Habitat use by the Vulnerable greater spotted eagle *Aquila clanga* interbreeding with the lesser spotted eagle *Aquila pomarina* in Estonia

Asko Lõhmus and Ülo Väli

Abstract Major threats to the Vulnerable greater spotted eagle *Aquila clanga* are habitat loss and hybridization with the lesser spotted eagle *Aquila pomarina*, but no quantitative studies have been carried out to understand these processes. In Estonia the known remaining *A. clanga* population comprises only five pure and nine mixed pairs. We describe their habitat at the scale of both the home range and nest site, and use logistic regression models for comparisons with random forest plots and nest sites of *A. pomarina*. The territories of *A. clanga* were characteristically near waterbodies, where the species' nesting preference was for dense forest with a pronounced old-growth structure. Habitats of the two species were distinct at both spatial scales. Open natural landscapes were favoured by *A. clanga* but avoided by *A. pomarina*. Within its home range *A. clanga* occupied old wet stands containing black alder, birch and pine, whereas *A. pomarina* preferred old spruce stands. Multivariate models, which summarized these differences between the two species, did not reveal distinct habitat features of mixed pairs compared with *A. clanga* pairs. Hence, interbreeding pairs may occupy previous *A. clanga* territories, and these deserve similar protection to those currently inhabited by *A. clanga* pairs.

Keywords *Aquila clanga*, *Aquila pomarina*, Estonia, greater spotted eagle, habitat selection, hybridization, lesser spotted eagle, nest sites, wetlands.

Introduction

The greater spotted eagle *Aquila clanga* is a globally threatened raptor sparsely distributed across a large area of temperate Eurasia (BirdLife International, 2000). It is categorized as Vulnerable on the IUCN Red List (IUCN, 2004). Habitat alterations through forestry and drainage activities have been identified as major threats, but the species' ecological requirements and adaptability to environmental changes are still poorly known (Meyburg *et al.*, 2001). Most descriptions of breeding habitat are either general landscape characterizations (Cramp & Simmons, 1980; Malchevskij & Pukinskij, 1983; Dombrovski *et al.*, 2000; Mischenko *et al.*, 2001) or anecdotal descriptions of one or a few nest sites (Glotov, 1959; Shepel, 1992; Ivanovsky, 1996; Dombrovski *et al.*, 2000). The only detailed descriptive study is by Pugacewicz (1995), focusing on 18 nest sites of nine pairs in north-eastern Poland. The only comparison of

Asko Lõhmus (Corresponding author) and **Ülo Väli*** Institute of Zoology and Hydrobiology, Centre of Basic and Applied Ecology, University of Tartu, Vanemuise 46, 51014 Tartu, Estonia. E-mail Asko.Lohmus@ut.ee

*Current address: Institute of Zoology and Botany, Riia 181, 51014 Tartu, Estonia.

nest sites and available habitat, looking at 13 nest sites in the Bryansk region, Russia, is a short note by Romanov (2001).

In Eastern Europe the species is sympatric with the lesser spotted eagle *Aquila pomarina*. Uniquely among wild raptor populations, these two species frequently hybridize (Zhezherin, 1969; Panov, 1989; Lõhmus & Väli, 2001; Dombrovski, 2002), as confirmed recently by morphological and genetic analyses (Väli & Lõhmus, 2004). Hybridization may pose a threat to the less numerous *A. clanga*, but the underlying mechanisms and possible conservation implications are unclear. While non-specific mate choice is the immediate cause of the formation of mixed species pairs, other factors may be operating. Habitat loss, in addition to its direct effect, may force the two species to breed in closer proximity and thus increase the frequency of hybridization.

Given the need for a greater understanding of the impact of hybridization, we explored the habitat relationships of *A. clanga* in Estonia, where one of the two remaining populations in the European Union breeds. The taxonomic status of *c.* 300 pairs of spotted eagles of both species (50% of the national total) has been monitored, revealing extensive hybridization in a situation where *A. pomarina* is at least 20 times more numerous than *A. clanga* (Väli & Lõhmus, 2000, 2004). In this study we describe *A. clanga* habitat at two scales:

the species' home range and nest site. At the home range (i.e. macrohabitat) scale we sought to determine the species' preferences by comparing the land cover of nesting territories with that of random plots, and to study segregation between *A. clanga* and *A. pomarina* we compared the land cover of nesting territories of the two species. At the nest site (i.e. microhabitat) scale, we examined preferences by comparing *A. clanga* nest sites and random plots, and to examine segregation between the two species we used all *A. clanga* nest sites and the nearest *A. pomarina* nest to each. We also compared the habitats of pure and hybrid pairs to elucidate the mechanism behind hybridization and to establish conservation needs for the nest sites of mixed pairs.

