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RESEARCH ARTICLE

Movements of birds of prey reveal the importance of tree lines, small woods and forest edges in agricultural landscapes

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Abstract
Context Small woody features (SWF; tree lines and small woods) in agricultural landscapes provide a substitute for forest conditions for a wide range of species and a suitable edge habitat for ecotone species. The importance of SWF for biodiversity is usually inferred from presence or abundance data for small animals. Although large animals, due to their lower density are less likely to be attributed with SWF, they may depend on these areas to effectively utilize the agricultural landscape matrix.
Objectives We followed movements of three avian predator species (northern goshawk, common buzzard, and lesser spotted eagle) in the breeding and post-breeding season to assess their dependence on SWF in agricultural landscapes and to determine the characteristics of woods influencing each species.
Methods We compared time spent flying and perching, where perching sites were classified as open space, forest interior, forest edge, and SWF. Next, the relative importance of SWF and forest edges, as well as specific characteristics of each habitat, were evaluated using resource selection functions.
Results All species spent most of the daytime perching, and preferentially utilized SWF and forest edges. Buzzards and eagles were not influenced by the characteristics of SWF, but goshawks preferred relatively large, dense patches.
Conclusions We conclude that SWF are crucial for exploitation of agricultural landscapes by avian predators by providing suitable perching sites for foraging. We also detected variation in the quality of perching sites, suggesting that for some species (like the goshawk), artificial perching sites cannot compensate for a lack of SWF.

Keywords Farmland · GPS telemetry · Raptors · *Accipiter gentilis* · *Buteo buteo* · *Clanga pomarina*

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Introduction

Forests are strongholds of biodiversity and habitats for a wide range of terrestrial species (FAO and UNEP 2020). However, in many parts of the world, agricultural landscapes are dominant, and woods remain only as islands in a farmland matrix. Still, such small woods and scattered trees are important for insects (Arthur et al. 2010; Rossi et al. 2016), birds (Hinsley et al. 1996; Dolman et al. 2007), bats (Law et al. 2000), and rodents (Moore et al. 2003) in transformed landscapes. Trees themselves offer habitats (e.g., branches, hollows, and wood fibers) that are crucial for many species originally found in forests, and there are hardly any substitutes for such habitats in open landscapes. Therefore, the presence of trees can fulfil the minimal habitat requirements for a wide group of species with a history of inhabiting forests (Martin et al. 2009). Additionally, small woods are crucial to maintain meta-populations of forest species in agricultural landscapes. They offer relatively long strips of edge habitat, which is suitable for ecotone specialists as well as for a wide range of species that forage in open spaces but breed in forests. The density of such species may even be highest in small woods (Bellamy et al. 2000). Many animal species use small woods as roosting sites or as observation or display posts. For such purposes, woods are usually beneficial, regardless of their size. Forest edges may play a similar role; they have high invertebrate and bird diversity (Máthé 2006; Šálek et al. 2010), and a high abundance (but not necessary diversity) of mammals (Stevens and Husband 1998; Fischer and Schröder 2014) and other animal groups (Helle 1985; Sekgororoane and Dilworth 1995; Šálek et al. 2010).

Unfortunately, small woods and scattered trees are declining in agricultural landscapes globally; in particular, mature trees are expected to vanish if current management practices continue (Gibbons et al. 2008). A decline of farmland trees is expected to affect a number of bird and bat species, including population decreases of 50% by the end of the century (Fischer et al. 2010). However, losses are usually directly linked to a decrease in the availability of breeding sites. This derives from the fact that simple presence-absence or abundance data have been used to analyze the determinants of the importance of trees and small woods. The utilization of woods by detailed analyses of single individuals has rarely been evaluated (but see Redpath 1995; Smedshaug et al. 2002). Therefore, the consequences of the loss of trees, small woods, and tree lines are not predictable for medium and large animals, which use such landscape elements to hunt or roost. Advances in GPS telemetry provide a basis for improving our knowledge of the importance of trees in farmlands (Tomkiewicz et al. 2010). This technology enables us to follow medium and large animals with sufficient precision to investigate behavioral patterns in mosaic landscapes. Additionally, fine-scale datasets for 'Small Woody Features' (SWF), including both linear and patchy features, have recently been released (Faucqueur et al. 2019; Copernicus 2020) and enabled us to analyze utilization of this habitat by few species inhabitanting agricultural landscape.

We focused on the use of SWF and forest edges by three birds of prey: northern goshawk *Accipiter gentilis* (hereafter goshawk), common buzzard *Buteo buteo,* and lesser spotted eagle *Clanga pomarina*. All are medium size (ca. 600–1600 g) tree-nesting species that breed in forests; however, they differ remarkably with respect to foraging ecology. The goshawk eats mostly other birds, hunting by short chases after spotting prey moving close to the perching site (Kenward 2006). The common buzzard hunts prey on the ground using different techniques, typically spotting prey from a perch (Wuczyński 2005; Walls and Kenward 2020). The lesser spotted eagle exhibits soaring, usually spotting small prey (small mammals, birds, and amphibians) during patrol flights, while perching or walking and attacking prey on the ground (Mirski 2010). Therefore, all of these species depend on perching sites while foraging to various extents.

