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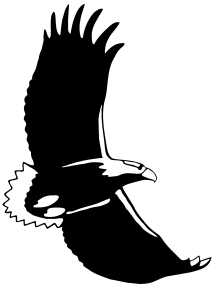
Journal of BirdLife Finland



Vol. 100 • No. 1 • 2023

The contents of pages 1–60 are peer-reviewed

BirdLife
SUOMI·FINLAND

Ornis Fennica

VERTAISARVIOITU
KOLLEGIALT GRANSKAD
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www.tsv.fi/tunnus

ISSN 0030-5685 • Listed in Current Contents and in Science Citation Index

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BirdLife
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Published by BirdLife Finland.
Printed in Finland by Lehtisepät Oy, Jyväskylä.

Ornis Fennica 100: 1–16. 2023

Distribution and habitat of the Eurasian Treecreeper (*Certhia familiaris*) in Corsica

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Received 12 February 2022, accepted 16 November 2022

The Eurasian Treecreeper is a forest bird distributed from South-Western Europe up to Northern Asia. Two phylogenetic groups have been recently identified within this species, one restricted to Corsica Island (Mediterranean) and the Caucasus region, the other distributed over most of Eurasia and in Northern Asia. Little is known on the natural history of the Corsican population. We present here new comprehensive data on its distribution and habitat. The Eurasian Treecreeper is found from sea level to the upper limit of the forest but absent from the treeless macchia, a dominant vegetation in Corsica. Breeding occurs in a variety of tree species with a strong preference for mature stands and large trees. Its preferred habitat consists of old stands of Corsican Pines and of Sweet Chestnuts, although they are not the commonest tree species in Corsica. The current decline of Sweet Chestnut orchards confers a particular importance to the future preservation of mature stands of Corsican Pine, a patrimonial habitat of great value hosting several endemic bird taxa.

1. Introduction

The Eurasian Treecreeper (*Certhia familiaris*) is a forest bird patchily distributed in the Palearctic, relatively common from the British Isles to Northern China and Japan, through Central Europe (Keller *et al.* 2020). The species comprises two phylogenetic lineages that diverged during the mid-Pleistocene (*ca.* 1 Myr): a paleo-endemic group with an allopatric range nowadays restricted to Corsica and the Caucasus region, and a more widespread lineage, distributed over most of Eurasia and in Northern China (Pons *et al.* 2015). The Corsican population, belonging to the subspecies *C. f. corsa*, differs from other populations in morphology (Pons *et al.* 2019) and voice (Chappuis 1976, Tietze *et al.* 2008). It is nearly completely isolated, genetic introgression with Italian or French populations being very rare (Pons *et al.* 2019). Thus, this endemic population represents an important conservation unit, but current knowledge on its natural history is scarce, restricted to a few data on distribution, ecology (Thibault & Bonaccorsi 1999), and density (Arrizabalaga *et al.* 2002). In the Red-list of birds of Corsica, the Eurasian Treecreeper is considered as "Near Threatened", with a "major priority of conservation" due to its endemicity (Linossier *et al.* 2017). It is the only representative of the *Certhia* genera on the island, whereas in many other European regions the Eurasian Treecreeper is syntopic with the Short-toed Treecreeper (*C. brachydactyla*), both species interacting ecologically (Clouet & Gerard 2020).

On the continent, the Eurasian Treecreeper is a good indicator of the forest maturity (Suorsa *et al.* 2005), breeding densities being three times higher in old-grown forests than in managed forests (Virkkala *et al*. 1994). Moreover, a physiological study suggested that poor food supply to chicks reared in dense young forests, compared to scarce old forests richer in invertebrates, may decrease the body condition and survival of nestlings (Suorsa *et al.* 2003). Ancientness and maturity are two major qualities of forest ecosystems (Cateau *et al.* 2015). Among the major Mediterranean islands, Corsica (8,722 km^2) still shelters forests (Quézel & Médail 2003), among which ancient forests cover less than 80,000 ha, including 15,000 ha of mature forest (Panaïotis *et al.* 2017, Torre 2014). Like most of the Mediterranean region, the largest part of the Corsican forests is composed of a mosaic of tree species, shaped by a long history of human activities. The most emblematic tree of the island, although covering only 17% of the total forested area, is the Corsican Pine (see Table 3 for scientific name of trees), an endemic subspecies of the Black Pine, also distributed in Southern Italy and Sicily (Farjon & Filer 2013). The Corsican populations diverged from the Italian group about 100,000 years ago and persisted *in situ* during the Last glacial Maximum (Afzal-Rafii & Dodd 2007). Pollen and charcoal studies showed that its range, although restricted to inland today, used to cover the whole island of Corsica in the past (Reille 1977; Thinon 1998). The Corsican Pine is recorded from sea level up to 1,969 meters (IFN 2003), but forests are distributed from Meso-Mediterranean vegetation zone (near rivers) up to Montane vegetation zone (Gauberville *et al.* 2019). Logging affected its range since the Neolithic period (Mazet *et al.* 2016) towards recent times (Bourcet 1996, Pia Rota & Cancellieri 2001), although an altitudinal reconquest started since the last century due to the abandonment of summer pastures (ONF 2006, Panaïotis *et al.* 2017). In terms of area, the Holm Oak occupies the first rank in Corsican forests with 46% of the forest cover. Coppices have been long favoured for grazing, pruning, clumping, and logging (for firewood, wood charcoal, or manufacturing) (Carcaillet *et al.* 1997). Another anthropic part of the forest is composed of Sweet Chestnut orchards (6% of the total forest of Corsica cover today) that were cultivated during the 16–19th centuries and then progressively abandoned during the 20th century due to cutting for manufacturing tannin, parasites and diseases that affected chestnut harvests, and fires that destroyed old stands (Pia Rota & Cancellieri 2001, Campocasso 2016). Cluster Pine (16% of the total forest cover today) is a typical fire-propagated Mediterranean species that occupies a large wooded area in Corsica, although old stands remain rare due to frequent fires. Beech (8% of the total forest cover) has a marginal distribution in the Mediterranean region with only two islands occupied (Quezel & Médail 2003, 158). The Cork Oak is a typical Mediterranean species that covers a large surface in plains (7% of the total forest cover), especially in the South and the East of the island. Traditionally planted with large spacing between trees producing an open forest cover, the Cork Oak forests were managed towards collecting corks and grazing cattle (Riffard *et al.* 2008); this usage also implied that the older trees were cut when cork production decreased, thus maintaining stands artificially younger. Finally, Fir is rarely represented in pure stand in Corsica with less than 1% of the total forest cover.

