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Nest site selection and turnover patterns in support of conservation decisions: Case study of the lesser spotted eagle in the core area of its global population

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ABSTRACT

Forest-dwelling raptors nest in the same close, mature forest stands over many years. As mature stands are targets for timber harvesting, the conservation of nest sites should be integrated into commercial forestry practices. Ecological data supporting conservation decisions are essential for ensuring effective conservation, and minimising costs and conflicts among different stakeholders. Here, we analysed nest site selection and nest site turnover patterns in a typical mature-forest-dwelling raptor in the core area of its global population. Our aim was to provide a basis for nesting habitat conservation in the context of commercial forestry. The lesser spotted eagle *Clanga pomarina* was found to prefer mature stands, located close to the forest's edge, for nesting. Pine stands were largely avoided by nesting pairs, but the composition of other tree species was similar to stands located in surrounding forests. The lesser spotted eagle occupied the nest for an average of three years, and the number of used nests within a territory increased progressively with the longevity of its occupation. Within a territory, the pair moved between alternate nests mostly up to 600 m. The results of this study suggest that long-term conservation approaches for mature-forest-dwelling raptors should use breeding territory, which contains several nest sites (or suitable stands) spaced at certain distances and covered by temporal buffer, as a target unit in conservation-supporting forestry practices.

1. Introduction

Raptors are long-lived territorial birds that occupy the same territory, year after year (Speiser and Bosakowski, 1991; Jenkins and Jackman, 1993; Forero et al., 1999). Most forest-dwelling raptors build stick nests on tall trees, which are usually located in mature forest stands (Bielański, 2006; Lõhmus, 2006). At the same time, mature trees and stands are targets for timber harvesting (Barrientos and Arroyo, 2014), resulting in the loss of nest sites and disturbance to breeding birds (Treinys and Mozgeris, 2006; Santangeli et al., 2012; but see Penteriani and Faivre, 2001). Therefore, forest logging is classed as the second most significant threat to raptor populations globally, after agri/aquaculture (McClure et al., 2018).

Raptors are mainly solitary breeders, tending to disperse over suitable landscapes in low densities (Newton, 2003). This makes it difficult to protect considerable share of population even by large protected areas (Petty, 1998). Most medium-sized and large raptors use the same nest for several years, but alternating among a few nests within their territory over the long term (Ontiveros et al., 2008; Kochert and Steenhof, 2012). This behavioural pattern justifies the widely-applied practice of establishing buffer zones (i.e. areas around nests where human activity is restricted), which helps to protect the raptors during the sensitive breeding period and saves their nest sites from destruction (Richardson and Miller, 1997; Lõhmus, 2005). In many European countries, this approach has been integrated into the national legislative framework (e.g. Helander and Stjernberg, 2002; Sielicki and Mizera, 2012; Mozgeris et al. 2015). Unfortunately, the effectiveness of current conservation practices has seldom been tested (Sutherland et al., 2004), including designated buffer zones, the sizes of which often have no obvious basis from behavioural studies for protecting the relevant species (Ruddock and Whitfield, 2007). Moreover, there are several constraints that limit the direct application of ecological data in supporting conservation decisions. For example, habitat preferences may vary between populations of the same species that breed in

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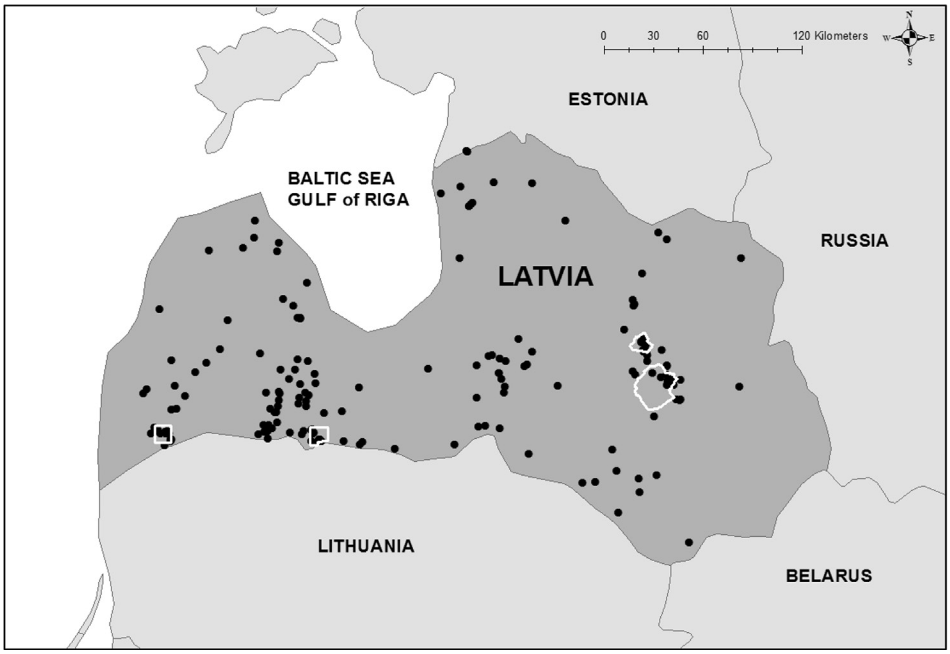

