009–2011) (white bars). Sample sizes for both periods are 50 and 197 breeding attempts, respectively

discriminators between nesting and random territories with an overall highly significant model ( $F_{7, 281} = 29.21$ ,  $P < 0.0001$ ). Five out of the seven variables were significant. Variables classified 85.5 % of all combined territories correctly. In the occupied nesting territories of white-tailed eagle were a higher abundance of fishponds, streams, lagoon and sea, water bodies, and semi-open areas compared to their availability in the landscape. During the four settlement phases, white-tailed eagle habitat preferences varied. During the first settlement phase, eagles preferred fishponds, streams, and wetlands compared to their availability in the country's landscape ( $F_{5, 210} = 37.59$ ,  $P < 0.0001$ ). During the second settlement phase, only the preference for fishpond was retained, while the new ones emerged, i.e. for lagoon and sea, water bodies, semi-open areas, and coniferous forests ( $F_{9, 209} = 12.73$ ,



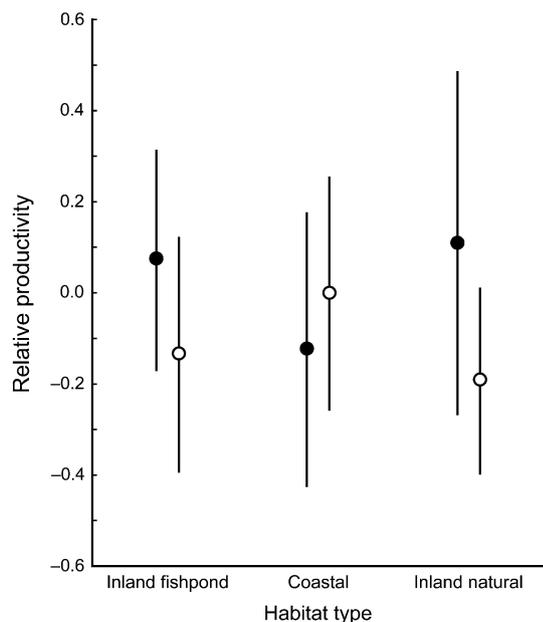
**Fig. 4** Number of white-tailed eagle pairs established in coastal (black bars), inland fishpond (grey bars), and inland natural (white bars) habitats during four settlement phases

$P < 0.0001$ ). During the third settlement phase, the preference for fishponds and water bodies were retained, while the preference for streams emerged again ( $F_{5, 217} = 9.62$ ,  $P < 0.0001$ ). During the last phase, preferences were the same as during the first phase: for fishponds, streams, and wetlands ( $F_{4, 226} = 31.08$ ,  $P < 0.0001$ ).

Relative productivity of white-tailed eagles did not differ between nesting territories in different habitat types ( $F_{2,83} = 0.03$ ,  $P = 0.97$ ), neither for territories established prior to or since 2001 ( $F_{1, 83} = 1.27$ ,  $P = 0.26$ ). Reproductive output in later established territories within the same habitat type was not significantly lower compared to early established territories ( $F_{2, 83} = 1.22$ ,  $P = 0.30$ ), although the pattern for inland habitats and coastal habitat was slightly different (Fig. 5). The abundance of preferred feeding habitats also did not explain observed variation of reproduction. The best model subset (i.e.  $\Delta AICc \leq 2$ ) included two meaningful models. The first one contained water bodies proportion (model weight = 0.22) and second the proportion of fishponds (model weight = 0.21). The mean relative productivity of nesting territory was not predicted by the area of these habitats within a 6-km radius around nest sites (GLM,  $P \geq 0.6$  in models with water bodies and fishponds).

**Genetic structure of population**

After alignment of newly obtained control region sequences, six different haplotypes already found elsewhere in the distribution range (A01, A02, B01, B03, B06, and B07) were identified among the sample of 45 individuals representing the population of white-tailed eagles breeding in Lithuania (Table 1). The haplotype diversity value was 0.711. The recovered Lithuanian population of white-tailed



**Fig. 5** Relative productivity of white-tailed eagles in nesting territories established in three habitat types prior to 2001 (black circles) and since 2001 (hollow circles). Confidence intervals at 95 % are shown. Sample size of nesting territories for inland fishpond habitat type prior to 2001 and since 2001 are 17 and 15, respectively, for coastal habitat type prior to 2001 and since 2001 are 11 and 15, respectively, for inland natural habitat type prior to 2001 and since 2001 are seven and 24, respectively

**Table 1** Absolute frequencies of the mtDNA control-region haplotypes in three habitat types in the Lithuanian population of white-tailed eagle ( $n = 45$ )

	A01	A02	B01	B03	B06	B07	Total
Coastal	5	4	2	2	0	0	13
Inland fish pond	10	1	4	0	2	1	18
Inland natural	5	1	8	0	0	0	14
Total	20	6	14	2	2	1	45