Combining GPS telemetry and available datasets, our aim was to determine the relative importance of SWF and forest edges for three birds of prey to evaluate factors influencing their utilization to guide landscape planning and conservation. In allowing for variation in SWF and species responses to habitat characteristics, these analyses may reveal different conservation goals for small woods in farmlands. First, we aimed to confirm that in open, agricultural landscapes, birds of prey spend most of the daytime perching, and the importance of perching depends on the main foraging strategy (i.e., goshawk and common buzzard are mostly hunting by perching, while lesser spotted eagle prefers to soar). Obviously, perching may be used also for other activities, such as resting and sleeping; therefore we paid special attention during data analysis to excluding other activities besides hunting. We also assumed that SWF and forest edges provide suitable edge habitats for many prey but also serve as lookout points for hunting; therefore, birds of prey perch in SWF and forest edges more often than in the forest interior and open spaces. Assuming that SWF holds mostly edge habitats and perches to scan open spaces, we expect these areas to be attractive, irrespective of their size or the distance to forest edges. SWF characteristics are mostly of secondary importance for birds of prey, except for species hunting by surprise on agile prey, such as the goshawk, which takes advantage of the canopy for camouflage. Therefore, we expect that the goshawk will use dense forests more often than other species.

Materials and methods

Tracking data

The study plot was northwest of Tartu in Southern Estonia (Fig. 1). The study area consisted of a mixture of forests, agricultural land, urban and rural infrastructure, lakes, river valleys and bogs (Online Resource 1). The direct study area, covering the extent of tracking data, reached 1011 km^2. As much as 46.6% of this land was managed for agriculture, 34.8% was afforested, 6.9% was constituted by river valleys, bogs and lakes, 4.0% by SWF, and the remaining 7.8% by wastelands, infrastructure, yards and other land-use categories.

The density of breeding pairs of the studies species reached 17.5 pairs/100 km^2 in case of common buzzard, 2.3 in goshawk and 1.8 in lesser spotted eagle (Väli unpubl. data). Using apex raptor decoys (white-tailed eagle and eagle owl) and large mist nets, 30 individuals of three different birds of prey species were caught and equipped with GPS-tracking devices (Online Resource 2). Tracking data for 26 individuals (16 common buzzards, six lesser spotted eagles, and four northern goshawks) were collected in 2019 (February–December) using GPS loggers manufactured by Ornitela. Four lesser spotted eagles were caught in 2011–2012 and equipped with Microwave GPS satellite transmitters; however, only data obtained in 2019 were used. GPS loggers were set to collect one fix every 10 min. If the battery charge was below 25%, the data collection interval decreased to one fix per hour. Satellite transmitters were programmed to collect data at 2 h intervals. Only data from breeding territories were used. Therefore, data up to winter were used for sedentary goshawks, while migration and wintering periods were excluded for the migratory lesser spotted eagles and common buzzards (Online Resource 2).

We aimed to analyze utilization of SWF and forest edges mostly for foraging. Therefore we have applied following procedure to omit data representing other main activities. All three studied species nest in forests. To exclude locations connected to breeding activity, all GPS fixes in a 150 m radius around each nest of followed individuals were excluded. To focus on potential foraging activity, locations from dusk to dawn were omitted using the *oce* package (Kelley and Richards 2020) in R 3.6.1, using GPS coordinates and timestamps to calculate the position of the sun at each location. Observations were excluded when the sun was equal to and below 0° over the horizon. This dataset was used to analyze time spent flying and perching (dataset 1; 57,497 GPS fixes) and was the base to prepare another two datasets. All GPS fixes from dataset 1 with a registered speed over 0 m/s were excluded, and the remaining data were used to analyze perching time in various habitats (dataset 2; 31,031 GPS fixes). To avoid autocorrelation issues, prior to habitat use modelling, dataset 2 was resampled to obtain one fix per hour by including only the first position registered at given hour (dataset 3; 13,733 GPS fixes). The effect of this operation was checked by comparing the average step length between original and resampled datasets using the *moveHMM* package (Michelot et al. 2016). The distance between consecutive positions was 1.9 times longer for the resampled data, which reached 956 m, on average (median = 812 m). Perching habitats between GPS locations were therefore considered independent.