Methods

Habitats

Since the late 1980s nesting territories (an area occupied by a pair of mated birds over successive years; Steenhof, 1987) and nests of spotted eagles throughout Estonia have been mapped. We examined all 14 nesting territories of *A. clanga* where nests have been found: five pure pairs and nine mixed pairs (i.e. with parents of different species). For comparison, we considered 143 *A. pomarina* nesting territories (Väli, 2003; Väli *et al.*, 2004) and randomly selected forest plots. To avoid pseudoreplication we only used the most recently occupied nest from each nesting territory for home range scale analyses. At the nest site scale we included all 22 known *A. clanga* nests (within the 14 nesting territories) to increase the accuracy of the analysis. This did not violate the assumption of sample independence because nests in the same territory were 390-1,110 m (median 590 m) from each other, whereas nest sites are selected at a much smaller scale by the birds. The sampling scheme is summarized in Table 1.

At the home range scale we followed methods previously applied to *A. pomarina* (Väli *et al.*, 2004). Land cover was examined within a 2-km radius of nest trees (of both species) and of 143 random points within the forest, using the CORINE Land Cover digital map, which is based on satellite images for 1993–1995 (Meiner, 1999). The 2 km distance incorporates most foraging flights of breeding spotted eagles (Komischke *et al.*, 2001; Scheller *et al.*, 2001; A. Lõhmus & Ü. Väli, pers. obs.). After exploring the intercorrelations of land cover variables, we selected for further analysis: (1) the area of forest where the species nest, (2) the open natural lands (i.e. floodplain meadows, transitional woodland/scrub, open fens and bogs) that are the preferred foraging habitats of *A. clanga* (Galushin, 1962; Pugacewicz, 1995), and (3) the reciprocal Simpson's index of landscape heterogeneity, calculated from the 20 original CORINE land cover types (all artificial surface types were pooled) as $D = \Sigma(p_i^2)^{-1}$, where p_i is the relative area of land cover type *i*. Using recent topographic maps (mostly at a scale of 1:10,000) we also measured the distances from each nest tree or random point to the nearest forest edge, field or meadow, house, road and water body (river or lake). Many distances were checked in the field and we made minor corrections in the few cases where map data and the real situation differed.

At the nest site scale we described *A. clanga* nest sites and three forest plots, in a random direction, 200, 500 and 700 m from each nest, and the nearest *A. pomarina* nest, to each of the 14 *A. clanga* nesting territories. We also described 14 *A. pomarina* nest sites randomly selected from the 143 *A. pomarina* nest sites. We measured the mean height, diameter at breast height and age (using standard dendrochronological techniques) of overstorey trees, and tree species composition within a 30-m radius of each nest. Given the importance of forest structural diversity for forest-dwelling raptors, we followed Lõhmus (2003) in calculating an index of old-growth forest structure as a sum of the following four indicators: (1) age structure of tree layer (1, even-aged; 2, multiple canopy layers have started to develop; 3, multi-cohort forest but no established gap dynamics; 4, multi-cohort

Table 1 Sampling design of the study in relation to its aims and spatial scales. See Appendix for a list of measured variables.

Aim	Home range (i.e. macrohabitat) scale Land cover within 2 km of and distances from:	Nest site (i.e. microhabitat) scale Forest composition and structure within 30 m, and canopy closure and soil moisture within 5 m of:
To study preferences (compare *A. clanga* habitat with random sites)	All 14 known nesting territories of *A. clanga* and 143 random plots	All 22 known *A. clanga* nests in 14 territories and 3 random plots per territory ($n = 3*14 = 42$)
To study species segregation (compare *A. clanga* habitat with *A. pomarina* habitat)	All 14 known nesting territories of *A. clanga* and 143 nesting territories of *A. pomarina*	All 22 known *A. clanga* nests in 14 territories and the nearest *A. pomarina* nest to each *A. clanga* territory ($n = 14$)