A01, A02, B01, B03, B06, B07—haplotype names described in previous studies (Hailer et al. 2007; Langguth et al. 2013)

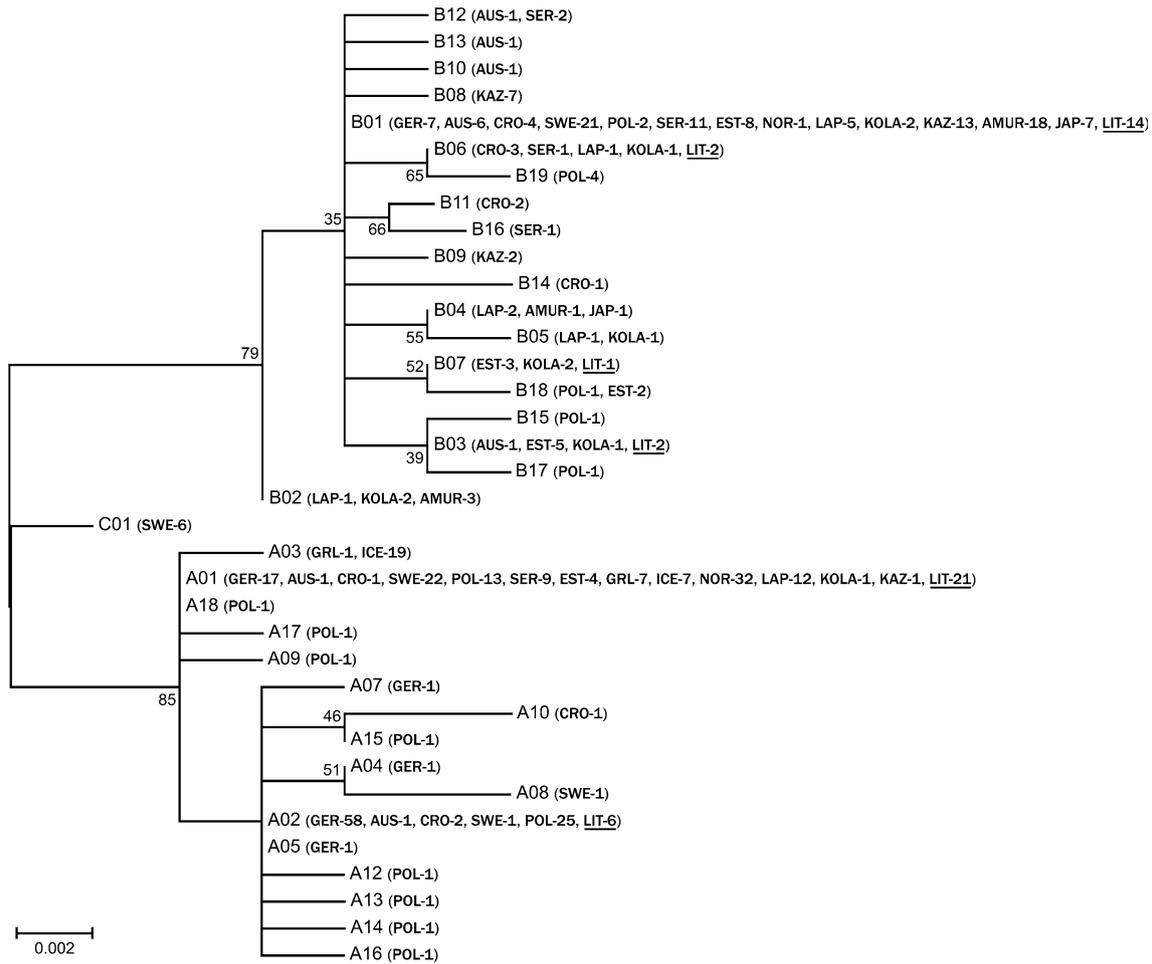
eagles harbour the same most frequent haplotypes A01 and B01 as was found in Sweden (Fig. 6). In Lithuanian white-tailed eagles the less common A02 haplotype was the most frequent in populations of Central (Poland) and Western (Germany) Europe. The rare haplotypes B03 and B07 found in Lithuania are distributed among populations situated in the northeastern region including Estonia, Kola, and Lapland. Another rare haplotype, B06, in Lithuanian white-tailed eagles was found in geographically distant populations including Kola, Lapland in the north, and in the Balkan region (Serbia, Croatia). Individuals belonging to most frequent haplotypes, A01 and B01, were

significantly differently distributed across the three habitat types in Lithuania ( $\chi^2_2 = 14.63$ ,  $P = 0.0007$ ) (Table 1). Half of all individuals belonging to A01 haplotype were concentrated in the inland fishpond habitat, while individuals with B01 haplotype most frequently were found in the inland natural habitat (57 %). Three nesting territories in the fishpond habitat harboured two unique haplotypes, while one unique haplotype was detected in a nesting territory located in the coastal habitat.