Environmental data

Data for SWF were downloaded as a vector database from the European Union's Earth Observation Programme (Copernicus 2020). The database covered patchy woody features (woods of 200–5000 m^2 with a minimum width of 30 m) and linear woody features (woods of at least 50 m long and up to 30 m wide; Copernicus 2020). However, based on satellite images, linear features were overrepresented and often covered patches with more complex shapes. Therefore, SWFs were not divided according to patchy or linear characters in our analysis. Assuming standard GPS accuracy reaching 15 m, a 15 m-wide buffer over SWF was applied in analyses linking this habitat type with locations of birds.

The forest interior and forest edges were distinguished on the basis of forest vector maps (selected for forests of at least 5200 m^2) downloaded from Estonian Land Board Geoportal. Forest edges were treated as a

30 m-wide (in both sides) buffer, established from the borderline of a forest polygon. The width of the buffer takes into account the mean GPS-tracking error (15 m) and assumed depth of 30 m of the forest margin, from which birds are able to see open space, either picking the tallest tree on the edge or hiding under the canopy to strike by surprise. This dataset was used to remove SWFs that could be duplicated with the Estonian forests layer. The intersection of the SWF and forest vector layer was excluded from the SWF layer. Finally, this dataset was used to measure the 'SWF area' in a local cartographic projection, the Estonian Coordinate System of 1997.

The distance between registered bird locations and the forest edge ('distance to forest') was calculated using the Nearest Neighbor plugin in QGIS 3.4.4 with the above-described vector datasets (raw, without buffers). Tree cover density ('TCD') was also evaluated based on satellite images from 2015. Data were downloaded from Copernicus (2020) at 20 m resolution, and each GPS location was extracted in QGIS 3.4.4.

Analyses

All statistical analyses were implemented in R 3.6.1 (R Core Team 2020). Using dataset 1, time spent perching and flying for each species were compared based on fixes with registered speeds equal to or less than 3 km/h (indicating perching) and speeds equal to or greater than 4 km/h (indicating flying; Nathan et al. 2012; Khosravifard et al. 2012). This division did not account for motionless "hanging" in flight by soaring lesser spotted eagles or hovering common buzzards. Considering the latter, given that in different studies, it constituted 0–3% of common buzzard observations (Walls and Kenward 2020), we considered this type of flight negligible to our dataset. Similarly, in case of "hanging" in flight by eagles, such flight lasts seconds, therefore its share in dataset is very low. Inter-specific differences were tested with generalized liner mixed models with individuals as random effects and binomial distributions using the *glmmTMB* package (Brooks et al. 2017) in the R environment. The assignment of fixes to the flying or perching set was treated as a binary dependent variable, and species was the only independent variable.

Dataset 2 was used to compare amount of time spent by each species in SWF, forest edges, forest interior, and open space. GPS fixes representing used habitats were set against random points accounting for available habitats. The latter was drawn in QGIS 3.4 for each individual. Using the number of acquired GPS fixes as a sample size, points were drawn for 100% minimum convex polygon (MCP) home range estimation for all individuals. Proportions of habitats for bird locations and random points were compared with the Kruskal–Wallis test with Dunn's post hoc multiple pairwise comparison test with Bonferroni adjustment.

To investigate the relative importance of SWF, forest edges, and various factors for each species, eight generalized linear mixed effects models were built for each species using the *glmmTMB* package. Models were fitted to binomially distributed data with individuals as random effects. As a binary response variable, we set GPS locations of tracked individuals (dataset 3) against random points in their MCP home ranges (described in the previous paragraph). Eight models differed in the number of explanatory variables, starting from the presence of SWF only, to the presence of SWF and forest edges, to factors describing both (Table 1). Prior to fitting the model, variables were scaled to adopt a similar range of values and thus to improve model performance. The best model was chosen based on the Bayesian information criterion (BIC). An output table was collated using the *sjPlot* package (Lüdecke 2020). Differences in daytime patterns of SWF selection for perching was tested between individuals of each studied species using Permutational Multivariate Analysis of Variance (PermANOVA) in *vegan* package (Oksanen et al. 2019). To evaluate daily patterns in the use of SWF and forest edges by birds of prey, separate generalized additive models were fitted for each of the habitats used by the three species depending on the time of day. Models were fit using the *mgcv* package (Wood 2017) with binomial distributions and individuals as random effects.

