

## The effects of habitat quality and female size on the productivity of the lesser spotted eagle *Aquila pomarina* in the light of the alternative prey hypothesis

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Habitat quality is an important but insufficiently understood concept in ecology and conservation biology, due to geographic and temporal variation as well as interaction with individual quality. In 1994–2002, we studied the Estonian population of the lesser spotted eagle *Aquila pomarina* in order to (1) explore the relative contributions of habitat and female size in reproductive success; (2) check for a switch to alternative prey in vole-poor years and the relevant variation in annual habitat quality as confirmed in the common buzzard *Buteo buteo* in the same area. We measured five landscape variables, the number of neighbouring conspecifics and the relative size of the female according to large moulted feathers in 77 nesting territories, and related this to the eagles' productivity in vole-rich and vole-poor years. Nesting lesser spotted eagles benefited from heterogeneous landscapes and suffered from the neighbourhood of conspecifics. There was no evidence that different-sized females used different habitats. In general, female size was positively related to productivity in vole-poor but not vole-rich years, but in the presence of competitors, large size appeared to be disadvantageous. The mean annual productivity of the eagle was well correlated with that of the buzzard, both having peaks after every three years. In contrast to the buzzard, the share of voles in the eagle's diet and its habitat quality did not differ significantly between good and poor years. We concluded that despite a superficial ecological similarity to the buzzard, the lesser spotted eagle did not behave as predicted by the alternative prey hypothesis, but the study confirmed that annual variation in prey utilization and relative habitat quality are parts of the same functional response. Non-switching to alternative prey may be related to a historical foraging strategy, used by the eagles before they spread to agricultural landscapes, since the current effects of body size strongly suggested food shortage in vole-poor years.

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Much of contemporary ecological research is devoted to habitat – its use by organisms and influence on life-history patterns and population viability (Block and Brennan 1993, Meffe and Carroll 1994, Sutherland 1996, Morrison et al. 1998). In most cases, however, both theory (e.g. Fretwell and Lucas 1969, Pulliam 1988, Pulliam and Danielson 1991; but see Rodenhouse et al. 1997) and its applications for biodiversity protection (Bernstein et al. 1995) make a simple separation of high-

and low-quality habitats. In reality, relative site quality may change over time but the relevant patterns are insufficiently understood (Hakkarainen et al. 2003, Lõhmus 2003). Also, although it has been generally acknowledged that habitat quality and individual quality act in concert while determining individual fitness, these aspects have been usually studied separately (but see Goodburn 1991, Hasselquist 1998, Newton 1998, Przybylo et al. 2001), particularly in applied research

on rare and threatened species where sampling is laborious or includes conservation risks.

In this paper, we explore annually changing habitat quality and individual quality in the well-known North-European system of vole 'cycles' (regular multiannual fluctuations of *Microtus*- and *Clethrionomys*-voles) and generalist predators (e.g. Hanski et al. 1991). According to the "alternative prey hypothesis", an important feature of generalist predators is their ability to switch to alternative prey when voles are scarce, and thus synchronize population dynamics of voles and the other species (Angelstam et al. 1984). Löhmus (2003) suggested that this is also a typical situation for annual changes in relative habitat quality for the predators, since alternative prey usually occupies different habitats than voles do. Indeed, during vole-lows the common buzzard *Buteo buteo* switches to alternative prey (Reif et al. 2001) and consequently its reproductive success depends on different habitat characteristics than in vole-rich years (Löhmus 2003). Here, we attempt to extend this documented habitat quality variation in a common species to a species of conservation concern.

