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ORIGINAL ARTICLE

# Agricultural land use shapes habitat selection, foraging and reproductive success of the Lesser Spotted Eagle *Clanga pomarina*

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**Abstract** Anthropogenic loss of biodiversity is often indicated by the disappearance of top predators. However, some of them have adapted to man-made agricultural landscapes. Among raptors, one such example is the Lesser Spotted Eagle. We compiled an exhaustive data set on foraging habitat composition of this species by direct field mapping and detailed land cover maps to study the effect of various agricultural management practices on its occupancy of home ranges and productivity, as well as on its habitat utilization and hunting success. Home ranges of the Lesser Spotted Eagle contained more natural grasslands (7.6%) and other agricultural biotopes (29.9%) than expected by random, and they preferred to breed close to managed agricultural biotopes. They hunted preferably on grasslands, where they spent 86% of their time, especially on managed grasslands, but avoided arable fields. In total, 51% of the Lesser Spotted Eagle attacks were successful, and we detected no differences in hunting success among habitats. Nests of successfully breeding birds were surrounded by more crops/cultivated grassland on a rotational basis (19.0%), as well as by managed natural grassland (1.1%), than those of unsuccessful pairs (16 and 0.7%, respectively). We also detected a negative impact of oilseed rape fields and mowed cultivated grassland on the reproductive success of the Lesser Spotted Eagle, but these effects were not consistent over the years. Our results suggest that, although the Lesser Spotted Eagle is well adapted to foraging in traditional farmland, it is threatened by changes in agricultural practices and an increasing sown area of some crops, such as oilseed rape. Cultivation of various crops and retaining of grasslands, interspersed with set-aside and non-agricultural habitat patches, promoted by the European Union greening policy, would be favourable to the Lesser Spotted Eagle.

**Keywords** Conservation · Foraging · Grassland · Habitat · Raptor · Sustainable agriculture

**Zusammenfassung**

**Die landwirtschaftliche Nutzung beeinflusst Habitatwahl, Nahrungssuche und Fortpflanzungserfolg von Schreiadlern *Clanga pomarina***

Der anthropogene Artenverlust zeigt sich oftmals im Verschwinden von Spitzenprädatoren. Einige dieser Spitzenprädatoren haben sich jedoch an die künstliche Agrarlandschaft angepasst. Bei den Greifvögeln ist der Schreiadler ein solches Beispiel. Wir haben mit Hilfe direkter Feldkartierung und detaillierten Landbedeckungskarten einen umfassenden Datensatz zur Beschaffenheit des Nahrungshabitats dieser Art zusammengestellt, um den Effekt verschiedener Agrarmanagementmethoden auf die Besetzung von Aktionsräumen und die Produktivität des Adlers, sowie seine Habitatnutzung und seinen Jagderfolg zu untersuchen. Die Aktionsräume der Adler enthielten mehr natürliches Grünland (7,6%) und andere Agrarbiotope (29,9%) als zufällig erwartet, und die Vögel zogen es

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vor, in der Nähe gemanagter Agrarbiotope zu brüten. Die Adler jagten vorzugsweise in Grünland, wo sie 86% ihrer Zeit verbrachten, insbesondere in gemanagtem Grünland, mieden jedoch Ackerflächen. Insgesamt waren 51% der Jagdversuche erfolgreich, und wir fanden keine Unterschiede im Jagderfolg zwischen Habitaten. Die Nester erfolgreich brütender Vögel waren von mehr Feldfrüchten/kultiviertem Grünland auf Rotationsbasis (19%) und gemanagtem natürlichen Grünland (1,1%) umgeben als die Nester erfolgloser Paare (16% bzw. 0,7%). Wir fanden außerdem einen negativen Einfluss von Rapsfeldern und gemähtem kultivierten Grünland auf den Fortpflanzungserfolg der Adler, doch diese Effekte unterschieden sich zwischen den Jahren. Unsere Ergebnisse deuten darauf hin, dass der Schreiadler, obwohl er gut an die Nahrungssuche in traditionellen landwirtschaftlichen Nutzflächen angepasst ist, durch Veränderungen der Agrarmethoden und eine Zunahme von Aussaatflächen für gewisse Feldfrüchte, z. B. Raps, bedroht ist. Die Erhaltung verschiedenartiger Feldfrüchte und Grünlandflächen mit eingestreuten stillgelegten Agrarflächen und landwirtschaftlich gänzlich ungenutzten Kleinbiotopen, wie von der EU-Begrünungspolitik gefördert, wäre vorteilhaft für den Schreiadler.