Results

Importance of perching behavior and perching habitat

All three species spent most of the daytime perching (Fig. 2). The goshawk and common buzzards perched, on average, for 89.8% ± 4.5% and 89.0% ± 4.0% of the day, respectively. Lesser spotted eagles perched

Table 1 Comparison of registered GPS locations of the three birds of prey species and random locations in an agricultural landscape of Estonia, as evaluated by Dunn's multiple pairwise comparison tests

	Open landscape	Forest edge	Forest interior
Common buzzard			
Forest edge	– 30.45***		
Forest interior	– 28.51***	5.12***	
SWF	– 24.10***	– 2.40*	– 5.64***
Northern Goshawk			
Forest edge	– 60.60***		
Forest interior	– 45.75***	11.30***	
SWF	– 49.60***	– 5.79***	– 14.07***
Lesser spotted eagle			
Forest edge	– 42.77***		
Forest interior	9.00***	40.12***	
SWF	– 29.96***	1.09^{ns}	– 32.24***

Positive and negative values indicate a preference for or avoidance of habitats in the columns vs. the rows

ns not significant

*$p < 0.05$, **$p < 0.001$, ***$p < 0.0001$

significantly less often, 72.2% ± 4.7% of the day ($\lambda = -1.10$, $p < 0.001$; Online Resource 3). The remaining portion of daylight was spent flying. All studied species selectively used open spaces, forests, and SWF (Fig. 3). We observed the greatest differences between time spent in selected vs. available habitats for the goshawk ($\chi^2 = 4826.4$, $p < 0.0001$) and lesser spotted eagle ($\chi^2 = 2945.03$, $p < 0.0001$), and we also detected a significant difference for the common buzzard ($\chi^2 = 1102.2$, $p < 0.0001$). Pairwise comparisons revealed that SWF was used more often than expected based on availability in almost all cases (except when compared with forest edge use by the lesser spotted eagle; Table 1).

Factors affecting the attractiveness of small woody features and forest edges

Generalized linear mixed effects models showed that a simple model including only SWF and forest edges best explained the perching behavior of the common buzzard. Lesser spotted eagles were additionally affected by the canopy density of forest edges. Goshawks showed the most complex pattern of SWF and forest edge use, as all tested characteristics were included in the most well-supported model (Table 2).

Common buzzards clearly preferred to perch in forest edges as well as in SWF over the forest interior and open spaces (Table 1). Lesser spotted eagles also preferred to perch in both of those habitats over the open space and forest interior; however, they had a slight preference for forest edges over SWF. Lesser spotted eagles preferentially perched in forest edges of slightly lower density. By contrast, goshawks clearly preferred SWF over forest edges, which were also utilized. In case of both habitats, goshawks selected ones with dense tree cover. They also preferred SWF with relatively large areas (c). All models explained a moderate percent of variation in perching behavior. The random effect of individuals was relatively weak, but was most pronounced in common buzzards (Table 3).

Small woody features and forest edges showed different patterns of utilization by birds of prey depending on the time of day (Fig. 4, Online Resource 3). Moreover, studied species showed different patterns of SWF use during the day (PermANOVA, $F = 2.100$, $R^2 = 0.154$, $p = 0.027$). Goshawks tended to use SWF more often than other areas in the late morning. Common buzzards selected small forests in the early morning and before noon but avoided SWF and forest edges in the afternoon. Lesser spotted eagles showed the most distinct daily patterns, choosing SWF