The lesser spotted eagle *Aquila pomarina* is a medium-sized European raptor, which has an unfavourable conservation status (Meyburg et al. 2001). In most of its range, the eagle preys upon small mammals, particularly voles (Palásthy and Meyburg 1973, Gedeon and Stubbe 1991, Haraszthy et al. 1996, Löhmus and Väli 2001, Scheller et al. 2001). When in sympatry, diet of this species is similar to that of the common buzzard, and in Byelorussia, both species have been claimed to use alternative prey in vole-poor years (Golodushko 1961). Therefore we studied the lesser spotted eagle in Estonia in order to explore the relative contributions of habitat quality and female size in reproductive success during vole-rich and vole-poor years. To our knowledge, this is the first attempt to explore habitat quality for this eagle, although many authors have quantitatively described its breeding habitat (Bergmanis et al. 1990, Drobels 1994, Vlachos and Papageorgiou 1996, Ivanovsky et al. 1999, Skuja and Budrys 1999, Langgemach et al. 2001, Scheller et al. 2001, Treinys 2004, Väli et al. 2004). Body size is one of the most commonly used indices of individual quality, but it has been rarely addressed in habitat studies on birds of prey (Korpimäki 1990, Hakkarainen and Korpimäki 1996, Rosenfield and Bielefeldt 1999, Valkama and Korpimäki 1999), and never in large species of conservation concern. Secondly, we compared the annual variation in habitat quality with that in the eagle's diet, to test the alternative prey hypothesis, which has been confirmed in the buzzard in the same area (Löhmus 2003, hereafter: the buzzard study).

## Material and methods

### Sample of nests

Nesting territories (an area occupied by a pair of mated birds over successive years; Steenhof 1987) of the lesser spotted eagle have been mapped and nests searched for all over Estonia since the early 1990s. We explored a subsample of 77 territories (15% of the national population; Löhmus and Väli 2001), for which female size estimates were available, 1994–2002. Only data from occupied nests were used to measure productivity – the number of large (well feathered) young per year (Postupalsky 1974, Steenhof 1987). Nests were considered occupied if they were at least well repaired and 'decorated' with green sprays (see Newton 1979: 89–90). In a few cases, an eagle pair brought greenery to more than one nest; therefore, possible alternative nests were always searched for near 'decorated' nests. To compare fluctuations in the productivity of the eagle and of the common buzzard, we compiled data for the latter from SE Estonia. This includes the raw data of Löhmus (2003) as well as of national raptor monitoring (Löhmus et al. 1997, Löhmus 2004).

### Classifying vole-years and analysing the eagle's diet

According to snap-trapping of rodents, diet analyses of birds of prey, and the results of the national monitoring project of raptors and owls (Löhmus 1999, 2004, and unpubl. data), the occurrence of *Microtus*- and *Clethrionomys*-voles peaked every third year since the early 1990s (1993, 1996, 1999, 2002; see also Fig. 1). Other years were classified as vole-poor. The number of analysed nestings varied between years due to logistic reasons (8–61, on average 27 nests annually), which means that both year types were not represented for all

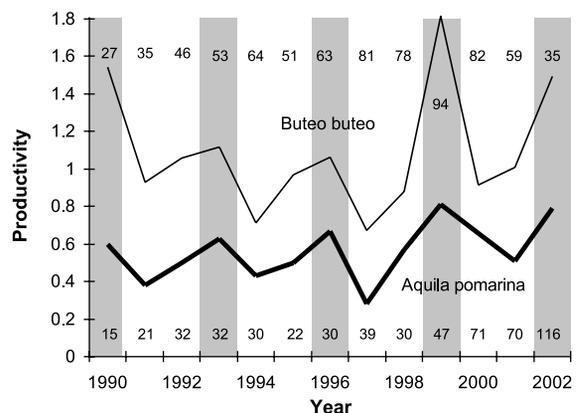


Fig. 1. Mean annual productivity of the common buzzard and lesser spotted eagle in Estonia, 1990–2002. The numbers denote sample sizes and the shaded years are those classified as vole peaks.

nesting territories. Size of the nesting population was very stable, hence the nests checked in only a few years did not belong to additional immigrants in these particular years.

We collected pellets and prey remains from the eagle nests in 1997–2002 (during two 3-year ‘cycles’; 6–40 nests annually). Since pellet analysis reflected diet composition of the closely related greater spotted eagle *Aquila clanga* most accurately (Väli and Lõhmus 2002), we determined prey according to the bones in pellets, using standard methods (Marti 1987) and reference collections. Prey items of one nest are not independent observation units, so the share of voles was first calculated for each nest and the annual averages of these percentages were then compared.

### Measuring landscape characteristics

In all analyses, each territory is represented only once. Habitat measurements were taken within 2 km around nest trees (or the central point between the nests of different years). The 2-km distance incorporates most foraging flights of breeding lesser spotted eagles in the Baltic region (Scheller et al. 2001; authors’ obs.). We measured the areas of land cover types from the CORINE Land Cover digital map, which is based on satellite images from 1993–1995 (Meiner 1999). The preliminary database contained 20 land cover types (compared with the original CORINE classification, we pooled all artificial surface types).