## Introduction

Humans have converted complex natural ecosystems into simplified managed agricultural landscapes (Stoate et al. 2001). Although many species could survive in sustainably managed heterogeneous agricultural landscapes, the replacement of traditional grassland by extensive arable fields, loss of landscape heterogeneity and intensification of land use progressively affect wildlife (Burel and Baudry 1995; Matson et al. 1997; Vitousek et al. 1997; McKinney and Lockwood 1999; Stoate et al. 2001; Robinson and Sutherland 2002; Benton et al. 2003). Future perspectives predict the expansion of this process. Therefore, retaining biodiversity in order to provide sustainable ecosystem services whilst reaching higher levels of food production will be the challenge for agriculture in the future (Tilman et al. 2002).

Predators, such as birds of prey, are good indicators of viable ecosystems, as their abundance is associated with a diverse prey base (Sergio et al. 2006). Several open-land raptors have been strongly influenced by agriculture (Sánchez-Zapata et al. 2003). As an example of conflict between European agricultural policy and nature conservation (Tella et al. 1998), changes in land use caused a drastic decline of the Lesser Kestrel *Falco naumanni* (Donázar et al. 1993). The same has been reported for the Little Owl *Athene noctua* (Šálek and Schröper 2008) and expected for Montagu's Harrier *Circus pygargus* (Butet and Leroux 2001; Arroyo et al. 2002).

The Lesser Spotted Eagle *Clanga pomarina* is a large raptor breeding in forests and foraging in open habitats nearby. During recent decades its numbers have been declining in many parts of its range (BirdLife International 2015). In Eastern Europe, which is the breeding stronghold of the species, the major threat to this raptor is the intensification of agriculture, which degrades its foraging areas (Bergmanis et al. 2006; Treinys et al. 2007). The Lesser Spotted Eagle prefers to hunt in grassland, which is supposed to determine its home range quality (Schneider-Jacoby 1996; Langgemach et al. 2001; Lõhmus 2001; Scheller et al. 2001; Mirski 2009; Zub et al. 2010). However, our previous studies have indicated that, although the Lesser Spotted Eagle prefers to breed in grassland-rich areas (Väli et al. 2004), the share of grassland is not positively linked to its reproductive success (Lõhmus and Väli 2004).

The aim of the current study is to analyse the controversial relationship between the Lesser Spotted Eagle and grasslands. We hypothesize that a formerly missed impact on reproductive success may be at least partly explained by methodology—the positive effect of grassland may have been masked by the limitations of previously used general land cover maps, such as CORINE (Meiner 1999; European Environment Agency 2012), and by the insufficient assessment of important biological characteristics. Also, the management of grasslands has not been taken into account in most previous studies. Here, we compile an exhaustive data set on the composition of the foraging habitat of the Lesser Spotted Eagle by direct field mapping and detailed digital maps to (1) study the effect of various crops and different types of grasslands on the occupancy of home ranges and productivity of the Lesser Spotted Eagle, and (2) analyse habitat utilization and hunting success of the Lesser Spotted Eagle in various agricultural biotopes.

## Methods

### Study area

The study was conducted in Estonia (57.5°–59.6°N, 21.8–28.2°E; 45,227 km$^2$), a flat lowland country situated in north-eastern Europe at the border between nemoral and boreal environmental zones (Metzger et al. 2005) and belonging to the Nordic vegetation growing zone (Peltonen-Sainio 2012). Approximately 50% of Estonia is covered with forests and ca. 25% with agricultural landscapes. The main cultivated crops are cereals (ca 30% of the utilised agricultural area), fodder crops (ca 20%) and industrial crops (mainly oilseed rape; ca. 10%); permanent grasslands form ca. 30% of the agricultural land (Eurostat 2012).

## Eagle data

In the current study, we included two temporally separated subsamples from an Estonian Lesser Spotted Eagle population, formed of 600–700 pairs. First, in 2004–2006 we studied 88 pairs of Eagles (43 pairs in 2004, 68 in 2005 and 17 in 2006) to (1) observe foraging birds, and (2) analyse general habitat composition of their home ranges from a digital map, as well as the detailed composition of agricultural biotopes and their management by field mapping. Second, in 2010–2012, we studied 241 pairs of Eagles (147 pairs in 2011, 163 in 2012 and 147 in 2013) and (1) analysed their habitat selection by comparing habitat composition at the Eagles' home ranges, as well as around random locations (in order to identify general landscape composition), using two types of digital maps, and (2) compared habitats around nests of unsuccessful and successful Eagle pairs.