**Discussion**

During 1985–2011, the white-tailed eagle population recovered from 0 to 120 pairs occupying a range of 34,000 km<sup>2</sup>. The habitat settlement pattern was not random as high-quality habitats were occupied first. Reproduction was similar across territories in different habitat types as well as among territories established during different years, supporting the ideal free distribution model. Eagles preferred aquatic habitats, but habitat preferences were not translated into fecundity of settlers. The population reproduced well with no evidence of anthropogenic suppression, but brood failures increased in later years, possibly indicating the growing effect of density-dependent regulation. Phylogenetically, the Lithuanian population is more closely related to the populations of Sweden, Poland, and Germany, while some similarity with Lapland, Kola, and Estonia populations was evident too. These findings indicate possible source populations directly or indirectly participating in the process of recovery of the formerly extinct Lithuanian population. Moreover, haplotypes distribution across the three habitat types in Lithuania was uneven.

Similarly to the population of white-tailed eagles in Lithuania, the populations in other European countries also rapidly increased over the same period from the early 1990s. Between 1991 and 2007, there was a five-fold rise in the population in Germany (Hauff 2009) and Finland (Stjernberg et al. 2005), while the total population of the species increased three-fold in all riparian countries of the Baltic Sea (Herrmann et al. 2014). White-tailed eagles increased in continental Europe as well, e.g. in Belarus (Dombrovski and Ivanovski 2005). Two complementary reasons enhanced the recovery of white-tailed eagles in the Baltic Sea region. First, the ban on DDT use and the gradual decrease of contamination in eggs of DDE and PCB over time improved reproduction of the white-tailed eagle (Helander et al. 2008). Second, winter-feeding during conservation projects essentially contributed to increased survival among yearlings and sub-adult birds (Stjernberg et al. 2005). The initial and subsequent sharp increase of



**Fig. 6** Maximum likelihood (ML) tree of the control region haplotypes distributed among all studied populations of white-tailed eagle showing differentiation of lineages disclosed in the phylogenetic analyses. Bootstrap values at relevant nodes are shown. Haplotypes identified in Lithuanian population (LIT) are *underlined*. Data for other geographical regions are taken from Langguth et al. (2013). Abbreviations of different populations: *AMUR* Amur river, eastern

Russia, *AUS* Austria, *CRO* Croatia, *EST* Estonia, *GRL* Greenland, *GER* Germany, *ICE* Iceland, *JAP* Japan, *LAP* Swedish Lapland, *LIT* Lithuania, *KAZ* Kazakhstan, *KOLA* Kola peninsula, northwest Russia, *NOR* Norway, *POL* Poland, *SER* Serbia, *SWE* Sweden. Actual number of each haplotype found in different population are shown in parentheses

Lithuanian breeding white-tailed eagle population may be attributed to immigrant settlers, just as in other recovered populations (e.g., Literák et al. 2007), as no evidence of breeding white-tailed eagles in Lithuania was found since the middle of the twentieth century, and starting from the 1970s, only solitary or small groups of immature birds were observed regularly (Dementavičius 2007). Later, birds of local origin complemented the breeding population (observation of ringed birds; D. Dementavičius unpublished data) as white-tailed eagles do not usually settle far from the natal area after maturation (Struwe-Juhl and Grünkorn 2007; Bělka and Horal 2009).

Our data suggest non-random, sequential habitat settlement. Early occupied habitat types (i.e. inland fishpond and coastal habitats) or sites (i.e. territories established prior to 2001), however, were not better in terms of reproductive

performance compared to later occupied habitat type (inland natural) and sites (since 2001). These findings are in agreement with assumptions of the ideal free distribution model. In raptor studies, assumptions of ideal behavior (i.e. recognition of high-quality sites and settlement accordingly) and despotic distribution (i.e. higher fitness in better sites) are frequently supported (review in Löhmus 2004; Wightman and Fuller 2006; Sergio et al. 2007). Evidence of despotic distribution, however, was not found for osprey *Pandion haliaetus* (Bai et al. 2009) or booted eagle *Hieraaetus pennatus* populations (Pagán et al. 2009), while rare support for ideal free distribution was found in the griffon vulture *Gyps fulvus* population (Fernández et al. 1998). Why did the white-tailed eagle not behave despotically? Brown (1969) proposed three critical levels of population density. At the first level, the population is not sufficiently

dense and individuals are not restricted to enter preferred habitat by other individuals. At the second level, early established individuals prevent newcomers occupying high-quality habitats and later birds breed in less suitable sites. At the third level, all suitable habitats are occupied and surplus potential breeders exist as floaters. We speculate that we studied the population at an intermediate position between the first and the second density levels, i.e. high-quality patches were occupied at a regional scale, and further increase in numbers resulted in higher habitat saturation through the establishment of territories in lower-quality sites.