We considered four variables used in the buzzard study: (1) the first principal component (PC1) of land cover areas, (2) share of wetlands, and (3) reciprocal Simpson’s index of landscape heterogeneity within 2 km, calculated from the 20 original land cover types as  $D = \sum(p_i^2)^{-1}$ , where  $p_i$  is the relative area of land cover type  $i$ , and (4) the number of conspecifics within 5 km as a measure of competition. PC1 was used because the areas of the original groups of land cover types (forests; wetlands and water bodies; natural grasslands and transitional woodland/scrub; agricultural areas; artificial surfaces) were strongly intercorrelated and their combination (derived from a correlation-based principal component analysis), explained 44% of the total variation (Table 1). PC1 distinguished between wild (low scores) and anthropogenic sites (high scores). Similarly to the buzzard study, the next component had an eigenvalue close to 1.0, and was primarily correlated with the area of wetlands – the least represented variable in PC1 (Table 1). Therefore, we included the original wetland area instead the second principal component. The number of conspecifics was estimated within 5 km to have a similar average number of conspecifics around eagle nests (1.6) as in the buzzard study (1.8), and thus, a comparable power of tests about intraspecific competi-

Table 1. Correlation coefficients of the five measured land cover proportions around lesser spotted eagle nests with the first two principal components from a principal components analysis (N = 77). The proportions were arcsine-square-root transformed prior to analysis.

Landscape variable (relative area)	Principal components	
	1	2
Artificial surfaces	0.41	0.46
Agricultural land	0.96	−0.14
Wetlands	−0.08	0.78
Natural grassland and scrub	−0.61	0.50
Forests	−0.86	−0.37
Explained variation%	44.1	24.7
Cumulative variation%	44.1	68.9

tion in these two studies. We also took into account that even in the case of strictly 2-km-radius home ranges there is overlap between neighbouring pairs up to a distance of 4 km, and the eagles often respond to flying intruders when these are still far away. The number of conspecifics was negatively correlated with landscape heterogeneity ( $r_s = -0.31$ , N = 77, P = 0.007), and though we retained both variables for comparison with the buzzard, we were cautious in interpreting their relative effects.

To compare the contributions of habitat and female quality, we added two species-specific variables to increase explanatory power of habitat model: (5) share of optimal (natural grassland; pasture; land principally occupied by agriculture, with significant area of natural vegetation) and (6) suboptimal foraging habitat (non-irrigated arable land; complex cultivation patterns; transitional woodland/scrub) within 2 km. This was based on observational studies, which have shown the preference for meadows and the opportunistic use of fields and scrubland by hunting lesser spotted eagles (e.g. Schneider-Jacoby 1996, Lõhmus 2001, Scheller et al. 2001).

### Measuring female size

Due to conservation concerns (e.g. Gregory et al. 2003) and time constraints, we did not trap the birds but used large moulted feathers to characterize female size. These feathers constitute a major part of tail and wing lengths (conventional body size measurements). Feather lengths do not change significantly in adult individuals during their lifetime and a sufficient individual variation allows distinguishing between individuals (Struwe-Juhl and Schmidt 2002).

The procedure comprised: (1) collecting feathers while visiting nests, (2) separating ten most reliably identified feather types for further analyses (three types of rectrices and seven outermost primaries; Table 2), (3) measuring lengths of flattened feathers at their nearest mm (as proposed by Busching 1984), (4) calculating relative

Table 2. Mean lengths ( $\pm$ SD) of large feathers of female lesser spotted eagles, which were used for the assessment of body size. Both rectrices (R) and primaries (P) have been numbered from the innermost to the outermost.