Thus Corsican forests are characterized by a mosaic of tree species managed by humans at all altitudes and a dominant pine forest at higher elevations. Based on its ecology on the continent, the presence of large trees is probably a consistent factor in the Eurasian Treecreeper habitat selection on the island, but its specific preferences are currently unknown. In this study, we gathered data on its breeding range, altitudinal limits, tree species preferences, and dendrological factors. Our main objective was to define the ecological characteristics of the Eurasian Treecreeper in Corsica. This approach is essential in elaborating and supporting conservation plans for the forests in Corsica that are, like several other forested ecosystems in Mediterranean basin, threatened by modifications of land-use and frequent fires.

2. Methods

The Eurasian Treecreeper (hereafter "the treecreeper") is a discreet forest bird with few vocalizations and a short singing period that can pass easily unnoticed (Chappuis 1994). This study was conducted in Corsica (42°N, 9°S) each year from 1st March to 30th June (the core of its breeding season) in 2013–2021, using playback experiments. We observed the behavioural response of individuals to 3-min playback sessions of the nominate subspecies song (Roché 1990). To prevent the arrival of remote birds, the range of the call produced by a 4-watt transmitter was settled to less than 200 metres (this was checked by testing the device in the forest). All observed individuals were recorded, regardless of the distance to the observer. The song of the Corsican taxon differs from that of Western mainland European birds (Chappuis 1976, Tietze *et al.* 2008), but males most often strongly reacted to the playback by showing various behavioural responses (alarm, song, silent with active display). Based on its ecological preferences elsewhere in Europe (Harrap & Quinn 1996), we avoided areas without vegetation and those covers by macchia (*i.e.,* a large part of Corsica) and collected information on 890 forested sites. Responses to playback (display or vocalisation) were treated as a territorial behaviour. However, when contacted only once during at least two visits in very small grove or coppice, birds were considered as erratic. Records of treecreepers outside the forests were obtained from the literature, websites, and our own fieldwork: these data were treated as "erratic". Several previous records from ornithological literature and the web, in which the identification at the species level was not confirmed (Eurasian vs. Short-toed Treecreeper a very rare visitor in Corsica), were not included in the analysis. On each location, we defined a circular plot of 20-m radius and recorded, in addition to the presence or absence of treecreepers, the geographical coordinates and elevation, the tree species (dominant and secondary), the minimum and maximum percentage of crown vegetation cover following the methods described in Prodon (1988), the height of the highest tree and its DBH (diameter at breast height).

In this study, we restricted the term "forest" to wooded stands larger than 15 ha, whereas "grove" corresponds to wooded stand smaller than 15 ha, and "coppice" to young stands that regrow after cutting, management (*e.g.*, clump), or colonize ancient cultures and orchards. Forest categories followed the nomenclature of the Institut Forestier National (IFN 2003): "forest" corresponds to stand dominated by a single tree species, with a cover superior to 40%; "open forest" corresponds to vegetation cover between 10 and 40%; "mixed forest" defines an assemblage of conifer and broad-leaved trees. We counted treecreeper territories in each of the seven most common tree species based on the IFN maps from 2016–2017 (IFN 2016–2017). However, discrepancies were sometimes found during fieldwork between the IFN maps and the observed dominant tree species (12.6% of the plots): in these cases our data were preferred over the data of IFN's. The mapping was conducted using the software QGIS 3.16 (QGIS Development Team 2016). Statistical analyses were performed using the free software BioStaTGV (https://biostatgv.sentiweb.fr/?module=tests) to compare the number of treecreeper territories between forest range areas (Chi²). Boxplots were drawn with the package ggplot2 (Wickham 2009) in R (R Core Team 2020) to show the altitudinal limits of the most common trees in occupied territories and the importance of each dendrometric variable according to the most common tree species. We used the package FactoMineR (Lê *et al.* 2008) to 1) perform a Principal Component Analysis in order to identify the variables most influencing the presence/absence of the treecreeper in the Corsican forests, and 2) produce logistic regressions that best explain the presence/absence variable over ecological (elevation) and dendrological quantitative characteristics, tested as independent factors. The normal distribution of values was evaluated by Shapiro-Wilk tests ($p<0.05$) and the homoscedasticity by Levene tests ($p>0.05$). The independence of variables was studied with Spearman's rank correlation coefficient: this analysis resulted in keeping only a selection of independent quantitative variables (see results). The logistic regression analysis was conducted using the glm R function, with no prior weight and using the default options. It was first conducted for all tree species, then conducted on the six common tree species for which the retained quantitative variables followed a normal distribution. We kept the most parsimonious models according to the AIC criteria (Akaike information criterion) (Burnham & Anderson 2002).