forest with canopy gaps of different sizes and different stages of regeneration); (2) the numbers of standing dead trees (1, <5%; 2, 6–10%; 3, >10% of living trees); (3) the numbers of logs (1, <5%; 2, 6–10%; 3, >10% of living trees); (4) the maximum decay stage of coarse woody debris (1, hard wood, not easily penetrable with a knife; 2, at least 1 cm of wood easily penetrable with a knife; 3, soft wood, crushable by hand). We visually estimated mean canopy closure (on a scale of 0-1) within 5 m of a nest tree or random point, and soil moisture on a four-point scale from dry (1) to wet (4).

Statistical analysis

After initial selection of habitat variables, we further reduced their number (Appendix) because of some strong intercorrelations. At the home range scale we used principal component analysis to reduce four of the five distances (to the nearest forest edge, field/ meadow, house and road) to one principal component ('fragmentation') that accounted for 63% of the variation. At the nest site scale nine of the 12 variables were intercorrelated, and were therefore reduced to two independent principal components. The first component ('large spruce', accounting for 29% of total variation) distinguished between old spruce-dominated forests with large trees (high scores) and wet thickets of birch (low scores). The second principal component ('alder swamp', accounting for 19% of total variation) ranged from young secondary stands of grey alder to old black alder-dominated swamps. In total there were therefore

10 habitat variables (five at each scale, of which seven were original variables and three principal components, see Appendix and Table 2).

The contributions of habitat variables in distinguishing between *A. clanga* nest sites and random sites (i.e. habitat preferences) and between the nests sites of the two species were explored with multiple logistic regression. We used the approach proposed by Hosmer & Lemeshow (1989): (1) We performed univariate analysis of each independent variable, omitting those having a likelihood-ratio test $P > 0.25$. (2) We built a preliminary multivariate model with the remaining variables, omitting those not contributing to the model. (3) We built and explored a multivariate model with the final set of variables. Because of the small sample sizes and low test power, we accepted variables with $0.05 < P < 0.1$ as marginally significant if these had clear biological relevance. All statistical analyses were performed with *Statistica version 6.0* (StatSoft, Inc. 1984–2001).

Results

The home range of *A. clanga* was characteristically near waterbodies and open natural lands (Table 2). Distance to waterbodies clearly separated nest sites from random forest plots; a similar tendency in *A. pomarina* was less pronounced and not significant (Fig. 1a). The two species were well segregated in their use of open landscapes (Table 2), such that *A. clanga* tended to prefer natural areas, whereas *A. pomarina* avoided these (Fig. 1b). The mean percentage cover of agricultural land within

Table 2 Univariate logistic regression models for distinguishing nest sites of *A. clanga* from random sites (preferences) and from nest sites of *A. pomarina* (species segregation). See Table 1 for the sampling scheme, and Appendix for list of variables.

Independent variable	Preferences				Species segregation			
	Coefficient $\pm$ SE	Log-likelihood	χ^2	P	Coefficient $\pm$ SE	Log-likelihood	χ^2	P
Home range scale ($n = 14$ *A. clanga*, 143 random plots, 143 *A. pomarina*)								
Constant		−47.2				−47.2		
% forest	−0.0081 ± 0.0160	−47.1	0.3	0.608	0.0049 ± 0.0186	−47.2	0.1	0.793
% open natural land	0.0298 ± 0.0196	−46.1	2.1	0.148	0.0746 ± 0.0265	−43.4	7.6	0.006[1]
Heterogeneity	0.02 ± 0.19	−47.2	0.0	0.918	−0.06 ± 0.23	−47.2	0.1	0.783
Fragmentation (D1)	−0.15 ± 0.30	−47.1	0.3	0.611	−0.93 ± 0.53	−44.8[2]	3.1	0.076
Distance to water body (km)	−0.69 ± 0.35	−44.3	5.8	0.016[1]	−0.51 ± 0.37	−46.0	2.4	0.121
Nest site scale ($n = 22$ *A. clanga*, 42 random plots, 14 nearest *A. pomarina*)								
Constant		−41.2						
% Scots pine	−0.016 ± 0.014	−40.3	1.7	0.196	0.0434 ± 0.0409	−23.3	1.5	0.215
Large spruce (S1)	1.38 ± 0.44	−34.2	14.0	<0.001	−0.60 ± 0.45	−23.1	2.0	0.157
Alder swamp (S2)	0.41 ± 0.28	−40.1	2.2	0.137	0.45 ± 0.31	−22.9	2.3	0.129
Old-growth structure	0.64 ± 0.17	−31.6	19.1	<0.001	0.22 ± 0.19	−23.3	1.5	0.221
Canopy closure	1.71 ± 1.42	−40.4	1.5	0.219	0.48 ± 1.81	−24.0	0.1	0.790