Feather	Length, mm	N
R1	249.9 $\pm$ 10.0	10
R2–R5	249.8 $\pm$ 8.3	46
R6	242.6 $\pm$ 10.2	19
P10	274.8 $\pm$ 7.9	13
P9	360.7 $\pm$ 7.4	11
P8	389.2 $\pm$ 12.2	20
P7	400.3 $\pm$ 12.1	24
P6	412.4 $\pm$ 14.3	10
P5	407.5 $\pm$ 8.5	6
P4	372.9 $\pm$ 10.2	11

deviations of feathers from average lengths of relevant feather types, (5) removing males' feathers from the sample, (6) repeating step (4) to get final relative length for each feather, and (7) averaging the mean relative lengths of all primaries (P) and rectrices (R):  $(\text{Size})_i = (\text{P}_i + \text{R}_i)/2$ , where  $i$  is the nesting territory. This gave us a normally distributed index of body size. Below, we present more details about the steps (5) and (7).

In contrast to females, breeding males attend nests very briefly in *Aquila*-eagles (e.g. Meyburg 1970, Väli and Lõhmus 2002), and in several raptors, males start moulting only at the end of the breeding season (e.g. Smallwood 1988 and references therein). Therefore, we expected that most moulted feathers at the nests belong to females and most of the few males' feathers can be separated by their smaller size (females are up to 10% larger than males; Cramp and Simmons 1980). We checked this by sexing two samples of feathers (potential male feathers and a random subset) using a molecular method. Due to cost, we were not able to analyse all feathers.

DNA was extracted using DNeasy Tissue kit (Qiagen) and manufacturer's directions. A part of the sex-specific chromo-helicase-DNA-binding (CHD) gene was amplified with primers P2 and P8 according to Griffiths et al. (1998); the product was cut with the restriction enzyme *VspI* and explored by electrophoresis in 2% agarose gel. In the lesser spotted eagle, the products of CHD-W and CHD-Z contain two and one restriction site, respectively, which gives three DNA bands for females and two bands for males (Väli 2004).

For compiling the first sample (potential males), we explored the range of relative lengths of feathers in each nesting territory, and selected the relatively smallest feathers in the decreasing order of deviation. Among the ten first feathers, eight belonged to males and twice we failed to extract the DNA. We ended this procedure when the 11th most deviating feather was found to belong to a female. Among 12 feathers of the random sample, 11 were of females and one of a male. Hence, there were probably a few males' feathers in the remaining sample but we considered it sufficiently

'pure' for our purposes, and only omitted the ten feathers of the first and the male's one from the second sample.

Step (7) was based on a comparison of the mean lengths of primaries and rectrices in the nesting territories (Fig. 2). Primaries varied less than rectrices, so that numerically similar deviations from the average were not comparable in the two feather classes. To overcome this problem, we used the regression equation of Fig. 2 to estimate the mean size of the missing feather class in the nesting territories for which we had only one. However, while lengths of different feathers within a class were relatively similar and the general relationship between the feather classes was strong, some large deviations indicated individual variation in body proportions (Fig. 2 residuals; see also Freeman and Jackson 1990). The existence of relatively long-winged or long-tailed individuals was proven twice (feathers from one year, once also confirmed by the DNA analysis), although some other deviations could reflect the change of adults over years. Such cases may add random noise to our data, since we were able to address the disproportion only when we had both feather classes in a territory.

## Statistical methods

The effects of habitat and female size on reproductive success were explored with multiple logistic regression models. The dependent variable was the relative mean productivity (higher or lower than the average) in a nesting territory in the specified year type (vole-poor or vole-rich). Original productivities were recoded because their values were highly variable and non-normal, since the eagle has almost without exception either one or no young annually and we had different sample sizes from different nests. The mean over a year type was taken to reduce deviations not related to year type and to avoid pseudoreplication. We used the approach proposed by

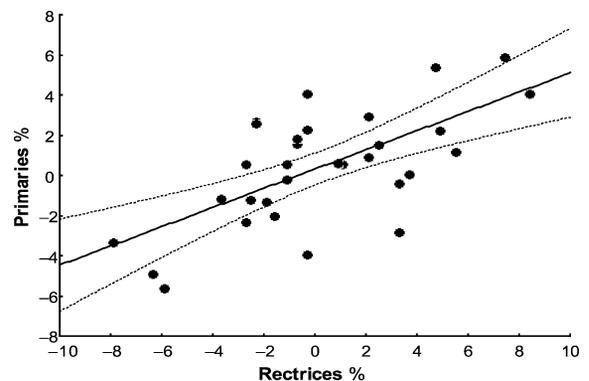


Fig. 2. Relationship between the relative length of female's primaries and rectrices in 31 nest sites of the lesser spotted eagle. The regression line ( $y = 0.479x + 0.314$ ;  $R^2 = 0.43$ ;  $P < 0.0001$ ) and its 95% confidence limits are shown.