Fig. 1. Location of lesser spotted eagle nest sites in state forests (black dots, n = 176) and the borders of four study plots (white lines) where nest turnover was analysed.

different geographical areas (Väli et al., 2004) or among different landscape types within a compact region (Skuja et al., in press). There may even be shifts in habitat preferences in an expanding (Bai et al., 2009; Treinys et al., 2016) or stable (Grašytė et al., 2016; Rumbutis et al., 2017) population. Thus, rigorous ecological knowledge on species nesting ecology is required to ensure cost-effective conservation.

The lesser spotted eagle *Clanga pomarina* is a medium-sized, migratory, forest-dwelling raptor, protected internationally by the Bern (Annex II), Bonn (Annex II) and CITES (Annex I) conventions, and the Bird Directive of the European Union (Annex I). Its global population of ca. 20,000 pairs is mostly distributed over a compact range in Central and Eastern Europe (Birdlife International, 2015). The highest density is recorded in Latvia, east of the Baltic Sea, where up to 20% (ca. 3800 pairs) of the global population breeds (Bergmanis et al., 2015). Fifty-two percent (3.38 Mha) of Latvia contains forests, and forest logging is an important economic activity, producing ca. 11 Mm^3 of timber annually (www.zm.gov.lv). This has resulted in the intensive loss of mature forests since the early 1990s, when socioeconomic transition occurred (Potapov et al., 2015). The lesser spotted eagle nests in mature trees, preferably in productive mature forests, as has been found in the countries neighbouring Latvia (Skuja and Budrys, 1999; Lõhmus, 2006; Treinys and Mozgeris, 2010). Consequently, well-developed forestry and the conservation of the mature-forest-dweller's nest sites and nesting-habitat availability are not compatible (Jiménez-Franco et al., 2018).

National legislation states that rare forest-dwelling birds, including the lesser spotted eagle, should be conserved in Latvia through the designation of microreserves. In microreserves, clear-felling is prohibited in a core area of 5–30 ha of forest around a nest. This core area is surrounded by a temporary buffer zone (up to 100 ha, including the core area) where forestry activities are restricted during the breeding season from 1st March to 31st July, according to the recommendations of experts (Order No. 940, 2012). However, the application of this system to lesser spotted eagle protection has faced several recent challenges. First, this approach, which was adopted in the mid 1980s, mainly focused on protecting very rare breeding species, such as the golden eagle *Aquila chrysaetos*, the white-tailed eagle *Haliaeetus albicilla* and the black stork *Ciconia nigra*. Second, annual timber harvesting has nearly doubled in Latvia since the early 1990s, following the restoration of independence and ownership restitutions. Third, after accession to the European Union in 2004, the implementation of the Bird Directive (2009/147/EC) resulted in an increase in efforts to discover lesser spotted eagle nest sites, and subsequently protect them through designating microreserves. The designation process has become highly dependent on subjective expert judgment, however, because of: (1) the six-fold increase in the area where felling restrictions can be applied; (2) the flexibility in determining a temporary buffer zone; and (3) an absence of data on lesser spotted eagle nest turnover patterns, as well as insufficient knowledge on nest site selection in Latvia. Consequently, a recent intensification of both processes – timber harvesting and the conservation of nesting sites of the lesser spotted eagle – has caused confrontation among forest managers, nature conservationists and decision-makers.

In this paper, using comprehensive data from Latvia, we have analysed nest site selection and nest site turnover patterns in the lesser spotted eagle to gain an understanding of how to integrate knowledge of the species' ecology into forest management. More specifically, we asked: (1) which forest characteristics shape the nest site preferences of the lesser spotted eagle, based on comparison with sites available in surrounding forests; (2) for how many years do eagles occupy the same nest; and (3) what is the distance between alternative nests used within the same breeding territory. Notably, to our knowledge, nest occupation longevity, as well as the spacing of nests within a breeding territory, have not yet been comprehensively analysed for this species. We expected to define the key features of stands suitable for nesting, the area of stands with restrictions against clear-felling within microreserves, and the area of temporal buffers to cover nest turnover of the species. After answering these questions, we developed a set of recommendations to enhance conservation of the lesser spotted eagle in the core area of its global distribution range. These recommendations are extendable to other regions, and thus could also serve as a model for protecting other, similar forest-dwelling birds.