[1]Univariate models, which appeared to be better than any further multivariate developments. The constants are −1.52 ± 0.42 for the preference model, and −3.18 ± 0.47 for the species segregation model.
[2]Sample size for *A. pomarina* = 134; Log-likelihood of constant = −46.3.
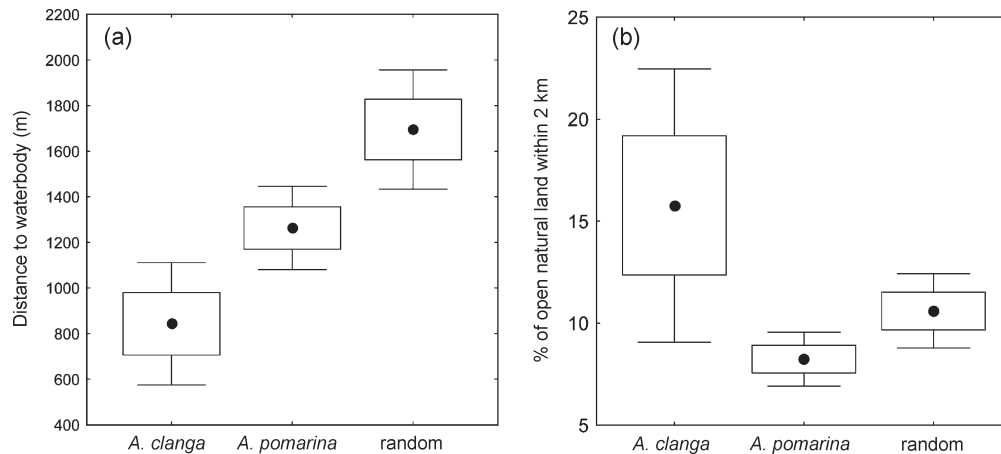
Fig. 1 Box plots of the average distance to the nearest waterbody (a) and the % of open natural lands (grasslands, bushy habitats, wetlands) within 2 km (b) of 14 *A. clanga* and 143 *A. pomarina* nests and 143 random forest points in Estonia. The boxes indicate the standard errors and the whiskers the 95% confidence intervals of the mean.

2 km of *A. clanga* nests was $27.7 \pm$ SD 17.2% ($n = 14$). The tendency of the habitat of *A. clanga* to be less fragmented than that of *A. pomarina* (P = 0.076; Table 2) disappeared in the multivariate analysis, and was probably related to the lower fragmentation of natural landscapes.

Within their generally wetland-dominated home ranges, *A. clanga* preferred old dense forest with a pronounced old-growth structure (Table 3). The importance of canopy closure became evident only after the two other important variables were taken into account (cf. the models in Tables 2 and 3). There was no clear gradual decrease in the likelihood of the eagles nesting at distances 200, 500 and 700 m from nests (Fig. 2), indicating that nest site selection occurred within <200 m radius.

The two species used different nest sites within the same landscapes (Table 3). *A. clanga* occupied wet forest containing black alder, birch and pine, whereas the nearest *A. pomarina* used significantly more old spruce forest stands. There was also a tendency towards a more

pronounced old-growth structure at *A. clanga* nest sites. All these species-specific differences in nest stands became significant in the multivariate model (cf. Tables 2 and 3), indicating some interaction between them. Using the species-specific models at the two spatial scales did not reveal a clearly intermediate or otherwise separate position of mixed pairs within the *A. clanga* sample (Fig. 3).