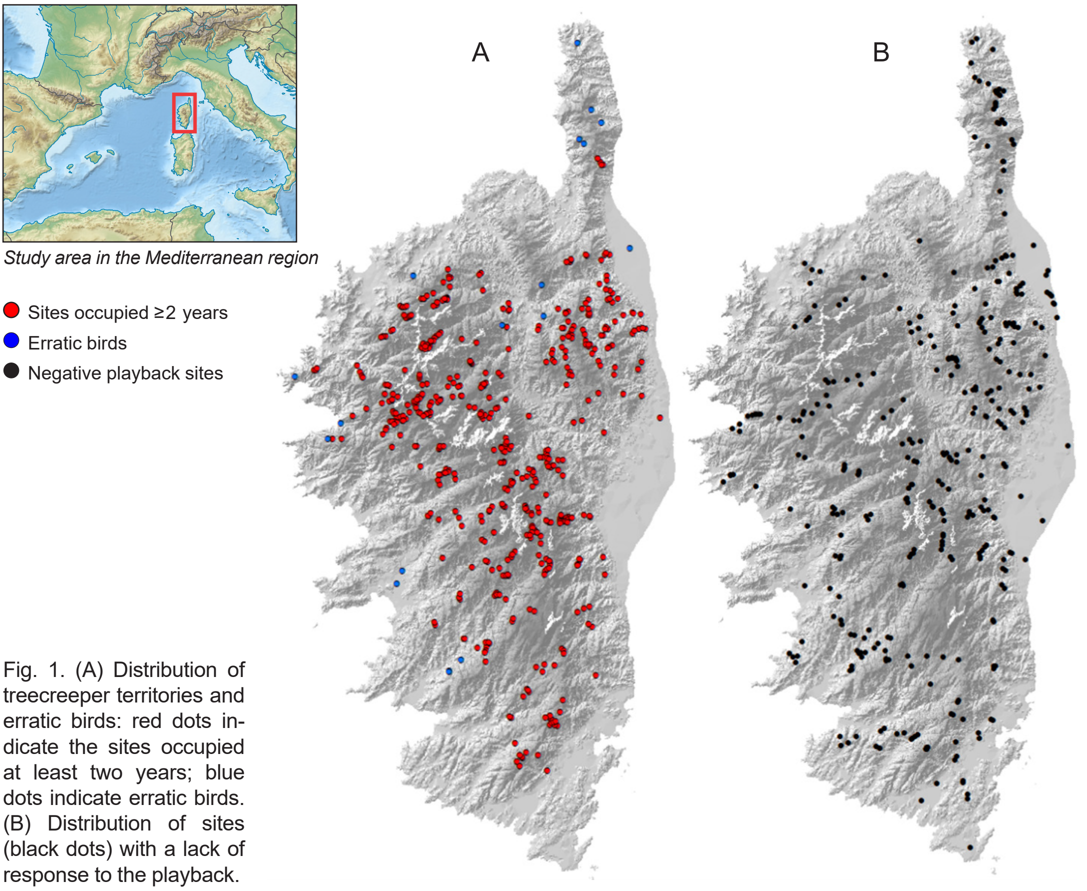


Fig. 1. (A) Distribution of treecreeper territories and erratic birds: red dots indicate the sites occupied at least two years; blue dots indicate erratic birds. (B) Distribution of sites (black dots) with a lack of response to the playback.

3. Results

3.1. Breeding range and dispersal

Over the 8 years of fieldwork, we mapped 517 sites occupied by territorial males or pairs, representing 60% of 890 sampled forested sites (Fig. 1a). Treecreeper territories range over a vast area covering most of the island, especially inland, avoiding the highest mountains (without forests) and the littoral (Fig. 1b), where treecreepers only occupy to a few scattered territories. These littoral regions also represent suboptimal habitats where erratic birds were found (Fig. 1a), composed of Cork Oaks with an open forested cover of Holm Oak coppices colonizing former orchards. The other sites occupied by erratic treecreepers corresponded to inland small forest patches, suitable in terms of habitat, but too restricted in area (less than 10 ha) to host a territory. The admixture of presence and absence data over inland area highlights the mosaic of vegetation found in Corsica, where groves and forests are patchily included within a vast zone of macchia.

3.2. Habitat preferences: forest categories

The treecreeper occupied all forested categories described by IFN (2016–2017), with nearly equal balance between conifers and broad-leaved trees in absolute number (Table 1), but not in relative numbers. Indeed, the ratio of Treecreeper sites compared to the total number of plots was significantly higher for conifers (73%), mostly Corsican Pine, than for broad-leaved trees (45%) ($\mathrm{Chi}^2_1=52.72$, $p<0.001$). The sampled treecreeper territories superimposed on a map describing the main categories of forested areas are shown in Figure 2. They were especially well-distributed in conifer forests along the mountainous central chain, and in broad-leaved forests in Northeast of the island. Conversely, they were absent from the broad-leaved forest (mainly Cork Oaks stands) in the Southeast region where visits by erratic birds were nevertheless observed.