2. Material and methods

2.1. Nest site preference

Data about the locations of lesser spotted eagle nests were collected in Latvia, located east of the Baltic Sea (56°53′N, 24°36′E, area of the country 64,589 km^2; Fig. 1). Information on nests located in state-owned forests was available from the database managed by Latvian State's Forests. The nests were found by: (1) foresters during their usual forestry activities (species checked by experts prior to information entry in the database); (2) ornithologists implementing the monitoring of lesser spotted eagles in study plots by observation of the birds' behaviour; (3) ornithologists during the Life Nature project LIFE13 NAT/LV/001078 'Conservation arrangements for the lesser spotted eagle in Latvia', by observation of bird behaviour, searching and checking large raptors nests; and (4) ecologists from the administrations of the protected areas.

The habitat preferences may change over long periods (e.g. Bai et al., 2009; Treinys et al., 2016), thus we included only recently-occupied (i.e. 2006–2017) nests. When several nests were located close each other (e.g. up to several hundred metres, indicating the same territory of a lesser spotted eagle pair and thus potentially introducing pseudo-replications), we included only one nest, which was occupied close to the middle of the 2006–2017 period.

A nest site was defined as a forest stand (mean size ca. 3 ha) containing a nest. Altogether, 176 nests were used to describe the nest site characteristics. To estimate nest site preferences, we compared lesser spotted eagle nest sites with the same number of randomly-chosen forest plots (hereafter – control plots) in state forests available within a 2-km radius around the nests. The 2 km radius around a nest represents the most important area of a breeding pair's home range (Scheller et al., 2001; Meyburg et al., 2004), where the individuals return to breed year after year (Dravecký et al., 2013; Väli and Bergmanis, 2017), and select their nest sites. This procedure was applied because habitat selection is a hierarchical process (Block and Brennan, 1993), thus erroneous conclusions are made when spatial scale is ignored (Jones, 2001); for example, when comparing nest sites with plots located in the landscape that are not inhabited by the species. A control point in the state forest layer was randomly selected, using a random point generator tool (ArcGIS 10.3). A stand containing a control point was used as a control plot.

We used the following explanatory variables: the age of the stand and the proportional volumes of pine, spruce, birch, black alder and aspen, additional spruce (presence/absence of solitary trees), the Shannon diversity index of the tree composition in the stand, the distance to forest edge (i.e. the shortest Euclidean distance to agricultural land patches with the codes 211, 231, 242 and 243 from the most recent Corine land-cover database, CLC 2012). To estimate habitat preference, we used nest stands and control forest stands that were ≥59 years old (58 years is the 10th percentile of nest stands used by the lesser spotted eagle; 158 stands represented the lesser spotted eagle and 74 stands were controls). We used binomial generalised linear models (GLMs; link = logit), where the control stands equalled 0 and the nest stands equalled 1 (package lme4; Bates et al., 2015). The dredge function from the MuMIn package (Bartoń, 2018) was used to build models with all possible combinations of explanatory variables. We used the information–theoretical approach for model selection and the multi-model inference procedure (Burnham and Anderson, 2002). Akaike's information criterion (AIC), with a correction (AICc) for small sample size, was used to select the best models from the model's set. The models were ranked by $\Delta AICc = AICc_i – AICc_{min}$ (where $AICc_{min}$ was the best model in a model set). Model weight was estimated through the normalised Akaike weights, $\exp(-0.5 \times \Delta AICc)/\Sigma_{r=1}^{R} \exp(-0.5 \times \Delta AICc_r)$. A threshold of $\Delta AICc \leq 2$ was used to separate models well-supported by the data from poorly-supported models. Due to high model selection uncertainty, we used a model averaging procedure to estimate the relative importance values for each explanatory variable included in the model from the best model's subset (Burnham and Anderson, 2002). The statistical environment R v.3.5.1 (R Core Team, 2018) was used for the calculations.

Forest type is one of the key characteristics representing the overall condition of a stand, including soil, humidity and plant species composition (forest typology classification: Bušs, 1981), and has been widely used to characterise bird nest sites in Baltic countries (Skuja and Budrys, 1999; Treinys and Mozgeris, 2006). We compared proportional distributions of nests and control stands over 19 forest types using the chi-squared test.

To test the country-wide spatial variation of distances to the forest edge from eagle nests (response variable), we used one explanatory variable – region (Latvian forests divided into eight geographical regions: https://www.lvmgeo.lv/en/maps) (GLM, link = identity; sample = 176 nest stands). To explain the stand age of the lesser spotted eagle nest sites (response variable), we included the dominant tree species and region as explanatory variables in the GLMs (link = identity; sample = 157 nest stands older than 59 years). We applied the model-ranking procedure described above.