Hosmer and Lemeshow (1989: 82–88): (1) performed univariate analysis of each independent variable, omitting those having likelihood-ratio test  $P > 0.25$ ; (2) built a preliminary multivariate model with the remaining variables, omitting those not contributing to the model ( $P > 0.05$  in likelihood-ratio and Wald tests; no clear change in the coefficients of other variables); (3) built and explored a multivariate model with the final set of variables.

For parametric tests and principal components analysis, the variables were checked for normality (Kolmogorov-Smirnov test) and proportions were transformed with arcsine-square-root (but for ease of interpretation, we present means and standard deviations in their untransformed states). Univariate relationships between the eagle's mean annual productivity and its diet composition and the productivity of the buzzard were explored with Spearman rank correlation. All tests were two-tailed. The calculations were performed with Statistica 6.0 software. For power analysis of paired t-tests, we used the program PS (Dupont and Plummer 1990).

## Results

Habitat quality models generally included the same variables with similar directions of effects in both year types. Independent of year, univariate analyses excluded four variables (areas of anthropogenic landscape, optimal and suboptimal foraging habitats and wetlands) as non-significant (Table 3). Multivariate models showed the independent contributions of two intercorrelated habitat variables (see Material and methods) – the positive effect of heterogeneity and negative effect of neighbouring conspecifics – in vole-rich years (Table 4). In vole-poor years, directions of the effects were the same, though their relative importance was less clear: univariate analysis listed the number of neighbours as statistically slightly more important than landscape

heterogeneity (Table 3) while the multivariate model suggested the opposite (Table 4).

Female size had no effect in vole-rich years (Table 3), but it was positively related to productivity in vole-poor years (Table 4). In the multivariate stage of analysis, the only biologically meaningful interaction among the important variables (those with  $P < 0.25$  in the univariate analysis) was likely to be the interaction between body size and the number of conspecifics, showing performance of different-sized birds under different competition pressures. This interaction term was negative, improved significantly the main-effects model for vole-poor years (model 1B in Table 4) and strengthened the positive independent effect of female size (model 1C in Table 4). Female size had no correlations with any of the habitat variables used in this analysis ( $r_s < 0.2$ ,  $P > 0.05$ ,  $N = 77$ ).

Similarly to the buzzard, productivity of the lesser spotted eagle fluctuated according to vole abundance, but there was no evidence of switching to alternative prey. In 1994–2002, the eagles produced on average  $0.82 \pm 0.38$  SD young per occupied territory ( $N = 132$ ) during vole peaks compared with  $0.55 \pm 0.37$  SD ( $N = 95$ ) in poor years in Estonia. The mean annual productivity of the eagle was well correlated with that of the common buzzard ( $r_s = 0.73$ ,  $N = 13$ ,  $P = 0.0049$ ), both having peaks after every three years (Fig. 1).

Fifty percent of 703 prey items were voles, including only two *Clethrionomys glareolus*, the rest being *Microtus* (344 individuals), or indeterminate (7). The 133 *Microtus*-voles identified to species included 70% of *M. agrestis* and 30% of *M. arvalis s. lat.* There was no clear relationship between annual productivity and the share of voles in the eagle's diet (Fig. 3;  $r_s = 0.42$ ,  $N = 6$ ,  $P = 0.36$ ). Moreover, the pairwise comparison of 22 nest sites with food samples from both year types showed no difference ( $t = -0.24$ ,  $df = 21$ ,  $P = 0.82$ ; means  $51 \pm 25$  and  $54 \pm 17$  SD percent for poor and rich years, respectively). The power of this latter test to detect a 10%-difference between means was 0.35, and the

Table 3. Univariate logistic regression models for productivity of the lesser spotted eagle in vole-poor and vole-rich years. 'LL' denotes log-likelihood for the model. The variables indicated with asterisk (\*) were retained for multivariate analysis.