Among the four categories of vegetation assemblage (forest, mixed forest, coppice and open forest), the treecreeper was significantly more often found in the first one ($\mathrm{Chi}^2_3=44.17$, $p<0.001$, Table 2). Frequent occurrence of treecreepers in coppices (37%) was unexpected, but our field surveys show that these territories often include plots of large trees favourable to treecreepers.

3.3. Habitat preferences: tree species

A total of 14 tree species have been identified in all sampled treecreeper territories when the stand was monospecific, and 16 when a secondary tree species was present. However only seven tree species were well-represented in treecreeper territories: Corsican and Cluster Pines, Sweet Chestnut, Holm and Cork Oaks, Beech, and Fir.

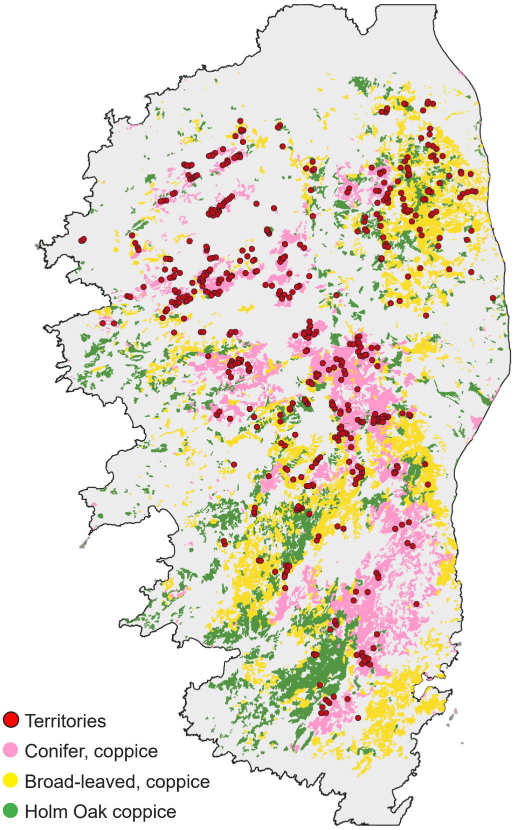


Fig. 2. Treecreeper territories on the vegetation map of Corsica (IFN 2003): conifer forests and coppices (mauve), broad-leaved forests and coppices (yellow), Holm Oak coppice (green). See Fig. 1 for reference location.

Table 1. Presence-absence of the treecreeper in the different plots presented in the IFN (Institut Forestier National) map.

IFN categories	Present	Absent	Total
Corsican Pine forest	101	28	129
Young forest of Corsican Pines	2	1	3
Cluster Pine forest	31	22	53
Pines forest	10	2	12
Mixed forest (majority of conifers)	5	3	8
Open mountain pine forest	15	4	19
Mixed conifer forest and coppice	19	3	22
Macchia with Cluster Pine	2	5	7
Macchia with pines	1	0	1
Conifers total	186	68	254
Sweet Chestnut forest	31	25	56
Holm Oak forest	5	0	5
Cork Oak forest	6	17	23
Broad-leaved forest	6	3	9
Beech forest	19	7	26
Mixed forest (majority of broad-leaved)	7	7	14
Open mountain broad-leaved forest	4	2	6
Mixed Holm Oak and coppice	26	18	44
Mixed Cork Oak and coppice	5	16	21
Mixed broad-leaved	34	43	77
Mixed pine forest and coppice (broad-leaved)	6	15	21
Coppice of Sweet Chestnut	1	0	1
Coppice of Holm Oak	15	32	47
Coppice of broad-leaved	7	16	23
Coppice of Beech	7	3	10
Macchia with Sweet Chestnut	3	13	16
Macchia with Holm Oak	9	10	19
Macchia with Cork Oak	4	9	13
Macchia with broad-leaved	4	9	13
Broad-leaved total	199	245	444

Table 2. Presence-absence of the treecreeper in the different plots of vegetation assemblage defined by IFN (Institut Forestier National).

IFN categories	Present	Absent	Total	% present
Forest (total)	238	119	357	66.7
Mixed forest and coppice	90	95	185	48.6
Coppice	30	51	81	37
Open forest	27	48	75	36

The Corsican Pine was present in *ca.* half of the territories, although its contribution decreased when including territories where this species is associated with a secondary tree species, while in the same situation the contribution of the Sweet Chestnut increases (Table 3).

Occurrence frequency of each tree species in the treecreeper territories according to the surface area of the main tree species in overall Corsican forests (open and mixed forest excluded) are presented in Table 4. Differences are highly significant ($Chi^2_6=65.07$, $p<0.001$, range areas of forests converted in log): Holm, Cork Oak, and Cluster Pine are under-represented, compared to Corsican Pine and Sweet Chestnut.

3.4. Habitat preferences: altitudinal distribution

Treecreeper territories were recorded from 12 m to 1,830 m above sea level (mean 960±345 m, median 974 m); 86% were located at medium elevations, between 501 m and 1,500 m (Table 5). The most frequent tree species on the territories corresponded to three categories: (1) Cork Oak at low elevation (below 500 m), (2) Sweet Chestnut, Cluster Pine, and Holm Oak at medium elevation (500–1,000 m), and (3) Beech, Corsican Pine, and Fir at high elevation (above 1,000 m) (Fig. 3). Rarer tree species on the territories were distributed at all elevation: Common Alder (12–628 m, n=3), Poplar (120 m, n=1), European Hop-Hornbeam (176–920 m, n=2), Italian Alder (505–791 m, n=3), Ash (796 m, n=1), Deciduous Oaks (375–1,098 m, n=9, median=814 m), and Birch (1,346 m, n=1).