The white-tailed eagles preferred aquatic habitats as expected, but the preferences varied between periods. Across the distribution range, white-tailed eagles breed in areas with ample supplies of prey—fish and water birds, i.e. near marine fjords, brackish water, lakes, rivers, in alluvial forests, and floodplains (Helander and Stjernberg 2003). We suggest that the observed variation in preferences during the recovery is a consequence of uneven settlement in different habitat types (see above) and landscape differences on a regional scale in the study area. Preferences for essential feeding habitats were not reflected in breeding performance. The lack of positive relationship between preferences and reproduction is rather common in raptors (review in Löhmus 2004; Bai et al. 2009), and several possible reasons could cause this, including the use of circular plots that do not precisely capture realized habitat size and composition (see Krone et al. 2013). Breeding performance of white-tailed eagles, however, varies very little at the regional scale, even with longitudinal and habitat differences (see in Helander et al. 2013). Survival rather than reproduction could be a more important component of white-tailed eagle fitness (Helander and Stjernberg 2003). Additionally, low variability in the quality of occupied sites (e.g., Pagán et al. 2009), abundance of high-quality sites at the present density level (see above) and reproduction dependence on individual age, but not on habitat (Forslund and Pärt 1995) could explain the neutral habitat preferences.

The reproductive performance of the recovered Lithuanian white-tailed eagle population is similar to populations in the Baltic Sea countries, where reproduction markedly improved since the early 1990s (Stjernberg et al. 2005; Krüger et al. 2010; Helander et al. 2013), indicating an overall decrease in environmental contamination. Enhanced nest site protection also contributed to improved reproduction (Kollmann et al. 2002). To evaluate the good status of the breeding performance of white-tailed eagles, reference values were developed for 5-year average productivity ( $>1.0$ ), brood size ( $>1.64$ ), and breeding success ( $>60\%$ ) based on available pre-1954 background reproduction data (Helander et al. 2013). As pre-1954 data from

many geographical areas were missing (Helander et al. 2013), we applied these indicators to Lithuanian population performance. Productivity during the two most recent 5-year periods (i.e. 2002–2006 and 2007–2011) of the studied population was 1.13 and 1.09, brood size 1.73 and 1.72, and breeding success 67 and 63 %, respectively. This suggests that the increased Lithuanian white-tailed eagle population is not suppressed by residual environment contamination, persecution, heavy disturbance at nest sites, or other forms of anthropogenic pressures.

We observed more frequent brood failures when the population nearly doubled. Reproduction decrease in increased populations is usually observed in territorial birds (Ferrer and Donazar 1996; Fasce et al. 2011; Nevoux et al. 2011; Grünkorn et al. 2014; but see e.g. Krüger et al. 2012). Two alternative mechanisms are frequently proposed to explain how increased density can affect reproduction. Under habitat heterogeneity hypothesis (HHH), reproduction declines in a growing population as a consequence of an increased proportion of individuals relegated to low-quality sites, while under the interference competition hypothesis (ICH), increased frequency of aggression leads to a uniform reproduction depression among territories (Ferrer et al. 2006 and references therein). Our finding could only be explained with caution within a fine-scale population regulation framework (namely under HHH or ICH). We studied the population at a regional level, which potentially encompasses variability not only among the territories, but across the landscape as well (Carrete et al. 2006; Sergio et al. 2007), although we did not find evidence for that. A left-skewed distribution of white-tailed eagle brood size and negative relationship between mean and skewness of productivity could indicate HHH (see Ferrer et al. 2006, 2008). This evidence for distinction between the two hypotheses in density-dependent population regulation in long-lived raptors, however, was questioned (Beja and Palma 2008). Moreover, we did not find evidence of habitat contribution to breeding performance in white-tailed eagles either at habitat type or at individual territory composition level. Interference competition may also have contributed to the observed brood failure increase. During population saturation in territorial animals, individual territories are compressed, costs of territory defense increase and, as a consequence, breeding performance decreases (Carrete et al. 2006 and references therein). Inter-nest distances markedly decreased when the population of white-tailed eagles increased (e.g., Stjernberg et al. 2003; author's unpublished data). Fatal fights between white-tailed eagle individuals, intrusions into established territories by subadults, and fights with territorial adults are well documented in increased populations (Stjernberg et al. 2003; Struwe-Juhl and Grünkorn 2007; Krone et al. 2013; Herrmann et al. 2014), while territorial

conflicts in air between adults were frequently observed during fieldwork in recent years by us. Some studies demonstrate a more complex pattern of density-dependent regulation and conceal obligate dichotomy between the importance of habitat heterogeneity and interference competition in the same population (e.g. Rodenhouse et al. 2003); these two mechanisms could act simultaneously with asymmetrical effect on different vital rates (Nevoux et al. 2011) or on the same vital rate in sites of different quality (Carrete et al. 2006; Grünkorn et al. 2014).