Independent variable	Poor years (N = 52 nesting territories)				Rich years (N = 71 nesting territories)			
	Coefficient $\pm$ SE	LL	$\chi^2$	P	Coefficient $\pm$ SE	LL	$\chi^2$	P
Constant		-36.01				-37.89		
Heterogeneity	0.28 $\pm$ 0.19	-34.70	2.62	0.106*	0.67 $\pm$ 0.28	-34.06	7.65	0.006*
Anthropogenic landscape (PC1)	-0.01 $\pm$ 0.28	-36.00	0.00	0.979	0.20 $\pm$ 0.29	-37.63	0.52	0.473
Area of meadows	-1.78 $\pm$ 2.24	-35.68	0.65	0.421	2.20 $\pm$ 2.13	-37.32	1.14	0.286
Area of suboptimal foraging habitats	1.94 $\pm$ 2.12	-35.58	0.86	0.354	-0.26 $\pm$ 2.20	-37.88	0.01	0.904
Area of wetlands	-1.37 $\pm$ 4.24	-35.95	0.11	0.746	6.56 $\pm$ 8.02	-37.42	0.92	0.337
Conspecifics	-0.34 $\pm$ 0.20	-34.45	3.10	0.078*	-0.53 $\pm$ 0.19	-33.85	8.07	0.004*
Female size	0.18 $\pm$ 0.10	-34.22	3.56	0.059*	-0.02 $\pm$ 0.09	-37.86	0.04	0.832

Explanations to variables: 'heterogeneity' – reciprocal Simpson's index of the diversity of land cover types within 2 km; 'anthropogenic landscape' – the first principal component of land cover areas within 2 km (see Table 1); 'conspecifics' – the number of other lesser spotted eagle nests within 5 km; 'female size' – an index of adult female size (% deviation from average where average = 0, see Fig. 2) derived from moulted feathers.

Table 4. Multivariate logistic regression models for productivity of the lesser spotted eagle in vole-poor and vole-rich years. 'LLmodel' denotes log-likelihood for the full model and 'LLvariable' for a model without that variable.

Model or variable	Coefficient $\pm$ SE	LLvariable	$\chi^2$	P
<b>1. Vole-poor years</b>				
1A. Preliminary multivariate model (LLmodel = -30.77)				
Constant	-1.07 $\pm$ 1.16			
Heterogeneity	0.38 $\pm$ 0.23	-32.35	3.16	0.075
Conspecifics	-0.29 $\pm$ 0.21	-31.72	1.90	0.168
Female size	0.25 $\pm$ 0.11	-33.77	5.99	0.014
1B. Final main-effects multivariate model (LLmodel = -31.72)				
Constant	-1.94 $\pm$ 0.99			
Heterogeneity	0.45 $\pm$ 0.23	-34.22	5.01	0.025
Female size	0.25 $\pm$ 0.11	-34.70	5.96	0.015
1C. Multivariate model with an interaction term (LLmodel = -27.86)				
Constant	-1.42 $\pm$ 1.24			
Heterogeneity	0.45 $\pm$ 0.25	-29.92	4.11	0.043
Conspecifics	-0.26 $\pm$ 0.25	-28.43	1.13	0.288
Female size	0.69 $\pm$ 0.27	-33.68	11.64	0.0006
Size $\times$ Conspecifics	-0.27 $\pm$ 0.14	-30.77	5.82	0.016
<b>2. Vole-rich years (LLmodel = -31.85)</b>				
Constant	-0.09 $\pm$ 1.29			
Heterogeneity	0.53 $\pm$ 0.29	-33.85	4.01	0.045
Conspecifics	-0.41 $\pm$ 0.20	-34.06	4.43	0.035

minimum detectable difference at  $\alpha=0.05$  and power = 0.8 was 18%.

## Discussion

### Habitat quality

Nesting lesser spotted eagles benefited from heterogeneous landscapes and suffered from the neighbourhood of conspecifics. The latter effect is known from several raptor populations, including those of eagles (Simmons 1993a, Anthony et al. 1994, Pedrini and Sergio 2002), and indicates a density-dependent mechanism of population limitation. In common buzzards in the same area, the negative influence of conspecifics was clear only in vole-poor years (Löhms 2003).