3.5. Habitat preferences: dendrometry

The vegetation cover varied between species, the extreme being observed for the Corsican Pine for which the minimum vegetation cover showed a large variation (Fig. 4a). The maximum vegetation cover was higher in the broad-leaved species compared to the conifers (Fig. 4b). The diameter was quite large for all species, with a mean of 0.48 meters (Fig. 4c). The values for Sweet Chestnut which tend towards trees larger than 1m in diameter can be explained by the old age of the orchards in Corsica. Finally, height was higher for conifers than for broad-leaved trees (Fig. 4d).

3.6. Models of habitat quality

Principal Component Analysis showed that within the variables influencing the presence/absence of treecreeper in the Corsican forests, height and elevation were correlated as well as the two variables describing the vegetation cover (Fig. 5) Thus, only three variables were kept in the logistic regression analysis: diameter, height, and maximum vegetation cover. Table 6 presents the best selected models of the logistic regression for each of the most common tree species (Beech, Sweet Chestnut, Cluster and Corsican Pines, Cork and Holm Oaks) and for all tree species together. Selected models underline the significant importance of diameter (excepted for the Cork Oak), height (excepted for the pines), and vegetation cover max. (excepted for the Beech) in explaining the presence of treecreepers (Table 7).

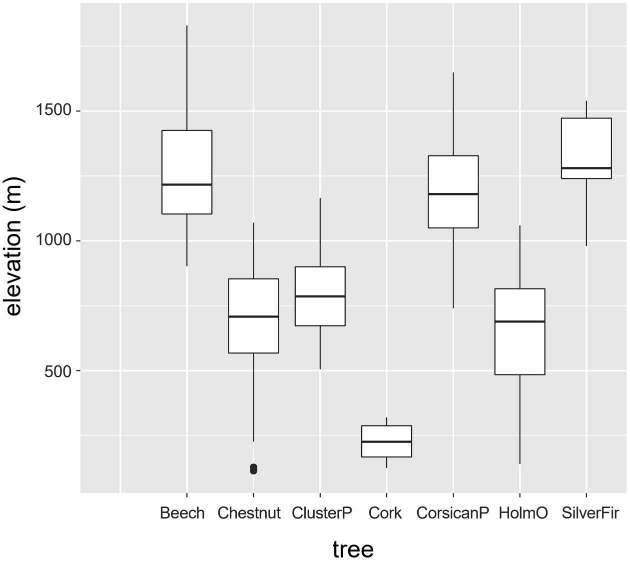


Fig. 3. Elevation of treecreeper territories in the seven main tree species.

Table 3. Distribution of tree species in the treecreeper territories (when pure [upper line] and when associated to a secondary tree [bottom lines]). Number in each cell indicates the number of sampled territories. Percentage on the third line indicates the ratio of tree species when “pure”, and % on the last line indicates the ratio when these trees are associated with others. Explanation of the acronyms used on the upper line is given in the first column.

	As	Be	Bi	CP	CA	CO	CoP	DO	EHH	Fi	HO	IA	Po	SC	total
Total pure	0	30	0	29	2	5	185	5	0	4	37	0		45	342
%		8.8		8.5	0.6	1.5	54.1	1.5		1.2	10.8			13.2	100
associated with:															
Ash (As) *Fraxinus ornus* L.						1				2	5			4	
Beech (Be) *Fagus sylvatica* L.							9								
Birch (Bi) *Betula pendula* Roth							5								
Cluster Pine (CP) *Pinus pinaster* Aiton							16				4			7	
Common Alder (CA) *Alnus glutinosa* L.							1							5	
Cork Oak (CO) *Quercus suber* L.											4				
Corsican Pine (CoP) *Pinus nigra* subsp. *laricio* Maire		3	1	2						2	4			7	
Deciduous Oak (DO) *Quercus* spp.							3				5			4	
Eur. Hop-Hornbeam (EHH) *Ostrya carpinifolia* Scop.														3	
Fir (Fi) *Abies alba* Mill.		4					7								
Holly *Ilex aquifolium* L.							1								
Holm Oak (HO) *Quercus ilex* L.				5	1	1	10	1				1	1	16	
Italian Alder (IA) *Alnus cordata* Loisel									1					10	
Poplar (Po) *Populus nigra* L.														1	
Strawberry tree *Arbutus unedo* L.				1							2				
Sweet Chestnut (SC) *Castanea sativa* Mill.	1	1		5		1	6	3	1		10	2			
Grand total	1	38	1	42	3	8	243	9	2	8	71	3	1	102	532
%	0.02	7.1	0.02	7.9	0.06	1.5	45.7	1.7	0.04	1.5	13.4	0.06	0.02	19.2	100

Table 4. Number of treecreeper territories in forests according to the total surface areas covered by the main tree species (from IFN 2016–2017)