No evidence of sporadic distribution of unique haplotypes in the recently recovered Lithuanian population was found. After comparison of the results of previous investigations carried out by other researchers (Hailer et al. 2006, 2007; Honnen et al. 2010; Langguth et al. 2013; Ponnikas et al. 2013) with the data derived during this study, an almost equal distribution of the most frequent haplotypes A01 and B01 was revealed in the Lithuanian white-tailed eagle population. The established haplotype structure and haplotype diversity value ( $H_d = 0.711$ ) in the Lithuanian population of white-tailed eagles confirms the significant impact of representatives of both haplogroups A and B onto the formation of the genetic structure of this recovered population. The results of genetic analysis indicate that the breeding population of this species in Lithuania was recently formed by birds of different origin—both by individuals from Eastern and Western/Northern Europe. A similar genetic population structure was earlier recorded for the tufted duck *Aythya fuligula* and for the whooper swan *Cygnus cygnus*, expanding their breeding range in the Baltic Region (Tubelytė et al. 2011; Butkauskas et al. 2012). Taking into account that some rare haplotypes (B03, B06, B07) were introduced by individuals ascending from several populations sharing these haplotypes with Lithuanian population, direct relationships between particular population could hardly be assumed. Nevertheless, the established haplotype structure and the highest haplotype diversity values of some European populations including Croatia (0.895), Serbia (0.667), Estonia (0.779), Sweden (0.642), Poland (0.732), Lapland (0.667), and Austria (0.773) suggest an intermediate level of haplotype diversity in the restored Lithuanian population (0.711). Considerably lower values of haplotype diversity were calculated for the populations in Greenland (0.250), Iceland (0.442), and Norway (0.060), which consist of representatives of haplogroup A. Similarly low values were also detected in the Amur (0.325) and Japanese (0.250) populations consisting of representatives of haplogroup B. Within Lithuania, individuals belonging to two different haplotypes (A01 and B01) were distributed unequally, especially across the two inland habitat types. Nesting sites belonging to different habitat types are spatially interspersed, hence this pattern could be hardly explained by

geographical location alone. Ponnikas et al. (2013) suggested that the Finnish white-tailed eagle population has ongoing immigration from neighbouring populations, which varies between years. Sites in the fishpond habitat were occupied earlier compared to sites in natural habitat, thus it may be supposed that source populations of immigrant birds varied in time. On the other hand, nesting site choice could be genetic, imprinted, or learned (Clark and Shulter 1999). Whatever the mechanism driving the habitat choice of the white-tailed eagle, settlement decision could be influenced by the origin of immigrants as well.

In summary, our data support a rare example of ideal free distribution at coarse-scale in a territorial, long-lived avian predator. But this finding should be treated with caution, as in a long-lived top predator such as the white-tailed eagle, (1) habitat choice consequence on reproduction could be evident after a time lag, e.g. due to increased reproductive performance with settlers age (Forslund and Pärt 1995) and/or gradual depletion of suitable patches in landscape at a regional scale during population increase; (2) main fitness component might be not reproduction as measured in this study, but survival. Increased brood failures when the population doubled indicate a growing effect of density-dependent regulation. The importance of only a single regulatory mechanism, whether habitat heterogeneity or interference competition, is less likely and the action of both could be expected depending on fitness component, landscape type, territory or individual quality. As white-tailed eagles in many raptor communities are free from predation and competition, further studies at coarse and fine scales of increasing or stabilized populations might better explain environmental factors, intraspecific competition and their complex interaction in population regulation. Neither the abundance of key feeding habitats within the nesting territory, nor general habitat type or establishment year was significantly related with reproduction. This limits the finding of simple criterion for setting conservation priorities for optimal high-quality sites, where higher breeding performance could contribute disproportionately to future population growth. Finally, our data on haplotype distribution differences among habitat types caution that sampling within a limited area or landscape type could lead to erroneous conclusions on the genetic structure of a targeted spatially widespread population.

**Acknowledgments** We thank Rūta Meleckytė for assistance in genetic analysis. We are also grateful to Jos Stratford for English editing.

**Compliance with ethical standards**

**Conflict of interest** The authors declare that they have no conflict of interest.

**Funding** This study was partly funded by the private limited company LITAGRA and the Ministry of Environment of the Republic of Lithuania.