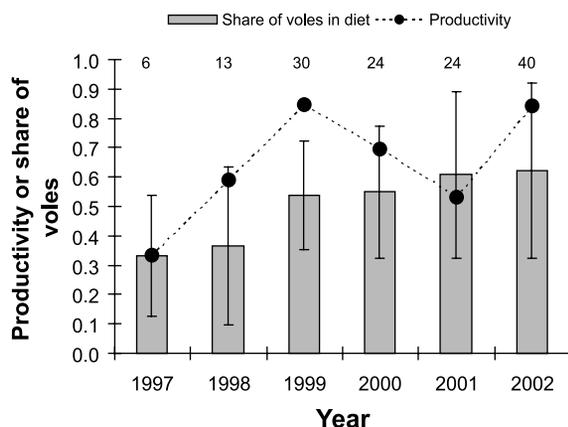


Fig. 3. The annual share of voles in the diet of the lesser spotted eagle in relation to its productivity. The lines on bars are standard deviations, the numbers indicate diet samples (no. of nests). See Fig. 1 for the sample sizes of productivity data.

The lesser spotted eagle has a long nesting season, making the continuous availability of suitable prey a prerequisite for successful reproduction. The diverse hunting techniques of the eagle enable it to forage in different habitats (Gedeon and Stubbe 1991), which could be important when vegetation growth makes prey locally inaccessible (e.g. Bechard 1982, Martin 1987, Preston 1990). This may explain the preference for heterogeneous landscapes by the species in Germany (Gedeon and Stubbe 1991, Langgemach et al. 2001) and the respective effect on productivity found by us.

However, the relationship between habitat characteristics and productivity of the lesser spotted eagle does not seem to be simple, since we have not found the eagle's preference for diverse areas in Estonia (Väli et al. 2004), and the strongest populations of *Microtus*-voles inhabit homogeneous landscapes (favouring common buzzards in vole-rich years; Löhms 2003). In line with the latter, the Estonian eagles prefer to nest near large meadows (Väli et al. 2004), which have been supposed to determine habitat quality for the species elsewhere (Langgemach et al. 2001, Scheller et al. 2001 and references therein). Yet, in our analysis, the eagles – despite their specialization on voles – did better in heterogeneous landscapes and were indifferent to the areas of foraging habitats (Tables 3 and 4). We explore this contradiction further below.

### Female size

We found four size-effects in breeding female lesser spotted eagles: (1) significant relationships between body size and productivity in vole-poor but not in vole-rich years, (2) generally higher productivity of large females, (3) lower productivity of large females in the presence of

competitors, and (4) the lack of correlation between body size and habitat variables. As discussed below, the effects (1) and (2) are best interpreted in the context of selection for large body size in female raptors, while the effects (3) and (4) reveal to rather poorly known aspects in avian ecology.

Birds of prey exhibit reversed sexual size dimorphism (RSD) with females larger than males. The evolutionary causes of RSD could be found in the breeding season (particularly the egg-laying or early incubation periods), when females mostly attend the nest and males provide the food (e.g. Lundberg 1986, Ferguson-Lees and Christie 2001), and should be reflected in size-dependent reproductive success. Indeed, longer-winged females and shorter-winged males are more productive in the sparrowhawk *Accipiter nisus* (Newton 1989). In three well-studied vole-eating birds of prey, reproductive parameters are positively related to female size (Korpimäki 1986, Saurola 1989, Village 1990, but see Massemin et al. 2000 about the lack of such evidence), while in two species hunting success during food-shortage is negatively related to male size (Hakkarainen and Korpimäki 1995, Hakkarainen et al. 1996). The studies that distinguished between vole-poor and vole-rich years either found body-size effects only in poor years (Hakkarainen et al. 1996, Massemin et al. 2000), or detected opposing trends in poor and good years (Hakkarainen and Korpimäki 1995). Hence, the year-dependent advantage of large size in female lesser spotted eagles is not an unexpected result, and it could be mostly related to the possibility of a large body to store more body reserves and/or to use them more efficiently (see Massemin et al. 2000 for the whole list of hypotheses of RSD evolution). Although year-effects could be expected also when large females improve the nestlings' food supply by providing larger prey, this is doubtful in spotted eagles, which have very low nestling mortality during late summer (Ü. Väli unpubl. data) and whose females bring few prey to young (Väli and Löhms 2002).