	Corsican Pine	Sweet Chetnut	Holm Oak	Cluster Pine	Beech	Fir	Cork Oak
Number of occupied treecreeper territories	243	102	71	42	38	8	8
Range areas in Corsican forests (ha)	29,741	10,183	80,668	28,100	13,928	258	11,643
Mean number of treecreeper territories / 100 ha	0.8	1	0.09	0.14	0.27	3.1	0.07

4. Discussion

4.1. Distribution and ecological characteristics

The data gathered for this study, with more than 500 sites investigated, provided a finer vision of the treecreeper distribution in Corsica than the information compiled in previous breeding bird atlases (Yeatman 1976, Chappuis 1994, Muller 2015). We confirmed that the treecreeper is present in forests from sea level to their upper limits, its range covering a large part of the island, except the treeless macchia, a dominant vegetation in Corsica. However, the median elevation of treecreepers' sites in Corsica was high (974 m), a result that we think is due to the current distribution of mature forests, more frequent in higher altitudes than on the littoral because of anthropogenic factors (Gamisans 2003). Although the treecreeper territories were found in various tree species assemblages, we demonstrated that the bird shows a marked preference for two tree species, the Corsican Pine and the Sweet Chestnut, that are not the commonest ones. This result supports previous observations, although conducted with different fieldwork methodologies, which estimated a density of breeding treecreepers twice higher in Corsican Pines (Arrizabalaga *et al.* 2002) than in Holm Oaks (Blondel *et al.* 1988). However, this preference is very likely explained by the fact that mature stands, developing a deep-seated bark favourable to invertebrates, are mainly found in Corsican Pine and Sweet Chestnut in Corsica. Thus, most of the Holm Oak range has been converted to coppices, unfavourable to the treecreeper, and the number of mature groves is very limited today, partly reduced by fires during the last fifty years. Similarly, the Cork Oak stands are too young, with a low vegetation cover, to be ecologically favourable to the treecreeper. In addition, many groves have been abandoned or transformed into subdivisions of private houses. The Beech covers a limited range and mature forests remain uncommon. When considering its vast surface, the Cluster Pine forest seems relatively under-occupied by the treecreeper. This can be explained by the great vulnerability of Pine forests to fires generating an over-representation of young stands. Lastly, other tree species woodlands like Fir or Birch, pioneering species growing in Corsican Pine cuttings, are not favourable to treecreepers probably because of their small surface areas. Similarly, the Common Alder, a species favourable to the treecreeper in marshy localities of the Caucasus (Harrap & Quinn 1996), had been over-exploited in Corsica and still declines today due to diseases and fires.

Table 5. Frequency of treecreeper territories according to the elevation above sea level (in meter)

Elevation	Number of territories (n = 532)
12–500	57
> 500–1,000	224
> 1,000–1,500	233
> 1,500	18

Forest habitat requirements of the treecreeper in Corsica are similar to those of mainland populations elsewhere in temperate continental Europe: a high rate of the vegetation cover with

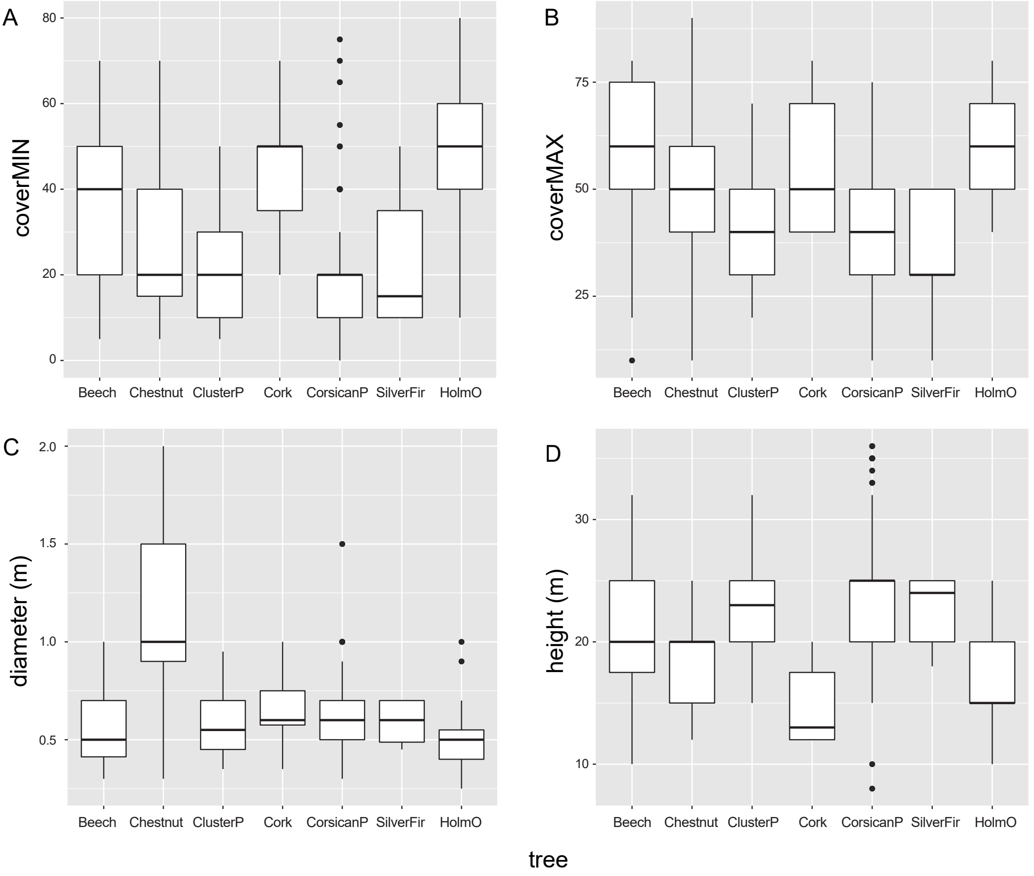


Fig. 4. Dendrometric variables for the seven main trees species in treecreeper territories: (A) minimum vegetation cover, (B) maximum vegetation cover, (C) tree diameter, and (D) tree height.