Discussion

The main results of our study were the importance of natural landscapes and natural forest structure for *A. clanga*, its habitat partitioning with *A. pomarina*, and the lack of clear differences between the nest sites of pure and mixed species pairs. The accuracy of these findings may be influenced by the small sample size, as we had to reduce the number of habitat variables and pool the mixed and pure *A. clanga* pairs. However, we explored

Table 3 Multivariate logistic regression models for distinguishing the forest of 22 nest sites of *A. clanga* from 42 random sites and from 14 nearest nest sites of *A. pomarina*. See Table 1 for sampling scheme and Appendix for list of variables.

Model or variable	Coefficient $\pm$ SE	Log-likelihood	χ^2	P
Preferences (Log-likelihood, model = 25.9; χ^2 = 30.5, P < 0.001)				
Intercept	-8.02 ± 2.48			
Large spruce (S1)	1.46 ± 0.58	-30.1	8.3	0.004
Old-growth structure	0.67 ± 0.21	-32.9	13.8	<0.001
Canopy closure	4.25 ± 2.11	-28.3	4.8	0.029
Species segregation (Log-likelihood, model = 18.0; χ^2 = 12.2; P = 0.016)				
Intercept	-2.89 ± 2.02			
% Scots pine	0.013 ± 0.085	-20.8	5.6	0.018
Large spruce (S1)	-1.17 ± 0.57	-20.5	5.1	0.024
Alder swamp (S2)	0.67 ± 0.37	-19.8	3.6	0.058
Old-growth structure	0.44 ± 0.26	-19.7	3.4	0.065
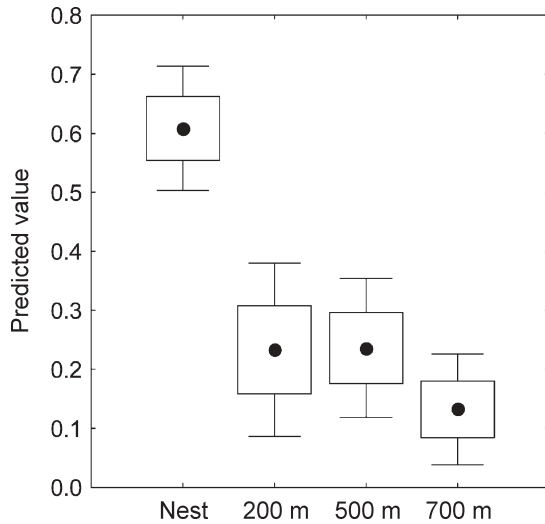
Fig. 2 Box plots of the mean probability values predicted by the preference model for nest sites of the greater spotted eagle ($n = 22$) and random sites 200, 500 and 700 m from the nests ($n = 14$ for each category). The model was based on the occurrence of large spruce, old-growth structure and dense canopy (see Table 2). The boxes indicate the standard errors and the whiskers the 95% confidence intervals of the mean.
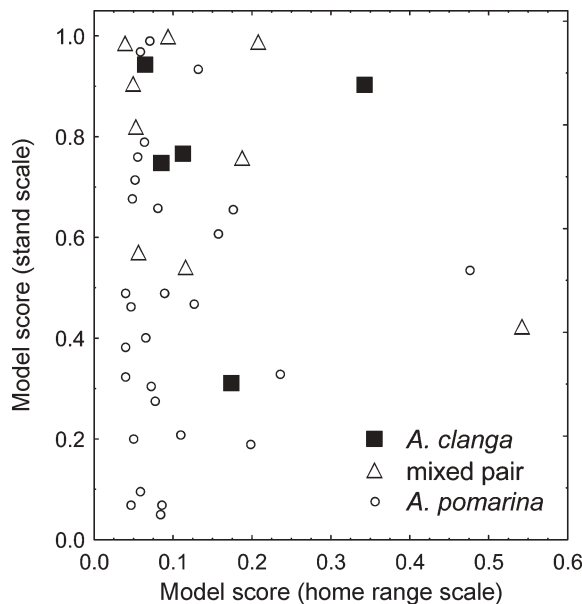
Fig. 3 Distribution of the nest sites of greater and lesser spotted eagles and their mixed pairs according to the values predicted by species-specific habitat models at home range and nest site scales (see Tables 2–3 for the models). *A. pomarina* points are shown only for comparison and are not meant to represent the whole population (the sample includes 14 sites near the nest sites of *A. clanga* and only 14 completely random sites).

the only taxonomically well-known mixed population of *A. clanga*, and we sampled at least 50–75% of the known *A. clanga* territories (Väli & Lõhmus, 2000).