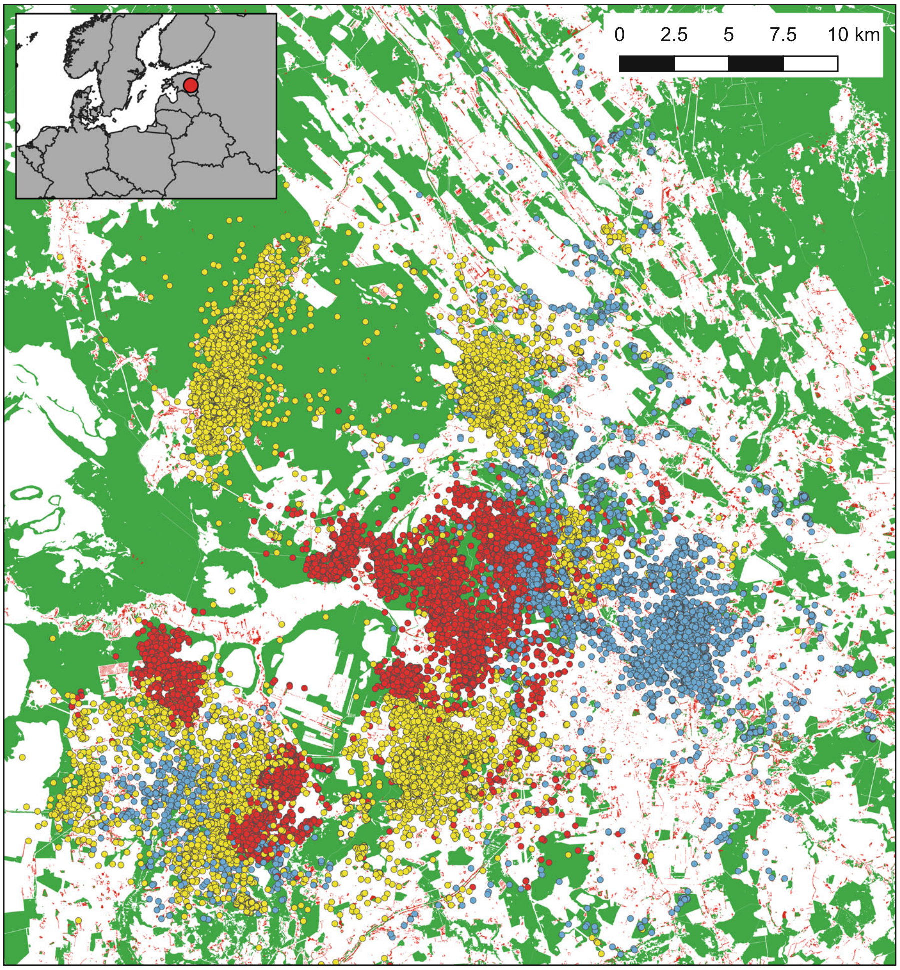

Fig. 1 Study area near Tartu, Estonia where three species were GPS-tracked to investigate the importance of small woody features and forest edges for hunting species. Red, yellow and blue dots show registered GPS locations of 16 tracked common buzzards (altogether 23,236 locations), ten lesser spotted eagles (22,252 locations) and four northern goshawks (11,809 locations), respectively. Small woody features are shown in red, and forests are shown in green polygons

and forest edges in the morning and afternoon but avoiding these areas midday.

Discussion

Importance of small woody features as perching sites in agricultural landscapes

Agriculture has tremendously altered landscapes previously dominated by forests (Williams 2000). Although many animals have adapted to this change, a minimal proportion of the historical habitat is necessary for breeding or shelter. Most forest-dwelling birds of prey adapted to hunting in farmland, and some even benefitted substantially from agriculture due to greater prey availability and habitat heterogeneity (Koks et al. 2007; Väli et al. 2017, 2020). Although raptor species previously inhabiting forests now live in nearly treeless habitats, like farmland and cities, conserved elements of their habitat are not limited to tree branches for nesting. Our data showed that different birds of prey typically require perching sites during the daytime, even species with soaring behavior, like the lesser spotted eagle. The frequency of perching did not differ significantly between the goshawk and common buzzard (utilizing various hunting techniques), but, as expected, was

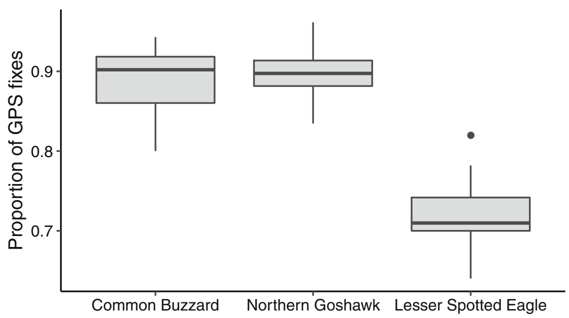

Fig. 2 Proportion of GPS fixes corresponding to perching compared with all fixes (both flying and perching) during daylight hours among three raptor species. Horizontal line shows the median, box shows the first and third quartiles, whiskers show 1.5 × inter-quartile range, and dots indicate outliers

clearly different in soaring eagles (Fig. 2, Online Resource 3). We paid special attention to focus on hunting while analyzing perching fixes, but we cannot exclude possibility that some other activities, such as resting, sleeping or preening were still included too. However, we believe that methods of data analysis enabled to exclude most other activities.

Perch-hunting requires minimal energy expenditure; therefore, it is a preferred hunting technique for many raptor species, especially those with a rather small wing surface, not typically adapted to use thermal uplifts (Newton 1979). Perch availability is also a strong determinant of habitat use in other birds of prey in different parts of the world (e.g., pale chanting goshawks and American kestrels; Malan and Crowe 1997; Sheffield et al. 2001). However, the importance of perching in birds of prey may have been underestimated in studies based on direct observations (Hantge 1980; Mirski 2010); our use of GPS-telemetry data addresses this limitation of previous studies. When perch-hunting is the dominant strategy, foraging conditions are expected to be highly limited in treeless landscapes. We even anticipate that the availability of SWF was crucial for the northern goshawk, a forest species in most of its range (Kenward 2006), to colonize farmland and urban areas (Rutz 2008). Without tree cover, it is difficult to surprise and chase agile prey in open spaces, particularly for species with short wings. However, soaring species, such as the lesser spotted eagle in this study, rely substantially on SWF. They are often forced to perch in the morning and evening, when there are no thermal uplifts (Elkins 2010). Perching sites are even more crucial for such species when the weather conditions are unfavorable for days or weeks during the chick-rearing season. Another reason for perching is safety during roosting, caring for plumage, and feeding. Contrary to ground sitting, perches offer far better visibility (Andersson et al. 2009), making them safer against attacks by mammalian predators and much better at spotting other birds of prey that could endanger them or their broods.