Nests of the Lesser Spotted Eagle have been searched for all over Estonia since the early 1990s, but there has been a significant increase of monitoring effort and the number of annually checked occupied nests has risen from ca. 15 to ca. 150 (Väli et al. 2011). In the current analyses we used only nests that were occupied by Eagles in a particular study year. Nests were considered occupied if they contained nestlings, eggs or remains of eggshells or were 'decorated' with green sprays of foliage. In the latter case, the occupying species was determined by observations, moulted feathers found at nests, nest material characteristics and other signs. As Eagles may seldom bring greenery to more than one nest, possible alternative nests were always searched for near 'decorated' nests, but eventually only one nest per territory was used in the analysis. The Lesser Spotted Eagle raises only one offspring usually [two fledglings could be found in only 1.9% of successful nests (Väli 2012)]. Therefore, we measured the reproductive success as a binary variable: no eggs laid or lost clutch or brood = 0, nests with large nestling = 1. Reproductive success of the Lesser Spotted Eagle is strongly correlated with the abundance of voles (Lõhmus and Väli 2004; Treinys and Dementavičius 2004; Väli 2012), which fluctuates with 3-year periodicity in Estonia (Lõhmus 1999). This justifies conducting the study over two 3-year periods.

The foraging of Eagles was studied by direct observations throughout their breeding season between April and August. Observers were located at open places with good visibility of the nest site and in its vicinity (up to 2–3 km from the nest site). Most of the records comprised those of flying Eagles because perching birds are hard to observe. As our aim was to compare hunting success in various biotopes, not effectiveness of various hunting types, having missed out perching birds should not have affected the results significantly. The total observation time of foraging Eagles was 2477 min, which was divided into 147 independent observation periods. To avoid pseudoreplication, only one attack per territory per observation period was included in the analysis (in total 135 attacks). For each attack, we registered its distance from the nest, used biotope, success of the attack and the prey item. As the Eagle carries its prey (usually voles, moles, frogs or small birds) in its beak, its hunting success is rather easy to record.

## Land cover data

According to the radio-telemetry data, the mean area of the Lesser Spotted Eagle home range in the Baltic region is 1143 ha [the maximum value for six studied birds was 1552 ha (Scheller et al. 2001)]; similar results have been recently also obtained using global positioning system telemetry (Väli et al., unpublished data). These data suggest that most foraging flights are performed within 2 km of the nest; 95.5% of our observations were made within 2 km of the nest too. Therefore, we used a circle with a radius of 2 km (1256 ha) as a proxy for home range, similarly to earlier studies (e.g. Lõhmus and Väli 2004; Väli et al. 2004; Treinys 2004). In a large sample this generalisation is valid as the spatial variability of home range shapes is evened out and, according to telemetry data (Väli et al., unpublished data), Lesser Spotted Eagle nests are situated close to the centre of the territory, not at its periphery, in mosaic Estonian landscape.

Three types of landscape data were used. First, for the general habitat selection analysis we measured proportions of habitat types from the Estonian Basic Map; second, the detailed habitat composition of home ranges and habitats used by hunting Eagles was recorded by direct mapping in the field; third, effects of the agricultural management practices were studied using field mapping and annually compiled digital Estonian Agricultural Register Maps. A detailed list of the landscape variables is presented in the "Appendix".

## Data analysis

Statistical analyses were conducted using the software R 3.2.3 (R Development Core Team 2015). In order to detect preferences in nest site selection, habitat utilization during hunting, as well as hunting success, we compared the biotopes used by Eagles with those available in the landscape using a $\chi^2$-test with Yates' continuity correction. In the habitat selection analysis, proportions of available habitats were described also around random points (the number of points was equal to that of the studied nests). Two limitations were taken into account here. First, in order to avoid describing landscapes in geographically different regions, random points were plotted at 10 km from the nest. Second, as the Lesser Spotted Eagle prefers to breed near woodland margins (in our sample, 2–411 m from the margin, 95% of nests closer to 187 m, $n = 278$), all random points were plotted closer than 187 m from the edge of woodland. Habitat selection, as well as impact of various biotopes on reproductive success, was explored using logistic regression models with nest site/random point (habitat selection analysis), or successful/unsuccessful nest (analysis of reproductive success), as binary dependent variables and year and total areas of biotopes as independent variables. The best model was selected by a backward stepwise procedure according to the Akaike information criterion. We used a simple logistic regression approach because mixed models with nest sites as random factors did not perform better.