Although the habitats of *A. clanga* vary across its distribution area, the importance of natural grasslands, wetlands and old natural forests is evident throughout its European range. In addition to Estonia, the extant Polish, Ukrainian and Byelorussian populations are also concentrated in large riverine or marshland areas (Strigunov, 1986; Pugacewicz, 1995; Belik & Vetrov, 1998; Dombrovski *et al.*, 2000). In Ukraine the species has completely disappeared from hillsides and dry forests where it was previously common (Belik & Vetrov, 1998), highlighting the importance of wetland habitat. The long history of agricultural development and deforestation in Europe is likely to have dramatically reduced the habitat for the species within the last two centuries.

The microhabitat preferences of *A. clanga* were less clear, because the independent contributions of several correlated features could have been concealed. The effect of the first principal component ('large spruce') probably reflects the eagle's preference for mature forest, which can be partly explained by the need for a large nest tree. The mean age (87 years, range 51–142 years) and diameter at breast height (48 cm, range 27–66 cm; A. Lõhmus & Ü. Väli, unpub. data) of 25 nest trees (the 22 in this study and three measured historically) in Estonia exceeds the mean values for trees at nest sites by 30–50%. The eagle could probably also occupy younger forest if remnant trees were present, and retention of old trees during forestry operations could improve the supply of nest sites for the species.

Our new findings are the importance of a naturally diverse forest structure and a high degree of canopy closure. These two variables (Table 3) were better correlated with the occurrence of eagles than the swamp type of the stands. Nesting in wet forests has been considered characteristic of *A. clanga* (Pugacewicz, 1995; Ivanovsky, 1996; Maciorowski *et al.*, 1996; Belik & Vetrov, 1998). Possibly, swamps are simply the typical forest type in the wetland-rich home ranges of the eagles, and may not be specifically selected. A preference for old-growth structure, independent of stand age and composition, has been previously demonstrated for five other forest-dwelling raptors, including *A. pomarina* (Lõhmus, 2003). This confirms that increasing structural diversity in forest increases the probability of raptor nesting and may be a successful restoration technique in degraded forests or plantations. A dense canopy has been considered a protection against overheating or predation in forest-dwelling raptors (Iverson *et al.*, 1996; Selås, 1996; Krüger, 2002), and may make *A. clanga* vulnerable to thinning of nest stands. The dense nature of its nest stands has been mentioned also by Maciorowski *et al.* (1996) and Mischenko *et al.* (2001) in Poland and Russia, respectively. Both canopy closure (in the preference model) and old-growth structure (in the species segregation model) tended to gain significance after

inclusion of other variables, particularly the first principal component ('large spruce'), which suggests that the internal structure of the stand may compensate for relatively young age or untypical tree composition.

The idea of partitioning of nesting habitat by the two spotted eagle species is not new (Pugacewicz, 1995; Ivanovsky, 1996) but we have quantified it for the first time and demonstrated it at both home range and nest site scales. Comparative studies on nest site characteristics of other sympatric tree-nesting raptors have repeatedly confirmed the theoretical prediction that species partition their habitat (or prey) to coexist (e.g. Schmutz *et al.*, 1980; Bosakowski *et al.*, 1992), including evidence of reduced habitat niches in the presence of competitors (Thiollay, 1993; Janes, 1994) or predators (Newton, 1986; Krüger, 2002). In all these cases either one of the species had a competitive advantage or the sympatric species had differing adaptations, whereas *A. clanga* and *A. pomarina* are similar morphologically and, at least in Estonia, largely share their foraging habitats and prey species (Väli & Lõhmus, 2000; Lõhmus, 2001; Väli, 2003).

There are no studies on habitat determinants of the productivity of *A. clanga* (i.e. its nest site quality) and these data are difficult to collect for such a rare species. However, the role of habitat in the reproductive success of *A. pomarina* has been established (Lõhmus & Väli, 2004). Given the similar reproductive parameters of the two species (clutch sizes, breeding frequencies, almost inevitable siblicide, and patterns of parental care; Cramp & Simmons, 1980; Väli & Lõhmus, 2002), a comparison of their reproductive rates in areas of sympatry could give an indication of the relative quality of their nest sites. In Estonia the recent average productivities of *A. clanga* and *A. pomarina* have been nearly identical (0.60 and 0.62 fledged young per occupied nest per year, respectively) and comparable with estimates from other regions (Väli & Lõhmus, 2000; Väli, 2003). Mean habitat quality therefore seems to be sufficient for the extant pairs of both species in Estonia, and their distinct habitat preferences may reflect real preferences rather than the exclusion of one species by the other.