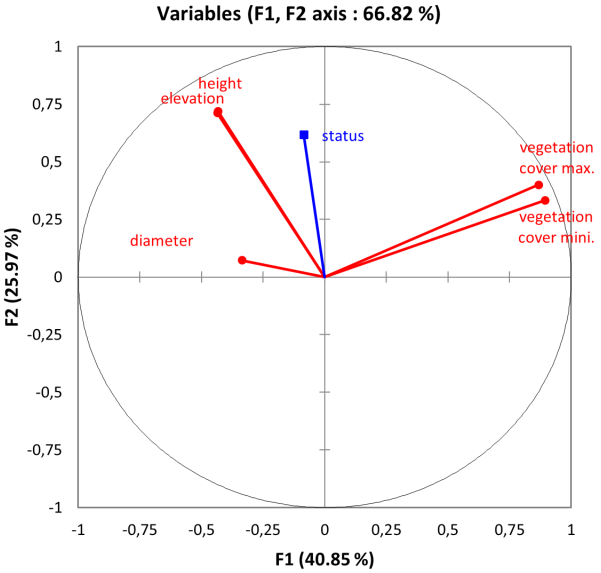


Fig. 5. F1-F2 Plane Factor Correlation Circle of the Principal Component Analysis. The active variables, corresponding to the description of the forest, are indicated in red, and the supplementary variable, that corresponds to the treecreeper's status (presence/absence) is indicated in blue.

Table 6. Selection of the best logistic regression models for all tree species together, and for each of the six commonest tree species; Fir was excluded of this analysis because of its small sample size.

Best logistic regression models	Variables	Number of variables	Deviance	Degree of freedom
Tree species all together	diameter, height, vegetation cover max.	3	1133.6	831
Sweet Chetnut	diameter, height, vegetation cover max.	3	251.7	182
Cork Oak	diameter, vegetation cover max.	2	37.5	40
Holm Oak	diameter, height, vegetation cover max.	3	232.5	177
Beech	diameter, vegetation cover max.	2	61.09	49
Corsican Pine	diameter, vegetation cover max.	2	209.9	250
Cluster Pine	diameter, vegetation cover max.	2	98.1	70

tall and large trees (*i.e.*, with a mean diameter superior to 40 cm) (Laurent 1987, Maumary *et al.* 2007). However, Martin (1982, 410) founded that in Corsica, comparatively to mainland, the treecreeper occupies a wider array of habitats ranging from forests to coppices (but see our comment for Table 2). Interestingly, in the British and Irish Isles where the Short-toed Treecreeper is absent, the Eurasian Treecreeper breeding populations are found in a wide range of habitats including lesser dense stands, parklands, gardens and even farmlands with well-treed hedgerows (Cramp & Perrins 1993, du Feu 2002). Thus, the absence of the Short-toed Treecreeper in Corsica did not lead to comparable niche expansion in the Eurasian Treecreeper, maybe in conjunction with the different origin of the lineages: recently divergent from the continent in British and Irish Isles *versus* a paleo-endemic in Corsica (Pons *et al.* 2015). The large altitudinal amplitude of the treecreeper territories recorded in Corsica is also noted elsewhere in Europe (Hagemeijer & Blair 1997, Keller *et al.* 2020), like for instance in France where the species is recorded in small numbers from the plains in Normandy, near the sea on the Riviera, and to the upper forest limit in the Alps and the Pyrenees (Muller 2015). A review of the habitats occupied across the geographical range of the treecreeper (Harrap & Quinn 1996) underlines the great adaptability of this species for which behaviour and social habits may be as important as ecological requirements and available habitat types in habitat choice.