Fig. 3 Proportion of perching sites during the daytime for GPS-tracked birds of prey according to habitat type in an agricultural landscape in Estonia. *SWF* small woody features

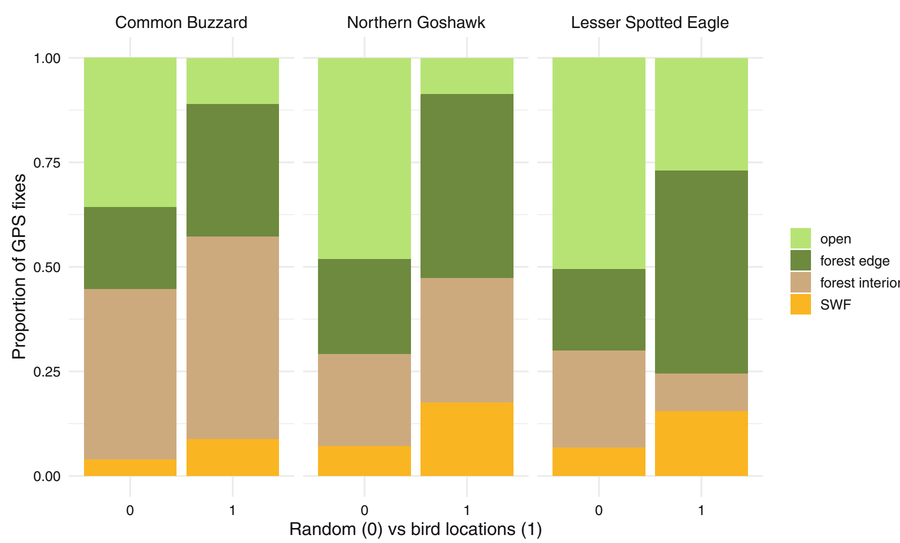

Table 2 Generalized linear mixed effects models explaining habitat selection with respect to small woody features (SWF) and forest edges by GPS-tracked birds of prey during foraging in an agricultural landscape of Estonia

Model	Predictors	Bayesian Information Criterion value		
		Common buzzard	Northern Goshawk	Lesser spotted eagle
1	SWF	14,936	10,382	11,403
2	SWF + forest edge	**14,275**	9979	10,555
3	SWF + SWF: TCD* + forest edge	14,278	9915	10,563
4	SWF + SWF: distance to forest + forest edge	14,279	9984	10,563
5	SWF + SWF: area + forest edge	14,283	9887	10,564
6	SWF + forest edge + TCD* of forest edge	14,282	9894	**10,552**
7	SWF + SWF:TCD* + SWF: distance to forest + SWF: area + forest edge	14,292	9843	10,580
8	SWF + SWF:TCD* + SWF: distance to forest + SWF: area + forest edge + forest edge: TCD*	14,298	**9758**	10,578

All models include individuals as random effects. A binary dependent variable was the response to GPS locations of followed individuals vs. random points. Bayesian information criterion values for the most well-supported models are shown in bold

**TCD* tree cover density

Factors affecting the utilization of small woody features by birds of prey

We confirmed that SWF and forest edges are highly important for perching birds of prey. SWF were used preferentially for perching over open spaces (incl. single trees), the forest interior, and forest edges by all tracked species, with the exception of lesser spotted eagles, which frequently used both, forest edges and SWF. Common buzzards and lesser spotted eagles perch on the ground, electric poles, and fences; therefore, the difference between the number of perching locations in open space and SWF or forest edges was striking (Table 2). Given the high availability of artificial perching sites in transformed, open landscape, our results reflect a difference in quality between such sites vs. SWF or forest edges. Bird-hunting northern goshawks clearly avoided perching in open spaces because they require canopy cover to surprise prey. However, the first two species mainly hunt small mammals on the ground and therefore often use artificial perches, electric poles, fences, etc. There is evidence that such species benefit from artificial perches (Widén 1994; Sheffield et al. 2001); however, these artificial perches have not been compared with natural perching sites, such as scattered trees, tree lines, SWF, and forest edges. Natural structures provide perching sites, but at their agriculturally unmanaged ground level they also provide a suitable habitat for small prey (Tattersall et al. 2000; Heroldová et al. 2005) and camouflage.

We expected that birds of prey use SWF mostly as perching sites for viewing open spaces and therefore most of their characteristics are irrelevant. Indeed, we found that common buzzards and lesser spotted eagles are not affected by the studied SWF characteristics. Northern goshawks preferred large SWFs, which may be explained by the relatively high variation in conditions to find suitable perching sites to hide and strike by surprise. Second, larger patches offer more nesting and roosting opportunities to avian prey species. It is also probable that forest species are preferred by goshawks over other avian prey. The common buzzard, as a flexible generalist, shows no particular preference for perching sites, as it hunts for diverse prey from various perches (Wuczyński 2005).