Given the habitat segregation between the two species, the absence of any obvious differences between the nest sites of pure and mixed pairs (Fig. 3) lends support to the suggestion that most interbreeding pairs are likely to occupy *A. clanga* territories (Lõhmus & Väli, 2001), and suggests that habitat for *A. clanga* is unsaturated in Estonia. This requires further study. Whilst being at the edge of the distribution range or extensive shooting of the species on migration and wintering grounds (Meyburg *et al.*, 2001) could explain the lack of adult birds, the fragmentation of natural landscapes over a certain threshold may have reduced territory occupancy

rates (e.g. Lande, 1987). In either case, frequent mating of single adults with surplus birds from the surrounding, denser *A. pomarina* population is an expected consequence. The nest sites of interbreeding pairs currently deserve similar protection to that provided to *A. clanga* pairs, as this will ensure the maintenance of high-quality habitats for *A. clanga* pairs should their numbers recover in the future.

Acknowledgements

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Biographical sketches

Asko Lõhmus' main research interests are forest ecology, wildlife-habitat relationships and conservation of birds, particularly raptors and owls. He leads the Conservation Biology working group at the University of Tartu and participates in the national planning of forest protection and species conservation in Estonia.

Ülo Väli is studying ecology, morphology and genetics of spotted eagles, and participates in conservation planning and implementation for these species in Estonia.

Appendix

Variable means ($\pm$ 95% confidence intervals, CI) at the home range and nest site scales and correlations of the variables with the principal components in random plots. See Table 1 for sample sizes.

Variable	Mean $\pm$ 95% CI	Correlation coefficient with principal components*
Home range scale		
% forest within 2 km	55.6 $\pm$ 7.1	independent variable
% open natural land within 2 km	15.8 $\pm$ 7.4	independent variable
Landscape heterogeneity	4.1 $\pm$ 0.8	independent variable
Distance (m) to nearest:		
Forest edge	109 $\pm$ 43	(D1)–0.74
Field or meadow	268 $\pm$ 170	(D1)–0.90
House	673 $\pm$ 159	(D1)–0.87
Road	624 $\pm$ 170	(D1)–0.63
Water body	843 $\pm$ 295	independent variable
Nest site scale		
% Scots pine *Pinus sylvestris*	6.8 $\pm$ 6.5	independent variable
% Norway spruce *Picea abies*	21.4 $\pm$ 10.8	(S1) 0.65
% aspen *Populus tremula*	11.4 $\pm$ 8.4	
% black alder *Alnus glutinosa*	15.7 $\pm$ 8.6	(S2) 0.67
% grey alder *Alnus incana*	8.2 $\pm$ 7.5	(S2)–0.59
% birch *Betula* spp.	31.4 $\pm$ 11.0	(S1)–0.55; (S2) 0.49
Stand age (years)	67.5 $\pm$ 7.1	(S1) 0.74; (S2) 0.50
Old-growth structure (scale of 4–12)	8.1 $\pm$ 0.8	independent variable
Tree height (m)	22.3 $\pm$ 1.2	(S1) 0.52
Tree diameter at breast height (cm)	31.7 $\pm$ 2.5	(S1) 0.83; (S2) 0.34
Soil moisture class (scale of 1–4)	3.1 $\pm$ 0.3	(S2)–0.52; (S2) 0.42
Canopy closure (scale of 0–1)	0.7 $\pm$ 0.1	independent variable

*The principal components were extracted separately for the distances (D1) and forest (S1, S2) characteristics. Prior to the extraction, distance to road was square-root transformed, other distances log-transformed, and proportions arcsine-square-root transformed. Weak correlations ($r = -0.3$–0.3) are not shown. In the text and Tables 2–3 the principal component D1 is referred to as 'fragmentation', and S1 and S2 as 'large spruce' and 'alder swamp', respectively.