Although 'overridden' by the general advantage of larger size, the negative effect of large body in the presence of competitors is a remarkable finding since it may reflect the cost of being large for female raptors. Blanckenhorn (2000) listed possible mechanisms that select against large body size, two of which (size-selective predation or parasitism; size-selective starvation) are applicable to female birds. The only one consistent with our data is the possibility that larger individuals require more food and suffer under resource limitation (when competition further reduces the availability of scarce prey), since the eagles are predated extremely rarely and we can not see a way how large size and density of conspecifics could interact in producing high parasite loads. Among non-passerines, a counterbalancing cost of large size has been shown also in

breeding herring gulls *Larus argentatus* (Monaghan and Metcalfe 1986).

Finally, though there is little doubt that better individuals may occupy better sites (e.g. Riddington and Gosler 1995, Hakkarainen and Korpimäki 1996, Newton 1998), we got additional support that this is not necessarily so. Although the lack of correlation between body size and habitat variables in the lesser spotted eagle may also be a Type II error, the result coincides with two other studies on raptors (Valkama and Korpimäki 1995, Rosenfield and Bielefeldt 1999). The reasons remain obscure, although in principle, such a pattern may occur in dense populations of site-tenacious and long-lived territorial birds, having very limited possibilities to select actively a territory on the basis of its quality (see Simmons 1993b).

### The alternative prey hypothesis

The share of voles in the summer diet of North-European vole-eating birds of prey usually differs many times between vole-poor and vole-rich years (e.g. Korpimäki and Sulkava 1987, Korpimäki 1988a, Spidsø and Selås 1988, Löhms 1999, Reif et al. 2001). Only one study has reported smaller than the 18%-difference, detectable at 80%-power in our study (15% in Ural owls *Strix uralensis* in Sweden, Lundberg 1981), but in this species much larger differences have been found in Finland and Estonia (Korpimäki and Sulkava 1987, Löhms 1999). In our study, the sample means were almost identical between years (51 and 54%). So we suggest that breeding lesser spotted eagles do not behave according to the alternative prey hypothesis in Estonia. We can not exclude the possibility that nonbreeding adults of this species switch to alternative prey but breeding of the eagle is likely to be determined when and where voles are sufficiently available.

Given this conclusion, one could expect that relative habitat quality should also be governed by the same features in different years. This was indeed the case, since the minor difference in the multivariate stage (which of two intercorrelated variables – landscape heterogeneity or number of conspecifics – was included in the final model; Table 4) was probably statistical, not biological (cf. James and McCulloch 1990). In contrast, the productivity of the common buzzard (a raptor switching to alternative prey) was related to different habitat variables or opposing directions of the same variables in different years (Löhms 2003). Hence, despite a superficial ecological similarity to the common buzzard, the lesser spotted eagle in roughly the same area and same time period differed in its functional response to changing vole densities.

Why did the eagles not switch to alternative prey, when conspecific and body-size effects strongly sug-

gested food-shortage during vole-scarcity? One reason could be that there are no suitable alternatives in the Estonian landscapes. For example, the near absence of *Clethrionomys glareolus* in the diet indicates that the eagle is not a successful hunter in forests – an important habitat for alternative prey for other birds of prey (e.g. Korpimäki 1988b). In Byelorussia, the eagle has been reported to switch to frogs (Golodushko 1961), which may have become less available due to worldwide declines (Alford and Richards 2000, Houlahan et al. 2000) and the overgrowth of traditionally managed flood-plain meadows in Estonia. The latter is the likely reason why lesser spotted eagles changed their habitat (from seminatural to agricultural lands) and diet (from diverse diet to *Microtus*-voles) in the second half of the 20th century in Estonia (Lõhmus and Väli 2001). Hence, the absence of the functional response to changing vole densities may also be related to a historical foraging strategy, used by the eagle before its spread to agricultural landscapes. This could also explain the inconsistency of preferred and high-quality habitats (see above). Causes of the dietary specialisation of the lesser spotted eagle clearly have importance for the conservation of this priority species and deserve further study.

In general, our falsification attempt lends further support to the idea that annual variations in diet and relative habitat quality are parts of the same functional response (Lõhmus 2003). The message for conservationists using data from common species to fill gaps of knowledge for managing threatened species, is that the key aspects of resource utilization (in our case – prey use) in target species should be quite well known before other aspects can be predicted.

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