## Results

### Home range composition and nest site selection

Home ranges of the Lesser Spotted Eagle contained an average 35–40% of regular agricultural biotopes (Tables 1, 2), which is significantly more than was available in the landscape (Table 3). Also the area of natural grassland was higher in the Eagles' home ranges (Table 3).

Detailed field mapping of agricultural biotopes (afforested areas and orchards excluded) showed that managed grassland covered 10.2% of the home range (or 31.2% of its agricultural biotopes), unmanaged grassland and fallows 13.6% (41.5%) and arable lands 8.9% (27.3%; see detailed data in Table 2). Among managed agricultural biotopes, the Lesser Spotted Eagle showed highest preference for the crop fields/cultivated grassland on rotation [which formed 18.0 ± 11.6% (± SD) of home ranges and 13.5 ± 13.5% around random points] and cultivated permanent grassland (6.2 ± 6.3 and 4.3 ± 5.1%, respectively; Table 4). Lower, but significant, preference for less common natural grasslands (1.0 ± 1.7 and 0.7 ± 1.3%, respectively) was also detected (Table 3).

### Habitat utilization by foraging Lesser Spotted Eagles

The Eagles spent most of their hunting time on grasslands (83.7% of 147 observations, 85.7% of the time; 2477 min) while arable lands were used much less often (10.9 and 9.3%, respectively; Fig. 1). In other biotopes, the Eagles were recorded only occasionally [waterbodies and their banks 2.7 and 3.3%, roadside 1.4 and 1.5%, forest (including clear-cuts) 1.4 and 0.3%]. Compared to their availability in home range, hunting Eagles preferred grasslands ($\chi^2_1 = 6.6$, $P = 0.01$) but avoided arable land ($\chi^2_1 = 15.3$, $P < 0.001$; Fig. 1). Among grasslands, the Eagles used managed grasslands (55.6% of 138 observations) slightly more often than unmanaged ones, which was significantly different ($\chi^2_1 = 4.2$, $P = 0.04$) from the relative availability of these biotopes (43% of grasslands were managed).

Most of the attacks in known habitats were made in grasslands, fewer in cereal fields (7.5%) and other biotopes (fallow 2.8%, side of waterbody 5.7% and roadside 0.9%), which is similar to the use of these biotopes ($\chi^2_2 = 0.1$, $P = 0.97$; Fig. 1). There were significantly more attacks on managed (62.5% of 72 attacks) than on unmanaged

**Table 1** Annual average biotope compositions (%; mean ± SD) of landscape and the surroundings of Lesser Spotted Eagle nests (within a 2-km radius) according to the Estonian Basic Map

| | 2010 | | 2011 | | 2012 | |
|---|---|---|---|---|---|---|
| | Random points | Nests | Random points | Nests | Random points | Nests |
| Regular agricultural biotopes | 21.0 ± 19.2 | 29.8 ± 15.9 | 23.1 ± 19.2 | 30.0 ± 16.2 | 25.2 ± 19.8 | 30.3 ± 16.2 |
| Natural permanent grassland | 5.5 ± 4.1 | 8.0 ± 5.2 | 5.4 ± 3.8 | 7.3 ± 5.0 | 5.3 ± 4.1 | 7.4 ± 5.3 |
| Other types of open landscape | 2.9 ± 3.6 | 2.5 ± 1.9 | 3.0 ± 3.5 | 2.7 ± 2.2 | 2.6 ± 3.5 | 2.8 ± 2.3 |
| Bushland | 0.5 ± 0.7 | 0.5 ± 0.5 | 0.4 ± 0.7 | 0.4 ± 0.4 | 0.4 ± 0.7 | 0.5 ± 0.6 |
| Forest | 55.1 ± 21.0 | 52.9 ± 16.0 | 53.1 ± 19.5 | 53.1 ± 16.2 | 51.0 ± 21.1 | 53.3 ± 16.5 |
| Mire and marsh | 8.5 ± 15.0 | 3.2 ± 5.5 | 8.2 ± 14.1 | 3.2 ± 5.7 | 9.6 ± 16.6 | 2.4 ± 4.0 |
| Exploited peatlands | 0.2 ± 1.1 | 0.3 ± 2.7 | 0.4 ± 1.7 | 0.0 ± 0.2 | 0.6 ± 2.4 | 0.3 ± 1.5 |
| Waterbody | 2.2 ± 5.7 | 0.8 ± 1.2 | 2.2 ± 5.9 | 0.7 ± 1.1 | 1.4 ± 3.7 | 0.7 ± 0.9 |
| Single farms | 1.8 ± 2.4 | 1.2 ± 1.0 | 1.9 ± 2.7 | 1.2 ± 1.1 | 1.8 ± 2.6 | 1.3 ± 1.1 |
| Urban landscape | 0.2 ± 0.5 | 0.1 ± 0.2 | 0.2 ± 0.5 | 0.1 ± 0.2 | 0.2 ± 0.4 | 0.1 ± 0.2 |