**Ethical approval** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

## References

- Aljanabi SM, Martinez I (1997) Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. *Nucl Acids Res* 25:4692–4693
- Bai M-L, Schmidt D, Gottschalk E, Muhlenberg M (2009) Distribution pattern of an expanding Osprey (*Pandion haliaetus*) population in a changing environment. *J Ornithol* 150:255–263
- Bakaloudis DE, Vlachos CG, Holloway GJ (2005) Nest spacing and breeding performance in Short toed Eagle *Circaetus gallicus* in northeast Greece. *Bird Study* 52:330–338
- Beja P, Palma L (2008) Limitations of methods to test density-dependent fecundity hypothesis. *J Anim Ecol* 77:335–340
- Bělka T, Horal D (2009) The White-tailed Eagle (*Haliaeetus albicilla*) in the Czech Republic. *Denisia* 77:65–77
- Brown JL (1969) Territorial behavior and population regulation in birds. *Wilson Bull* 81:293–329
- Butkauskas D, Švažas S, Tubelytė V, Morkūnas J, Sruoga A, Boiko D, Paulauskas A, Stanevičius V, Baublys V (2012) Coexistence and population genetic structure of the Whooper Swan *Cygnus cygnus* and Mute Swan *Cygnus olor* in Lithuania and Latvia. *Cent Eur J Biol* 7:886–894
- Carrete M, Donazar JA, Margalida A (2006) Density-dependent productivity depression in Pyrenean Bearded Vultures: implications for conservation. *Ecol Appl* 16:1674–1682
- Clark RG, Shulter D (1999) Avian habitat selection: pattern from process in nest-site use by ducks? *Ecology* 80:272–287
- Cramp S, Simmons KEL (eds) (1980) *The birds of the Western Palearctic*, 2nd edn. Oxford University Press, Oxford
- Dementavičius D (2007) White-tailed Eagle (*Haliaeetus albicilla*) in Lithuania: population numbers and trends 1900–2007. *Acta Zool Lituan* 17:281–285
- Dombrovski VC, Ivanovski VV (2005) New data on numbers and distribution of birds of prey breeding in Belarus. *Acta Zool Lituan* 15:218–227
- Fasce P, Fasce L, Villers A, Bergese F, Bretagnole V (2011) Long-term breeding demography and density dependence in an increasing population of golden eagles *Aquila chrysaetos*. *Ibis* 153:581–591
- Fernández C, Azkona P, Donazar JA (1998) Density-dependent effect on productivity in the Griffon Vulture *Gyps fulvus*: the role of interference and habitat heterogeneity. *Ibis* 140:64–69
- Ferrer M, Donazar JA (1996) Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish Imperial Eagles. *Ecology* 77:69–74
- Ferrer M, Newton I, Casado E (2006) How to test different density-dependent fecundity hypotheses in an increasing or stable population. *J Anim Ecol* 75:111–117
- Ferrer M, Newton I, Casado E (2008) Density dependence hypotheses and the distribution of fecundity. *J Anim Ecol* 77:341–345
- Fischer W (1959) *Die Seeadler*. Neue Brehm-Bücherei. A Ziemsen Verlag, Wittenberg
- Forslund P, Pärt T (1995) Age and reproduction in birds: hypotheses and tests. *Trends Ecol Evol* 10:374–378
- Forsman D (1999) *The Raptors of Europe and the Middle East: a handbook of field identification*. T & AD Poyser, London
- Fretwell SD (1972) *Populations in a seasonal environment*. Princeton University Press, Princeton
- Fretwell SD, Lucas HL Jr (1970) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor* 19:16–36
- Grünkorn T, Potiek A, Looft V, Jonker RM, Chakarov N, Krüger O (2014) Territory quality affects the relative importance of habitat heterogeneity and interference competition in a long-lived territorial songbird. *J Avian Biol* 45:15–21