In accordance with our prediction, we found that goshawks, which hunt other birds by surprise, show a preference for woods of greater density. The probability of perching, both at forest edges and SWF, increased as the tree cover density increased. This shows that, at least for some species, not only the availability, but also the quality of SWF matters. Interestingly, we observed the opposite pattern for lesser spotted eagles, which preferred to perch at forest edges with lower cover densities. In the latter species,

Table 3 Summary of the best generalized liner mixed effect models explaining the importance of small woody features (SWF), forest edges and factors characterizing these areas in three birds of prey species GPS-tracked in an agricultural landscape of Estonia

Predictors	Common buzzard			Northern Goshawk			Lesser spotted eagle		
	Estimate	CI	p	Estimate	CI	p	Estimate	CI	p
(Intercept)	− 0.29	− 0.53 to − 0.06	**0.015**	− 0.93	− 1.23 to − 0.64	**< 0.001**	− 0.63	− 0.85 to − 0.40	**< 0.001**
SWF	0.58	0.45 to 0.72	**< 0.001**	1.13	0.97 to 1.28	**< 0.001**	1.27	1.14 to 1.39	**< 0.001**
Forest edge	1.27	1.17 to 1.37	**< 0.001**	1.01	0.89 to 1.13	**< 0.001**	1.60	1.48 to 1.71	**< 0.001**
SWF: area				0.76	0.59 to 0.93	**< 0.001**			
SWF: TCD				0.58	0.43 to 0.74	**< 0.001**			
SWF: distance to forest				0.07	− 0.05 to 0.20	0.271			
Forest edge: TCD				0.49	0.39 to 0.59	**< 0.001**	− 0.17	− 0.26 to − 0.07	**0.001**
Random effects									
σ^2	3.29			3.29			3.29		
τ_{00}	0.22 $_{ind}$			0.09 $_{ind}$			0.12 $_{ind}$		
ICC	0.06			0.03			0.04		
N	16 $_{ind}$			4 $_{ind}$			10 $_{ind}$		
Observations	11,150			7,790			8,526		
Marginal R^2/Conditional R^2	0.078/0.137			0.130/0.152			0.139/0.170		

TCD tree cover density

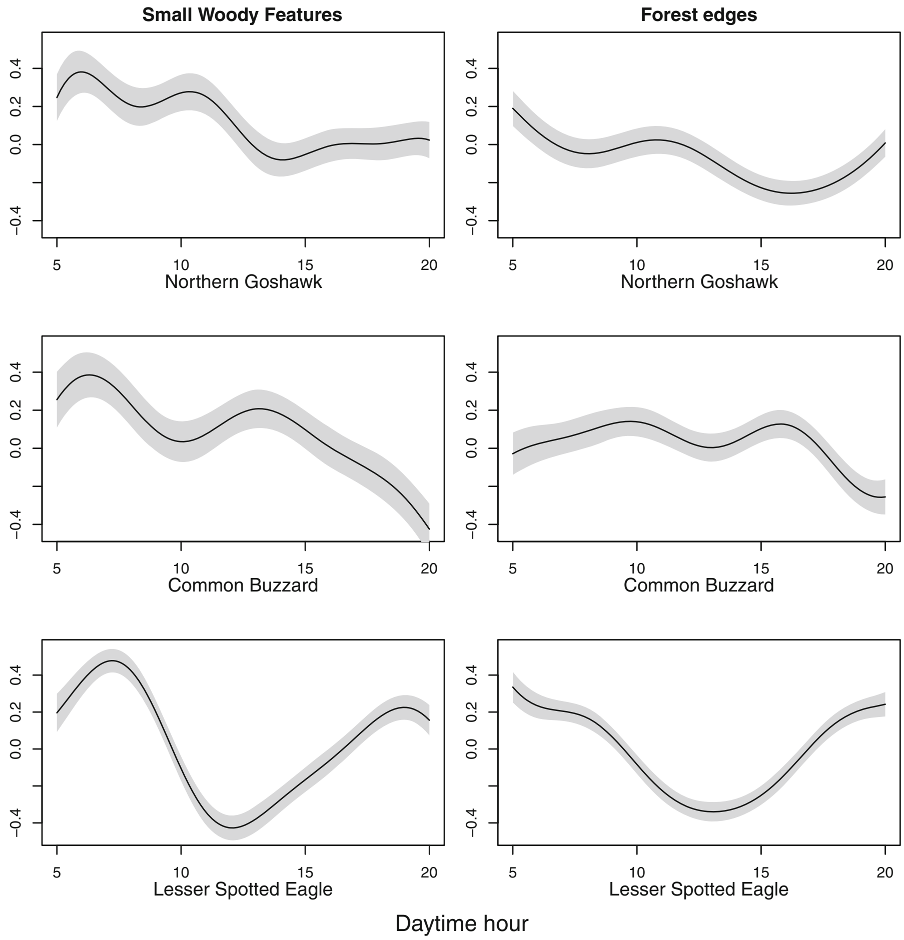

Fig. 4 Daytime patterns (local time) of the utilization of small woody features in an agricultural landscape of Estonia by three GPS-tracked birds of prey species revealed by generalized additive mixed models