**Table 2** Annual biotope compositions (%; mean ± SD) of the surroundings of Lesser Spotted Eagle nests (within a 2-km radius) according to the field mapping data. Non-agricultural habitats added from the Estonian Basic Map

| Biotope | 2004 | 2005 | 2006 |
|---|---|---|---|
| Mowed natural grassland | 1.8 ± 2.6 | 1.9 ± 2.8 | 1.6 ± 3.0 |
| Mowed cultivated grassland | 5.7 ± 6.1 | 8.1 ± 7.3 | 7.6 ± 7.6 |
| Pasture | 1.6 ± 3.5 | 1.4 ± 2.0 | 0.8 ± 2.0 |
| Unmanaged natural grassland | 5.1 ± 4.1 | 4.7 ± 3.1 | 6.2 ± 6.6 |
| Unmanaged cultivated grassland and set-aside | 7.8 ± 6.1 | 9.4 ± 7.0 | 7.9 ± 5.8 |
| Cereals | 8.4 ± 9.7 | 6.4 ± 5.8 | 6.8 ± 7.4 |
| Oilseed rape | 1.5 ± 2.4 | 0.8 ± 1.3 | 2.3 ± 3.9 |
| Vegetables | 0.3 ± 0.8 | 0.2 ± 0.6 | 0.2 ± 0.7 |
| Orchard | 0.3 ± 1.4 | 0.1 ± 0.6 | 0.4 ± 1.6 |
| Bushland and afforested agricultural landscape | 2.6 ± 1.4 | 2.8 ± 1.9 | 2.6 ± 1.5 |
| Forest | 54.2 ± 16.2 | 57.2 ± 16.1 | 54.7 ± 19.2 |
| Mire and marsh | 9.8 ± 11.1 | 6.2 ± 8.9 | 7.7 ± 12.6 |
| Waterbody | 1.0 ± 1.3 | 0.9 ± 1.1 | 1.2 ± 1.2 |

**Table 3** Best models describing habitat selection of the Lesser Spotted Eagle according to the Estonian Basic Map and the Estonian Agricultural Register Map of Managed Agricultural Land Units in 2010–2012

| | Estimate ± SE | *Z* | *P* |
|---|---|---|---|
| *Estonian Basic Map* | | | |
| Intercept | −1.968 ± 0.184 | −6.51 | <0.001 |
| Regular agricultural biotopes | 0.001 ± 0.000 | 4.53 | <0.001 |
| Natural grassland | 0.008 ± 0.001 | 5.55 | <0.001 |
| *Database of managed agricultural land units* | | | |
| Intercept | −0.672 ± 0.141 | −4.78 | <0.001 |
| Natural grassland | 0.008 ± 0.004 | 2.04 | 0.041 |
| Cultivated permanent grassland | 0.003 ± 0.001 | 2.64 | 0.008 |
| Crop field/cultivated grassland | 0.002 ± 0.000 | 3.69 | <0.001 |

grasslands (37.5%), when compared with their availability ($\chi^2_1$ = 4.7, $P = 0.03$), but the ratio was similar to the use of these biotopes ($\chi^2_1 = 0.6$, $P = 0.43$).

Of the attacks, 51% were successful ($n = 102$ attacks with a known result); 50% of 80 attacks were successful in grasslands and 46% of 15 attacks in arable fields, which were not significantly different from parity. Similar success of attacks was recorded in managed grasslands (51% of 45 attacks), and although success was lower in unmanaged grasslands (33% of 27 attacks) the difference was not significant ($\chi^2_1 = 1.5$, $P = 0.22$).

Of the observed prey, 55.8% were small mammals and 44.2% were amphibians ($n = 43$). Mammals were caught mostly in grasslands (70.8%), less in cereal fields (20.8%), and only occasionally in other arable fields (4.2%) and fallow (4.2%); amphibians were also caught mostly in grasslands (73.7%; but 26.3% on flood-plain meadow), but also near waterbodies (21.1%) and in clear-cuts (5.3%).