- Hailer F, Helander B, Folkestad AO, Ganusevich SA, Garstad S, Hauff P, Koren C, Nygård T, Volke V, Vilà C, Ellegren H (2006) Bottlenecked but long-lived: high genetic diversity retained in White-tailed Eagles upon recovery from population decline. *Biol Lett* 2:316–319
- Hailer F, Helander B, Folkestad AO, Ganusevich SA, Garstad S, Hauff P, Koren C, Masterov VB, Nygård T, Rudnick JA, Shiraki S, Skarphedinsson K, Volke V, Wille F, Vilà C (2007) Phylogeography of the White-tailed Eagle, a generalist with large dispersal capacity. *J Biogeogr* 34:1193–1206
- Hauff P (2009) Zur Geschichte des Seeadlers *Haliaeetus albicilla* in Deutschland. *Denisia* 27:7–18
- Helander B, Stjernberg T (2003) Action plan for the conservation of White-tailed Sea Eagle (*Haliaeetus albicilla*). BirdLife International report to the Bern Convention on the Conservation of European Wildlife and Natural Habitats, Strasbourg
- Helander B, Bignert A, Asplund L (2008) Using raptors as environmental sentinels: monitoring the white-tailed sea eagle *Haliaeetus albicilla* in Sweden. *Ambio* 37:425–431
- Helander B, Bignert A, Herrmann Ch, Stjernberg T (2013) White-tailed Eagle productivity. HELCOM core indicator report. [http://helcom.fi/Core%20Indicators/HELCOM-CoreIndicator-White-tail\\_Eagle\\_productivity.pdf](http://helcom.fi/Core%20Indicators/HELCOM-CoreIndicator-White-tail_Eagle_productivity.pdf). Accessed 20 Dec 2014
- Herrmann C, Krone O, Stjernberg T, Helander B (2014) Population development of baltic bird species: White-tailed sea Eagle (*Haliaeetus albicilla*). HELCOM Baltic sea environment fact sheets. <http://www.helcom.fi/baltic-sea-trends/environment-fact-sheets>. Accessed 20 Dec 2014
- Hollander FA, Van Dyck H, San Martin G, Titeux N (2011) Maladaptive habitat selection of a migratory passerine bird in a human-modified landscape. *PLoS One* 6:e25703
- Honnen AC, Hailer F, Kenntner N, Literák I, Dubská L, Zachos FE (2010) Mitochondrial DNA and nuclear microsatellites reveal high diversity and genetic structure in an avian top predator, the white-tailed sea eagle, in central Europe. *Biol J Linn Soc* 99:727–737
- Kekkonen J, Seppä P, Hanski IK, Jensen H, Väisänen RA, Brommer JE (2011) Low genetic differentiation in a sedentary bird: house sparrow population genetics in a contiguous landscape. *Heredity* 106:183–190
- Kollmann R, Neumann T, Struwe-Juhl B (2002) Bestand und Schutz des Seeadlers (*Haliaeetus albicilla*) in Deutschland und seinen Nachbarländern. *Corax* 19(Special Issue 1):1–14
- Kristan WB III, Johnson MD, Rotenberry JT (2007) Choices and consequences of habitat selection for birds. *Condor* 109:485–488
- Krone O, Berger A, Schulte R (2009) Recording movement and activity pattern of a White-tailed Sea Eagle (*Haliaeetus albicilla*) by a GPS datalogger. *J Ornithol* 150:273–280
- Krone O, Nadjafzadeh M, Berger A (2013) White-tailed Sea Eagles (*Haliaeetus albicilla*) defend small home ranges in north-east Germany throughout the year. *J Ornithol* 154:827–835
- Krüger O (2002) Analysis of nest occupancy and nest reproduction in two sympatric raptors: common buzzard *Buteo buteo* and goshawk *Accipiter gentilis*. *Ecography* 25:523–532
- Krüger O, Grünkorn T, Struwe-Juhl B (2010) The return of the White-tailed Eagle (*Haliaeetus albicilla*) to northern Germany: modelling the past to predict the future. *Biol Conserv* 143:710–721