2.2. Nest turnover patterns

Lesser spotted eagle nest occupation and turnover was monitored in four study plots, where eagles were censused from mid-April to 10th May and then from mid-June to mid-August. The census started in 1994 in the Murmastiene plot (460 km^2), in 2002 in Žūklis (94 km^2), in 1988 in Bukaiši (106 km^2) and in 2008 in Mazgramzda (100 km^2) (Fig. 1; for a description of the plots and the detailed field procedure, see Bergmanis et al., 2015). Altogether, 793 nest occupations were observed in 80 lesser spotted eagle breeding territories. For each eagle territory (an area that contains one or more nests within the home range of a mated pair or a single individual), we calculated the: (1) longevity of territory occupancy (we included only the years when any known nest in a territory was occupied); (2) number of nests within a territory during its occupancy; (3) longevity of nest occupancy (total number of years when a nest was occupied); (4) nest change distance (distance between two nests occupied in consecutive years; Fig. 2); and (5) distance between nests (the mean distance between all nests found within a territory during its occupation; Fig. 2).

We applied the GLMs to test: (1) whether the number of nests within a territory (response variable) depended on the study plot and the longevity of territory occupancy (explanatory variables); and (2) whether the distance between the nests within a territory (response variable) depended on the study plot, the longevity of the territory occupancy and the number of nests occupied within a territory (explanatory variables). The structures of the models and their errors, as well as the link functions, are presented in Table 2. We used the same model selection and multi-model inference approach described above. The 'predict' function (type = 'response') was used to predict: (1) the number of nests within a territory if occupation of that territory was to last for 5, 10, 15 and 20 years; and (2) the mean distance between nests if a pair of eagles was to occupy 2, 3, 4 and 6 nests.

3. Results

3.1. Nest site preference

The descriptive characteristics of the nest sites are presented in Appendix. The nest sites of the eagles differed significantly from the control plots, as indicated by five models that were supported by the data (i.e. $\Delta AICc \leq 2$; Section A in Table 1). Averaging of these supported models indicated that lesser spotted eagle nest sites were best characterised by proximity to agricultural land, greater stand age and a low proportion of pine compared to control stands available in surrounding forests. The nest sites' proportional distributions over forest types were similar to the control stands ($\chi^2 = 22.6$, df = 18, $P < 0.21$; see Suppl. mat. 1), indicating that eagles did not prefer or avoided certain forest type stands.

The strong preference of lesser spotted eagles for proximity to agricultural areas was retained across Latvia (Fig. 3) because the GLM

Fig. 2. Example of measured distances between lesser spotted eagle nests: (1) two measurements (distance between nests occupied in 2002 and 2003, as well as distance between nests from 2003 and 2004) were taken and used separately for the variable 'nest change distance'; (2) the mean of three measurements (i.e. distances between nests from 2002 and 2003, 2003 and 2004, 2002 and 2004) were used for the variable 'distance between nests'.

to explain the variation of distance to forest edge by region (ΔAICc = 1.77), based on the evidence ratio, was 2.4 times less likely than the intercept GLM (ΔAICc = 0.00) (Section B in Table 1). Nest stand age was best explained by the dominant tree species, together with the geographical region (for estimates see Suppl. mat. 2); the GLM including these two explanatory variables was 1.9 more likely, based on the evidence ratio, than the second-ranked GLM, with dominant tree species as the only variable (Section C in Table 1). Hardwood deciduous trees (oak or ash) and pine dominated among the oldest nest stands, spruce stands were medium-aged and stands with dominant aspen, birch and black alder in the first layer of trees were the youngest (Fig. 4).

3.2. Nest turnover patterns

Lesser spotted eagles occupied territories for an average of 9.9 years ± 5.4 SD (n = 80). The longest occupation of a territory lasted 23 years out of 31 years when the territory was controlled. Nests were occupied, on average, for 3.00 years ± 2.64 SD (range 1–14 years; n = 267). The longest uninterrupted reoccupation of a nest was for 12 years. Within their territories, eagles occupied from one to nine nests (on average, 3.3 nests ± 1.7 SD, n = 80). The number of nests occupied within a territory was best explained by the longevity of territory occupancy, and the model including only this explanatory variable was supported by the data (Section A in Table 2). Hence, the number of nests within a territory progressively increased with time of territory occupancy (GLM: $P < 0.05$). According to the predictions estimated from the model, we calculated the number of nests during territory occupancy for 5, 10, 15 and 20 years (Table 3).

New nests were built (or the eagle moved to a formerly-occupied nest) a mean 427 m ± 395 SD (n = 255) from the previous one. Most (78%) of such 'movements' were within a radius of 600 m, while the

Table 1
Summary of models estimating (A) differences in stand features (explanatory variables) between nests sites and control plots (response variable), (B) variation in distance from lesser spotted eagle nests to forest edge (response variable) among regions (explanatory variable), and (C) lesser spotted eagle nest stand age (response variable) variation relationship with dominant tree species and region (explanatory variables). + and − indicate value increase and decrease (respectively) in lesser spotted eagle stands compared to control forest stands. RVI – relative variable importance, estimate ± standard error (bold coefficients $P < 0.05$) taken for variables in the average model, calculated from the best model's subset (i.e., ΔAICc < 2).