**Table 4** Best models describing reproductive success of the Lesser Spotted Eagle according to the field-mapped agricultural biotopes (2004–2006) and the Estonian Agricultural Register Map of Managed Agricultural Land Units (2010–2012)

| | Estimate ± SE | *Z* | *P* |
|---|---|---|---|
| *Field-mapped agricultural biotopes* | | | |
| Intercept | 0.86 ± 0.39 | 2.20 | 0.028 |
| Year 2005 | 0.92 ± 0.46 | 2.01 | 0.044 |
| Year 2006 | 0.99 ± 0.69 | 1.43 | 0.152 |
| Mowed cultivated grassland | −0.01 ± 0.00 | −2.01 | 0.040 |
| Oilseed rape | −0.01 ± 0.01 | −1.84 | 0.066 |
| *Database of managed agricultural land units* | | | |
| Intercept | −0.20 ± 0.28 | −0.71 | 0.474 |
| Year 2011 | 0.30 ± 0.28 | 1.07 | 0.294 |
| Year 2012 | 0.87 ± 0.30 | 2.84 | 0.004 |
| Natural grassland | 0.01 ± 0.01 | 1.84 | 0.066 |
| Crop fields/cultivated grassland | <0.01 ± 0.00 | 2.49 | 0.013 |

## Effect of agricultural land use on reproductive success

The mean number of offspring per occupied nest was 0.56 in 2004, 0.75 in 2005 and 0.71 in 2006; 0.59 in 2010, 0.66 in 2011 and 0.76 in 2012. Hence, the reproductive success of the Eagles fluctuated significantly between years in both studied 3-year cycles (Table 4).

In 2004–2006, the reproductive success was negatively influenced by the area of mowed cultivated grasslands and oilseed rape (Table 4). However, the relationships were not consistent over the years. The negative effect of mowed cultivated grassland was found only in 2005 [6.3 ± 5.3% (± SD) around successful and 12.7 ± 9.4% around unsuccessful nests, $Z = -2.80$, $P = 0.005$], which was a

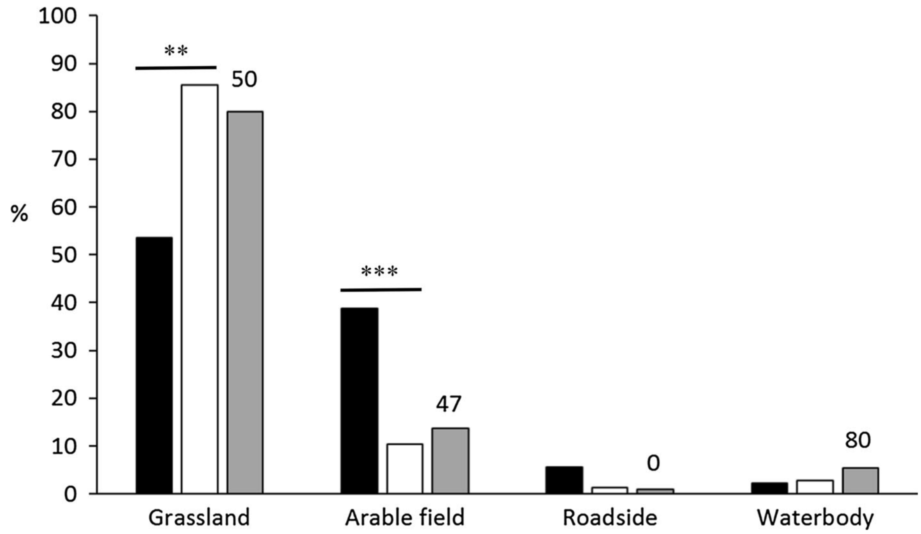


**Fig. 1** Shares of various habitat types in landscape of home ranges (*filled bars*), observations of foraging Lesser Spotted Eagles (*empty bars*; $n = 147$) and their attacks on prey (*grey bars*; $n = 106$). Significant differences (**$P < 0.01$, ***$P < 0.001$) and estimates of hunting success (%) are presented *above the bars*

good breeding year for Eagles, and that of the oilseed rape only in 2004 (0.4 ± 0.8% around successful and 2.8 ± 3.0% around unsuccessful nests, $Z = -2.57$, $P = 0.010$), which was a poor breeding year, but no effects were found in other years. In 2010–2012, when only managed agricultural biotopes were analysed, we found a slight positive effect of managed natural grassland, as well as crop fields and cultivated grassland on a crop rotation basis (Table 4). Nests of successfully breeding Eagles were surrounded more by crops/cultivated grassland on a rotational basis (19.0 ± 11.3%), as well as by managed natural grassland (1.1 ± 1.9%), than those of unsuccessful pairs (16.0 ± 11.9 and 0.7 ± 1.2%, respectively).