the canopy may limit the visibility of prey on the ground (whereas goshawks also attack flying birds) and therefore rather loose stands are more suitable for perch-hunting. Accordingly, variation in the properties of SWF is important to provide suitable conditions for different predatory species. It is worth to mention, that the difference in variance explained by random effect of the species was only about twice higher between the least and most numerous species although the difference between number of individuals was four times higher. This shows the effect of uneven sample sizes was rather weak in our dataset.

Finally, our tracking analysis showed that the utilization of SWF changes throughout the day. Temporal variation was more pronounced for SWF than for forest edges (Fig. 4). SWFs were typically used by goshawks in the mornings until noon, common buzzards in the mornings and midday, and lesser spotted eagles in the mornings and evenings. The latter species, which prefers to hunt by soaring, is forced to hunt by perching in the absence of thermal uplift potential. Therefore, beyond irregular weather conditions, daily solar radiation rhythms make this soaring species dependent on suitable perching sites, like SWF. In the first two species, which are forest inhabitants in the first place, broad SWF utilization in the mornings reveals their high importance during the main hunting period (Rutz 2006; Lang et al. 2019). Comparing the pronounced SWF daily utilization rhythms with the rather "flat" pattern of forest edge utilization highlights the importance of the former in the daily routine of the birds.

Overall, our findings illustrate the complex relations between predators and SWF scattered in agricultural habitats; these relationships are determined by hunting technique, time of day, and, in some cases, characteristics of the forest patch. Revealing these relations would have been very difficult with traditional methods; our animal tracking approach provides new insight into the use of small landscape features by large and mobile species.

Conservation of small woody features and tree lines

Our results show that the importance of SWF and forest edges in agricultural landscapes differs among birds of prey with considerable differences in ecology. Unfortunately, small woods, tree lines, and single trees are declining in agricultural landscapes, mostly due to farming polices and infrastructure development. For example, in the European Union, under the Common Agricultural Policy, agriculturally unproductive pieces of land are not eligible for financial support for management (Reif and Vermouzek 2019). Therefore, such landscape features as SWF, bushes, and tree groups are replaced with cultivated land. Agri-environmental schemes often fail in their mission to sustain biodiversity (Pe'er et al. 2014), which is linked to loss in unmanaged habitats. The latter threat of tree removal in the course of infrastructure development is mostly linked to the expansion of road networks. Old tree lines are often removed when roads are modernized to accommodate greater traffic and larger machinery. Such tree lines contribute substantially to the availability of forest-like habitats in agricultural landscapes and are favored by many species (Wuczyński et al. 2011).

To support birds requiring perching sites, conservation programs often involve the construction of artificial perches. These are often found to benefit birds of prey (Widén 1994; Sheffield et al. 2001); however, our results show that they cannot fully replace the benefits of SWF for the whole raptor community. Artificial perches are not suitable for species hunting on agile prey and requiring canopy cover. Moreover, such artificial constructions are not a substitute for woods in farmland used by generalists, showing a high preference for forests, like the common buzzard in our case or the tawny owl (Redpath 1995). Additionally, the understory in small wood patches is most often unmanaged, offering suitable habitat for small mammals, birds, insects, and plants to reproduce and function on a meta-population basis. This benefits birds of prey and many other species, and increases biodiversity.

Conclusions

Our results show that utilization of SWF and forest edges by birds of prey may be complex and governed by range of factors, such as time of the day, wood size and its characteristics, but also differs depending on foraging ecology of particular species. We found that SWF together with forest edges are generally important for birds of prey in farmlands as perching sites, but probably also as remnants of forest or edge habitat, that are generally deficient in open landscapes. Such woods, irrespective of their size, should be protected to maintain the diversity of avian predators in agricultural landscapes. Moreover, in treeless areas, small wood patches and tree lines should be planted to provide conditions suitable for the full food chain in semi-natural and artificial farmland conditions. Diverse conditions of farmland woods (dense and loose, deciduous and coniferous) are also important for various species in the raptor guild, therefore landscape management should favor diversity of SWF and forest edges.

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Author contributions PM designed the methodology; ÜV and PM led the tagging birds of prey; PM conducted data analysis; ÜV and PM wrote the manuscript.

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Data availability Raw data (referred to 'dataset 1' in Methods) is available at Mendeley Data repository, https://doi.org/10.17632/xxsdzhwct8.1

Compliance with ethical standards

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

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