Model	Explanatory variables						ΔAICc	Weight
(A) Nest vs. control								
	Forest edge	Age	Pine	Aspen	Bl.alder	Add.spruce		
No. 1	−	+	−				0.00	0.303
No. 2	−	+	−		+		0.60	0.224
No. 3	−	+	−			+	1.05	0.179
No. 4	−	+	−	−			1.33	0.156
No. 5	−	+	−		+	+	1.59	0.137
Estimate ± se	**−0.004 ± 0.001**	**0.04 ± 0.01**	**−1.42 ± 0.67**	−0.68 ± 0.78	1.16 ± 1.0	0.34 ± 0.33		
RVI	1.00	1.00	1.00	0.16	0.36	0.32		
(B) Distance to forest edge								
No. 1	Null						0.00	0.708
No. 2	Region						1.77	0.292
(C) Nest stand age								
No. 1	Dominant tree	Region					0.00	0.659
No. 2	Dominant tree						1.31	0.341
No. 3		Region					32.36	0.00
No. 4	Null						35.31	0.00

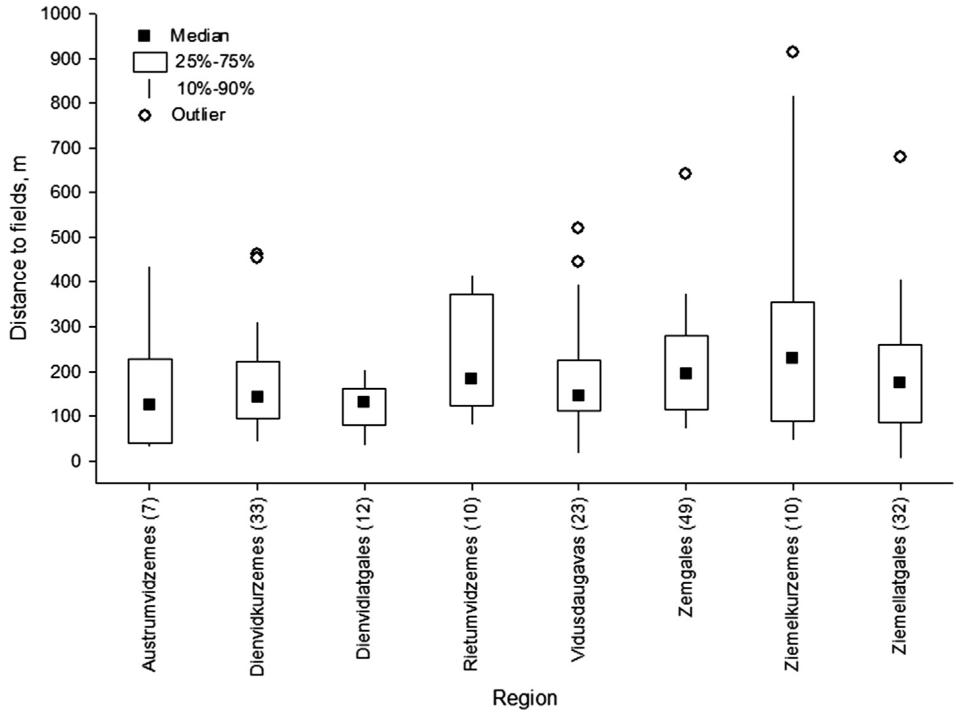

Fig. 3. Distances from lesser spotted eagle nests to nearest agricultural areas (i.e. forest edge) in different Latvian regions (number of nests in brackets).