## Discussion

The current study confirmed that home ranges of the Lesser Spotted Eagle contain more grasslands, and other types of agricultural land, than expected by the general landscape composition, and that the Eagle prefers foraging on grasslands. However, the effect of grassland was not as straightforward as it initially seemed. Hunting success was not higher on grasslands nor was the reproductive success positively related to the area of grasslands in the home range. The management of grasslands had usually, but not always, a positive effect both on nest site occupancy and reproductive success. Finally, arable land was avoided during foraging and the sown area of oilseed rape negatively correlated with reproductive success.

Lesser Spotted Eagles built their nests in areas where the share of agricultural land was higher than available in the landscape. Hence, existence of suitable foraging areas shapes the distribution of the species in Estonia similarly to other European regions (Mirski 2009; Zub et al. 2010; but see Väli et al. 2009). Probably the preference of agricultural landscape just reflects the positive effect of grassland, as arable fields are usually avoided (Treinys 2004; Väli et al. 2004; Mirski 2009; Zub et al. 2010).

However, such simple interpretation of the preference patterns is not sufficient in Estonia, even if it is in the countries with a higher proportion of agricultural land. Estonian agricultural landscape is usually a mosaic of relatively small fragments of grassland and arable fields, which are interspersed with forest patches, or surrounded by larger forests. This forms a perfect habitat for the bi-biotopic Lesser Spotted Eagle. Second, various crops are grown on a rotational basis, and grasslands are usually included in rotations. Eagles are long-lived species and home ranges are used by the same birds for several years (Danko et al. 1996; Dravecký et al. 2013; Väli and Bergmanis 2017). Hence, rotation of various crops must influence their habitat selection process, and selection could be based only on grasslands, not on crop fields. Summarising, landscape heterogeneity in space and time probably strongly influences habitat selection of the Lesser Spotted Eagle in Estonia.

The current study confirmed the importance of grasslands for foraging Lesser Spotted Eagles. Grasslands contained more prey, which was indicated by a higher number of attacks compared to that in arable fields, although the hunting success was similar in both. However, as found in a previous study using a coarser level of resolution (Lõhmus and Väli 2004), our work did not reveal a direct positive effect of grasslands on the productivity of Eagles. However, we did sometimes note a positive impact of managed grasslands.

Why did grasslands have only a limited, and in some respects even controversial, effect? The simplest explanation is that the effect depends on the type of grassland and its management. Although unmanaged grasslands are rich in various prey, these are not accessible under tall vegetation. Alternatively, uncropped margins of arable biotopes may provide enough prey for successful breeding in years of abundant prey, whereas single-year anthropogenic intensively managed grassland is a poor habitat for many prey species (Reidsma et al. 2006). Whether the latter forms an ecological trap for the Lesser Spotted Eagle, as suggested in the current study by the negative impact on reproductive success in a good breeding year, deserves further research. Secondly, reproductive success of the Lesser Spotted Eagle is determined also by weather conditions and the abundance of its main prey (Väli 2012), which is also indicated by the strong year-effects registered in the current study. Such influence may be more substantial in agro-ecosystems at high latitudes where weather conditions and vole abundances fluctuate more (Hanski et al. 1991; Peltonen-Sainio 2012).

The effect of habitats on reproduction may vary between raptor species, even though they seem ecologically similar. For example, according to the current study, the sown area of oilseed rape negatively influences productivity of the Lesser Spotted Eagle, but, according to Panek and Hušek (2014), it is positively correlated with the breeding success of the Common Buzzard *Buteo buteo*. Although responses to environmental factors may vary geographically, this probably does not explain the controversy, because also Estonian Common Buzzards breed successfully near rape fields and often forage at their margins, as indicated by the telemetry data (Väli et al. 2015). Perhaps the Common Buzzard, mostly using a sit-and-wait strategy (Sachteleben 1993), could take better advantage of a rich rodent supply of uncropped field margins, whereas the Lesser Spotted Eagle, that mostly hunts on the wing and sometimes even on foot (Scheller et al. 2001; Mirski 2010), depends more on open land and cannot catch rodents when these are hidden under the dense cover of rape stalks. This indicates that one should be careful when using common surrogate species to draw conclusions regards a rare one, which is not uncommon practice in conservation biology (Caro and O'Doherty 1999; Wiens et al. 2008).