- Krüger O, Chakarov N, Nielsen JT, Looft V, Grünkorn T, Struwe-Juhl B, Møller AP (2012) Population regulation by habitat heterogeneity or individual adjustment? *J Anim Ecol* 81:330–340
- Langguth T, Honnen AC, Hailer F, Mizera T, Skoric S, Väli Ü, Zachos FE (2013) Genetic structure and phylogeography of a European flagship species, the White-tailed Sea Eagle *Haliaeetus albicilla*. *J Avian Biol* 44:263–271
- Literák I, Mrlík V, Hovorková A, Mikulíček P, Lengyel J, Št'astný K, Cepák J, Dubská L (2007) Origin and genetic structure of White-tailed Sea Eagles (*Haliaeetus albicilla*) in the Czech Republic: an analysis of breeding distribution, ringing data and DNA microsatellites. *Eur J Wildlife Res* 53:195–203
- Löhmus A (2001) Habitat selection in a recovering Osprey *Pandion haliaetus* population. *Ibis* 143:651–657
- Löhmus A (2004) Raptor habitat studies—state of the art. In: Chancellor RD, Meyburg B-U (eds) *Raptors Worldwide*. WWGBP/MME, Budapest, pp 279–296
- Mac Sharry B (2012) User manual for range tool for article 12 (birds directive) and article 17 (habitats directive). European Topic Centre on Biological Diversity, Paris
- Nevoux M, Gimenez O, Arlt D, Nicoll M, Jones C, Norris K (2011) Population regulation of territorial species: both site dependence and interference mechanisms matter. *Proc R Soc B Biol Sci* 278:2173–2181
- Oehme G (2003) On the methods, terminology and criteria in population studies of the White-tailed Eagle. In: Helander B, Marquiss M, Bowerman B (eds) *Sea Eagle 2000*. Swedish Society for Nature Conservation, Stockholm, pp 25–26
- Pagán I, Martínez JE, Calvo JF (2009) Territorial occupancy and breeding performance in a migratory raptor do not follow ideal despotic distribution patterns. *J Zool* 279:36–43
- Ponnikas S, Kvist L, Ollila T, Stjernberg T, Orell M (2013) Genetic structure of an endangered raptor at individual and population levels. *Conserv Genet* 14:1135–1147
- Pulliam HR, Danielson BJ (1991) Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *Am Nat* 137:50–66
- Rodenhouse NL, Sherry TW, Holmes RT (1997) Site-dependent regulation of population size: a new synthesis. *Ecology* 78:2025–2042
- Rodenhouse NL, Sillett TS, Doran PJ, Holmes RT (2003) Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season. *Proc Roy Soc B-Biol Sci* 270:2105–2110
- Roques S, Negro JJ (2005) MtDNA genetic diversity and population history of a dwindling raptorial bird, the red kite (*Milvus milvus*). *Biol Conserv* 126:41–50
- Rozas J, Sánchez-DelBarrio JC, Messeguer X, Rozas R (2003) DnaSP, DNA polymorphism analyses by the coalescent and other methods. *Bioinformatics* 19:2496–2497
- Sergio F, Newton I (2003) Occupancy as a measure of territory quality. *J Anim Ecol* 72:857–865
- Sergio F, Pedrini P, Rizzolli F, Marchesi L (2006) Adaptive range selection by golden eagle in a changing landscape: a multiple modelling approach. *Biol Conserv* 133:32–41
- Sergio F, Blas J, Forero MG, Donázar JA, Hiraldo F (2007) Sequential settlement and site dependence in a migratory raptor. *Behav Ecol* 18:811–821
- Stjernberg T, Koivusaari J, Högmänder J (2003) Population trends and breeding success of the White-tailed Sea Eagle in Finland, 1970–2000. In: Helander B, Marquiss M, Bowerman B (eds) *Sea Eagle 2000*. Swedish Society for Nature Conservation, Stockholm, pp 103–112
- Stjernberg T, Koivusaari J, Högmänder J, Ollila T, Ekblom H (2005) Population trends and breeding success of the White-tailed Sea Eagle *Haliaeetus albicilla* in Finland, 1970–2005. Status of raptor populations in Eastern Fennoscandia. Proceedings of workshop, Petrozavodsk, pp 151–159
- Struwe-Juhl B (2000) Funkgestützte Synchronbeobachtung—eine geeignete Methode zur Bestimmung der Aktionsräume von Großvogelarten (*Ciconiidae*, *Haliaeetus*) in der Brutzeit. *Populationsökol Greifvogel Eulenarten* 4:101–110
- Struwe-Juhl B, Grünkorn T (2007) Ergebnisse der Farbberingung von Seeadlern *Haliaeetus albicilla* in Schleswig-Holstein mit Angaben zu Ortstreue, Umsiedlung, Dispersion, Geschlechtsreife, Altersstruktur und Geschwisterverpaarung. *Vogelwelt* 128:117–129
- Tamura K (1992) Estimation of the number of nucleotide substitutions when there are strong transition-transversion and G+C-content biases. *Mol Biol Evol* 9:678–687
- Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: molecular evolutionary genetics analysis version 6.0. *Mol Biol Evol* 30:2725–2729
- Thompson JD, Higgins DG, Gibson TJ (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucl Acids Res* 22:4673–4680
- Tome D (2003) Nest site selection and predation driven despotic distribution of breeding long-eared owls *Asio otus*. *J Avian Biol* 34:150–154
- Tubelytė V, Švažas S, Sruoga A, Butkauskas D, Paulauskas A, Baublys V, Viksne J, Grishanov G, Kozulin A (2011) Genetic diversity of Tufted Ducks (*Aythya fuligula*, Anitidae) in Eastern Europe. *Cent Eur J Biol* 6:1044–1053
- Vaitkus G, Juzefaitė V (2004) CORINE land cover 2000 in Lithuania. final report. Environmental Protection Agency, Vilnius
- Väli Ü, Treinys R, Poirazidis K (2004) Genetic structure of Greater *Aquila clanga* and Lesser Spotted Eagle *A.pomarina* populations: implication for phylogeography and conservation. In: Chancellor RD, Meyburg B-U (eds) *Raptors Worldwide*. WWGBP/MME, Budapest, pp 473–482
- Wightman CS, Fuller MR (2006) Influence of habitat heterogeneity on distribution, occupancy patterns, and productivity of breeding peregrine falcons in central West Greenland. *Condor* 108:270–281
- Zimmerman GS, LaHaye WS, Gutiérrez RJ (2003) Empirical support for a despotic distribution in a California Spotted Owl population. *Behav Ecol* 14:433–437