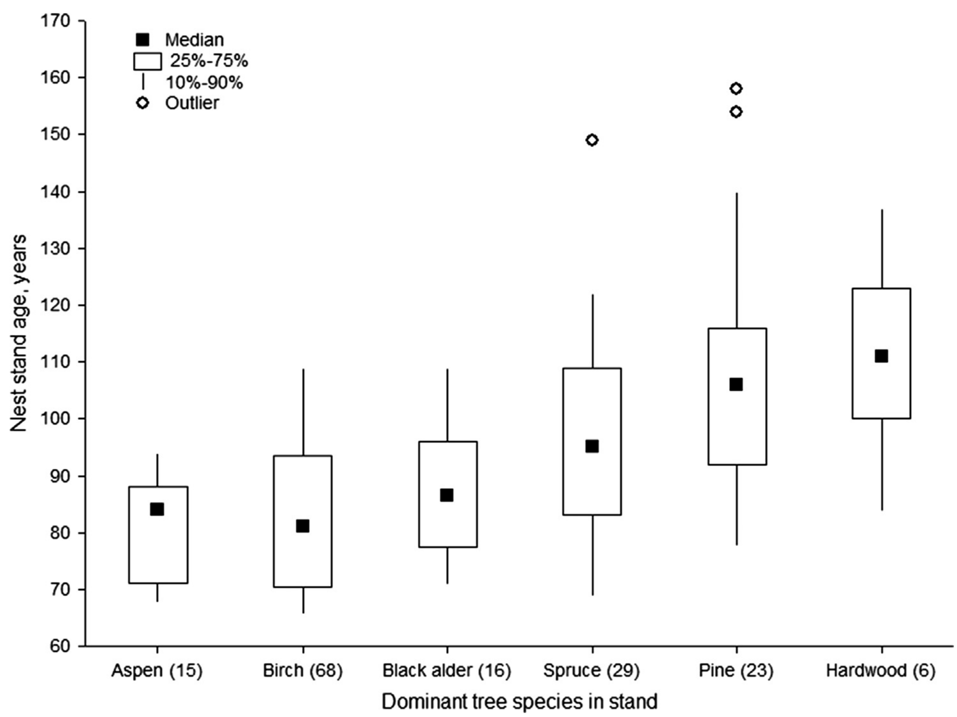

Fig. 4. Lesser spotted eagle nest stand age according to dominant tree species in the stand (number of nests in brackets).

rest were scattered over a wide array of distances (Fig. 5). In territories where at least two nests were registered during the study years, the nests were located at an average of 449 m ± 316 SD (n = 75) from each other. The mean distance between nests in a territory was only explained by the number of nests in the territory (Section B in Table 2); the nests were located more distantly from each other when there were more nests in the territory (GLM: 59 m ± 22 SE). The estimated predictions for mean distance between nests within territories containing two to six nests are presented in Table 3.

4. Discussion

The lesser spotted eagle preferred mature stands, located in the vicinity of the forest edge, for nesting in the most densely populated area of their entire distribution range. Pine stands were avoided, but otherwise the stands with nests were similar to the ones available in the surrounding forests. Territories were occupied for a decade, on average, but the occupation of nests within a territory lasted ca. three times less. This resulted in an increase in the number of nests used progressively, along with the longevity of territory occupation. Within a territory, the

Table 2
Comparison of model ΔAICc and AICc weights to test relationships between (A) number of nests within the territory (response variable) and (B) distances between nests within the territory (response variable) and study plot, longevity of territory occupancy and number of nests within the territory (explanatory variables). At the bottom of both model blocks, the structure of the errors and links are presented.

Model	Explanatory variables			ΔAICc	Weight
(A) Number of nests					
No.1		Longevity		0.0	0.95
No.2	Plot	Longevity		6.1	0.05
No.3	Plot			22.8	0.00
Null model				32.1	0.00
Error structure – Poisson, link = log					
(B) Distances between nests					
No.1			No. of nests	0.0	0.63
No.2	Plot		No. of nests	2.6	1.18
No.3	Plot			4.1	0.08
Null model				4.9	0.05
No.4	Plot	Longevity		6.0	0.03
No.5		Longevity		6.9	0.02

Error structure – normal, link = identity.

Table 3
Predicted values for number of nests within territory occupied for 5, 10, 15 and 20 years, and for mean distance between nests in territory for 2, 3, 4 and 6 nests.

Predicted number of nests for four periods of territory occupancy	Predicted mean distance between nests in territory for different nest numbers
5 years/2.2 nests	2 nests/366 m
10 years/3.1 nests	3 nests/425 m
15 years/4.3	4 nests/485 m
20 years/5.9	6 nests/603 m

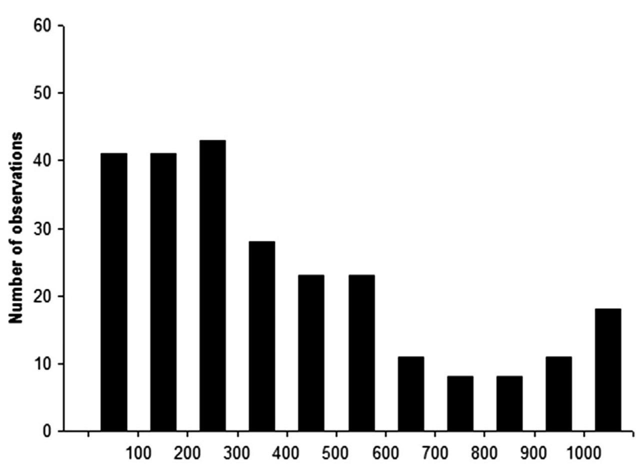

Fig. 5. Distribution of recorded lesser spotted eagle nest change distances in 100-m intervals (n = 255).

eagles moved among alternate nests that were located mostly up to 600 m from each other. The results of this study support the designation of microreserves, consisting of several mature stands distributed near forest edges that are covered by larger temporal buffers, as a suitable measure for the conservation of the lesser spotted eagle in the long term.