In general, we detected a positive effect of grasslands, but also a negative effect of oilseed rape fields on the Lesser Spotted Eagle. In light of these findings, recent trends in agriculture in Estonia, as seen overall in Europe, are alarming for this protected raptor species. The demand for oilseed rape is increasing along with that for biofuel production. For example, the sown area of oilseed rape increased from 600 ha in 1990 to 98,000 ha in 2010 in Estonia; more recently, the sown area of maize [which is also an unsuitable foraging habitat for raptors (Ursúa et al. 2005; Cardador and Mañosa 2011)] has increased in a similarly drastic manner [from 2000 to 8,500 ha in 2011–2015 (Statistics Estonia 2016)]. Fortunately, some recent positive trends for the Eagles were also noted. In 2010–2015 the sown area of oilseed rape decreased by ca. 30%, while the area of permanent grassland stopped decreasing (Statistics Estonia 2016).

Most grasslands at high latitudes are managed by mowing or grazing in order to avoid afforestation. This maintains suitable foraging habitat for many raptors. Obviously the management should not be too intensive, as maximum species richness is found in moderately managed grassland, e.g. under light grazing regimes and mowed semi-natural meadows (Reidsma et al. 2006; Billeter et al. 2008). Unfortunately, livestock husbandry is progressively intensifying in Estonia and elsewhere, as is the use of fertilisers, and single-mowed hay is being replaced by repeatedly harvested silage, whereas the optimal management for grassland-dependent raptors in northern latitudes are traditional forms of seasonally changing outdoor-indoor animal husbandry. Thus, there is a need for the maintenance of traditional agricultural practices wherever possible, and for diverse farmland use, including permanent late-mowed grassland, elsewhere (Benton et al. 2003). This proposal fits well with the suggestion to increase crop diversity in order to improve resilience to major future challenges for humankind, such as climate change (Howden et al. 2007; Reidsma and Ewert 2008).

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## Appendix

See Table 5.

**Table 5** Description of the landscape data sets used

| Study subject | Study years | Data source | Habitat type |
|---|---|---|---|
| General habitat composition of home ranges and its impact on habitat selection | 2004–2006, 2010–2012 | Estonian Basic Map (1:20,000) (Estonian Land Board 2013) | 1. Regular agricultural biotopes (arable fields and cultivated grassland, which is either permanent or inter-annually replaced by arable fields on a crop rotation basis) |
| | | | 2. Natural permanent grassland |
| | | | 3. Bushland |
| | | | 4. Forest |
| | | | 5. Mire and marsh |
| | | | 6. Exploited peatlands |
| | | | 7. Waterbodies |
| | | | 8. Farms |
| | | | 9. Urban landscape |
| Detailed habitat composition of home ranges, reproductive success and habitat utilisation by foraging Eagles[a] | 2004–2006 | Field mapping | 1. Managed natural grassland |
| | | | 2. Managed cultivated grassland |
| | | | 3. Unmanaged natural grassland |
| | | | 4. Unmanaged cultivated grassland |
| | | | 5. Set-aside arable land |
| | | | 6. Cereal crop field (oat, wheat, rye, barley) |
| | | | 7. Oilseed rape field[b] |
| | | | 8. Other managed agricultural land (potato, vegetable, strawberry fields, orchard) |
| | | | 9. Bushland and afforesting agricultural land |
| | | | 10. Forest |
| | | | 11. Mire and marsh |
| | | | 12. Waterbodies |
| Home range composition of foraging habitats according to their management, and its effect on reproductive success[c] | 2010–2012 | Estonian Agricultural Register Map (Estonian Agricultural Registers and Informational Board database) | 1. Managed natural grassland |
| | | | 2. Managed cultivated permanent grassland (multi-species grassland, which has had no crops for at least 4 years) |
| | | | 3. Crop fields and cultivated grassland on a crop rotation basis |
| | | | 4. Managed fallows (vegetation height less than 20 cm), which is maintained by regular ploughing or harrowing) |
| | | | 5. Orchards |

[a] We first analysed the effect of original biotopes but, thereafter, in order to increase the power of analysis, pooled agricultural biotopes into biologically significant groups: managed grasslands (*1, 2*), unmanaged grasslands (*3–5*), cereal fields (*6*), oilseed rape fields (*7*)

[b] In two home ranges in 2004 also 23.7 ha of structurally similar maize was included

[c] We excluded inter-correlated but rare and probably biologically insignificant managed fallows and orchards (*4, 5*) from the analysis

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