4.1. Nest site preference pattern

The lesser spotted eagles were not selective towards stand features, compared with the availability within a breeding territory, except for an avoidance of pine and a preference for maturity. Low selectivity at the nest stand scale might be explained by the hierarchical habitat selection model (Johnson, 1980), suggesting that decisions have already been made at a higher-order selection stage when the territories are first established. This is supported by our findings because the frequency distribution of nest stands by forest type was similar to the control stands available in the eagle territories, but differed from the Latvian forest stands. Differences in forest tree species composition between lesser spotted eagle breeding territories and the available forests in the landscape have been also found elsewhere in Europe (Langgemach et al., 2001; Lõhmus, 2006; Treinys and Mozgeris, 2010). A low selectivity of stand composition is favourable also in terms of conservation, because it results in larger availability of stands for protection of nesting habitat within occupied breeding territory.

The preference for mature stands was not unexpected because this is a very prominent feature of the lesser spotted eagle in different parts of its distribution range (see below). A well-expressed preference towards mature forests means that 72% of Latvian lesser spotted eagles nest in stands that have already reached the age for clear-cutting in commercial forests. The age of the stand was best explained by the tree species and, to some extent, the region in Latvia. Similar stand ages (ca. 85 years) to those in Latvia have been reported elsewhere, despite having different climatic conditions, tree compositions and soil types (Estonia: Lõhmus, 2006; northeastern Poland: Mirski, 2009; Lithuania: Treinys et al., 2011). Moreover, breeding densities vary geographically (Treinys et al., 2017), therefore a stronger pressure to nest in younger stands may be expected in denser populations, following the sequential habitat occupation model (Brown, 1969; Sergio et al., 2007). A geographically stable preference of the lesser spotted eagles for forests of similar age, however, negates behavioural plasticity, and indicates that this species is highly sensitive to a decrease in mature forest availability during timber harvesting, and depends on the wide-ranging integration of appropriate nesting habitat protection into forestry practices.

The lesser spotted eagle strongly prefers the forest edge (average distance ca. 200 m). Again, nesting close to a feeding habitat (meadows and other agricultural areas) is typical of the species across its European distribution, as indicated by the similar average distance to forest edge reported in different countries (averages ranged from 174 to 219 m: Langgemach et al., 2001; Väli, 2003; Mirski, 2009; Treinys et al., 2011). This is probably related to the need for balancing energy expenditure in frequently transporting small principle prey items (voles and amphibians of < 50 g) to the nest (Zub et al., 2010). The strong preference for the forest edge further limits the availability of suitable nesting patches in forest landscapes for this species. This means that not only the proportion of mature stands in forests is important, but also that the spatial pattern of such stands should be considered when planning the protection of a species with such a specific habitat preference.

4.2. Nest turnover patterns

The lesser spotted eagle faithfully occupies its territories, with an average occupation longevity of a decade, with the longest record being more than two decades. The longest occupation might be explained by hypothetical breeding life of the lesser spotted eagle: the maximum known age being 26 years and sexual maturity is reached at four years (Meyburg et al., 2005; Dravecký et al., 2008). On the other hand, it is well known that territories are occupied for many years, usually exceeding the life span even of long-lived birds (Lõhmus, 2001; Sergio and Newton, 2003; Kochert and Steenhof, 2012; Ramírez et al., 2016). New lesser spotted eagle mates, or even new pairs, may replace individuals that have disappeared from their breeding territories (Väli and Bergmanis, 2017), resulting in the continuous and long-term occupation of territories. This strongly advocates for the mapping of existing nest sites when setting conservation priorities, and not only relying on potential habitat planning.

Within the breeding territories, the lesser spotted eagle occupied an average of 3.3 nests, with the highest number of nests being nine. The number of occupied nests increased progressively with the longevity of territory occupation. The Spanish imperial eagle *Aquila adalberti* uses an average of 3.5 nests (range = 1–11) in their territories, and the mean number of used nests significantly increases through the years of territory occupancy (Margalida et al., 2007). In a community of booted eagle *Aquila pennata*, common buzzard *Buteo buteo*, and northern goshawk *Accipiter gentilis* the average occupation time of the available nests by any species was 3.3 years (Jiménez-Franco et al., 2014). The building of nests is an energy-costly activity for a bird (Collias and Collias, 1984); however, the life-span of nests constructed in trees is sufficiently long (median 12 years: Jiménez-Franco et al., 2014) for later reoccupancy during the lifetime of a territory holder. There may be different reasons to switch between nests, including avoidance of ectoparasites, substitution of at least one mate in the pair, and disturbance by, or competition with, other raptor species (Margalida et al., 2007; Ontiveros et al., 2008; Kochert and Steenhof, 2012).

The Latvian lesser spotted eagles switched between nests located an average of 430 m from each other. The median distance of 302 m between changed nests was observed in black kite *Milvus migrans* (Forero et al. 1999). The Spanish imperial eagle has alternative nests distributed at greater distances (mean 1.26 km: Margalida et al., 2007). These suggest that strategies for the protection of the habitats of long-lived, site-tenacious raptors should incorporate species-specific patterns of using multiple nests, and the spacing between the nests within breeding territories.

4.3. Conservation implications

First, the detected pattern of using multiple nests supports the designation of microreserves to protect nesting lesser spotted eagles in the core area of the global population of the species. As certain key characteristics of nest site selection are geographically stable, this approach will most likely be successfully applicable elsewhere across the range. Recommendations for practical conservation are summarised in Table 4. Second, our results indicate that the lesser spotted eagle adapted to alternate among several nests, situated in their breeding territories, and the number of nests tends to increase with the years of territory occupation/observation similarly as in other raptors (Margalida et al., 2007; Ontiveros et al., 2008; Kochert and Steenhof, 2012). Therefore, breeding territories containing several nests, spaced at certain distances, should be target units for a long-term conservation approach for these raptors (Slater et al., 2017). In other words, our study indicates that the protection of only currently occupied nests, usually by a 100–200 m buffer, is only a short-term measure for protecting nesting habitat and ensuring the undisturbed breeding of raptors, and could be insufficient for the long-term in forests with the intensive harvesting of mature stands. Third, as distances between alternative nests vary among raptor species, untested application of distances reported in one species may compromise the conservation of other species. On one hand, it may be detrimental for the species in question if temporal or spatial buffers are too small or, on the other hand, it might unnecessarily raise the conservation costs if they are too large, considering birds nesting behaviour. Finally, we encourage the continuous updating of information on the occupation of breeding territories, as well as on species biology, at reasonable time intervals, and an appropriate adjustment of microreserve borders, to be sure that the allocated costs are applied to area still utilized by species (Mozgeris et al., 2015).

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Declaration of Competing Interest

Ugis Bergmanis and Katrīna Amerika are employees of the Joint Stock Company 'Latvia's State Forests'. Ülo Väli and Rimgaudas Treinys have no conflicts of interest.

Table 4
Recommendations for protection of nest sites of the lesser spotted eagle using a breeding territory occupied by pair as one unit.

Features	Background/explanations
Suitable stands: birch, aspen, black alder, spruce, oak, ash as dominant tree in stand	Pine stand may be selected only if territory is located in pine-dominated forest, eagles nest in pine stands in that forest, other tree species make up a 20%–30% proportion of the first layer in the stand.
≥65 yr for birch and aspen, ≥70 yr for black alder and spruce, ≥80 yr for pine, ≥85 yr for oak, ash as dominant tree in stands	Approximate values of 10% of nest stands by dominant tree species (see Fig. 4)
Stand size 1.4–4 ha, total area of all stands 4–16 ha	25–75% of stands with nest site available for this study (n = 176). Total area accounted for 3–4 nests/potential stands
3–4 suitable forest stands (including known nests) within breeding territory	Estimated number of nests used during 10 and 15 yr is 3 and 4, respectively. Several stands guarantee the availability for building of new nests in the long-term
Suitable stands within breeding territory spaced at average distances of 400–500 m	Estimated average distance of 420 and 480 m between 3 and 4 nests within breeding territory, respectively
Suitable stands and zone of temporal protection located within 400 m of forest edge	90% of nests are build up to 400 m from agricultural areas
Zone of temporal protection of 100-ha area encompassing known nests or set-aside stands. Felling activities restricted during April–August	100 ha is an approximation of an area covered by a circular 600 m buffer zone (113 ha). Most observed eagle nest changes occurred within that distance, therefore such an area protects known and future nests from disturbance and brood losses.
Update of information on territory occupancy and adjustment (if needed) of protected area every 10–20 yr	Average and maximal longevity of territory occupation was 10 and 23 years, respectively

Appendix

Descriptive statistics for the lesser spotted eagle nest sites (n = 176, except for nest tree n = 173).

Variable	Mean ± sd	Prc10%	Prc25%	Median	Prc75%	Prc90%
Distance to edge, m	197 ± 151	43	96	161	255	392
Stand age, yr	85 ± 26	58	70	85	101	113
Proportion of tree species in stand, %						
Pine	12 ± 25	0	0	0	10	50
Birch	39 ± 30	0	10	30	60	90
Spruce	19 ± 24	0	0	10	30	50
Aspen	14 ± 19	0	0	10	20	40
Black alder	10 ± 21	0	0	0	10	40
Hardwood	5 ± 15	0	0	0	0	10

	Pine	Spruce	Birch	Aspen	Black alder	Oak	Ash	Other
Proportion of nest trees, %	2.3	33.5	30.6	12.7	4.1	13.9	2.3	0.6
Proportion of nest stands by dominant tree species, %	13.6	19.3	43.2	8.5	9.7	1.2	2.8	1.7

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.06.004.

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