4.2. Future changes in the Corsican forests

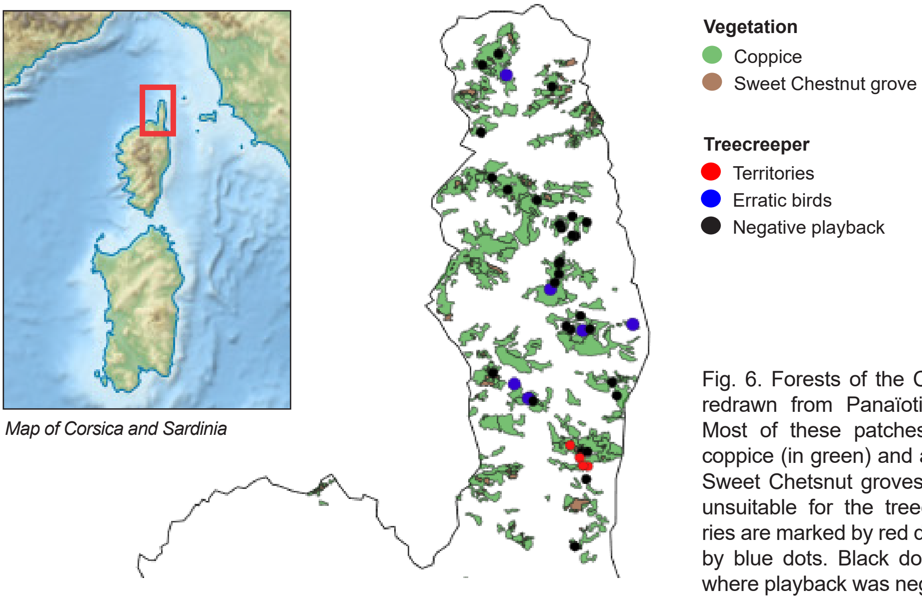
A significant reduction of mature stands, estimated at least to 43%, occurred in Corsica since the mid-19th century (Panaïotis *et al.* 2017). Such an important reduction was due to several factors, mainly anthropogenic: fires for pasture, logging for industrial combustible (Fontana 2004), for firewood or for the construction of railway ties (see https://youtu.be/ns.JoJS1-7Jw for Fium'Orbo), and important cutting in several public forests during 1970-90 period (*e.g.*, see Cerutti 1976 for Valdoniello forest). Conversely, natural regrowth was estimated to 25,000 ha per decade (Panaïotis *et al.* 2017), thanks to abandoned pastures recolonized by Corsican Pines in the mountains, gardens and terrace cultivations replaced by oaks and broad-leaved trees, and to the aging of Holm Oaks previously exploited for wood charcoal. These new forested areas will however not be suitable for treecreepers before at least several decades (Panaïotis *et al.* 1997), although the Holm Oak annual grown rate (m^3 ha^{-1}) can be especially high in Corsica (Bonin & Romane 1996), and might accelerate recolonization, especially in macchia which constitutes a step towards the formation of a forest. On the other hand, the abandonment of cultivated Sweet Chestnut groves reaching today a range of only *ca.* 1,300 ha (de Casabianca 2016) implying the death of the old trees and their natural replacement by others tree species, broad-leaved or conifers, would lead to the increase of unsuitable habitats for the treecreeper. Our field observations in the Cap Corse (North

Table 7. Parameters of the different selected models.

Parameters	Estimation	Std	z–value	Pr(>IzI)	Sig.
"Tree species all together" model					
intercept	–7.639114	0.564713	–13.527	<0.001	***
diameter	1.887201	0.256453	7.359	<0.001	***
height	0.262479	0.021905	11.983	<0.001	***
vegetation cover max.	0.047304	0.005145	9.194	<0.001	***
"Sweet Chestnut" model					
intercept	–7.7289	1.44166	–5.361	<0.001	***
diameter	1.39761	0.48224	2.898	<0.01	**
Height	0.24835	0.07209	3.445	<0.001	***
vegetation cover max.	0.05983	0.0108	5.54	<0.001	***
"Cork Oak" model					
intercept	–9.30897	3.4038	–2.735	<0.01	**
diameter	4.21003	2.31434	1.819	0.068	ns
vegetation cover max.	0.13593	0.05327	2.552	<0.05	*
"Holm Oak" model					
intercept	–10.13607	1.68221	–6.025	<0.001	***
diameter	9.59439	1.74827	5.488	<0.001	***
Height	0.21402	0.0797	2.685	<0.01	**
vegetation cover max.	0.04898	0.0145	3.377	<0.001	***
"Beech" model					
intercept	–7.05211	2.5481	–2.768	<0.01	**
diameter	11.38164	3.39641	3.351	<0.001	***
vegetation cover max.	0.05522	0.03093	1.786	0.074	ns
"Corsican Pine" model					
intercept	–8.17944	1.54965	–5.278	<0.001	***
diameter	14.51936	2.31462	6.273	<0.001	***
vegetation cover max.	0.09086	0.02176	4.176	<0.001	***
"Cluster Pine" model					
intercept	–8.23425	1.93935	–4.246	<0.001	***
diameter	10.05891	2.53804	3.963	<0.001	***
vegetation cover max.	0.09836	0.02765	3.557	<0.001	***

Corsica) illustrate well this situation, with a few treecreeper breeding territories found in small Sweet Chestnut groves [a recent colonization according to Marzocchi (2018)], whereas in the former gardens recolonized recently by broad-leaved trees, the observed treecreepers were only erratic (Fig. 6).

Forest fragmentation poses a major threat to animal and plant species (Rogan & Lacher 2018), and several major negative consequences have been identified in Europe for treecreepers (*Certhia* spp.): increase of nest predation (Huhta *et al.* 2004) and decline in abundance (Basile *et al.* 2016). In Corsica, treecreeper number may



Map of Corsica and Sardinia

Fig. 6. Forests of the Cap Corse (map redrawn from Panaïotis *et al.* 2017). Most of these patches, composed of coppice (in green) and a few very small Sweet Chetsnut groves (in brown), are unsuitable for the treecreeper. Territories are marked by red dots, erratic birds by blue dots. Black dots indicate sites where playback was negative.

locally increase in the future, if the global forest area continues to grow, and most importantly, to mature, at least in areas where seeds and soil are still present. But, conversely the decline of the Corsican Pine forest, the main mountain habitat for treecreepers today, is a major concern knowing that recurrent fires and logging, lead to a significant loss of habitats. This also holds for the endemic and threatened Corsican nuthatch (*Sitta whiteheadi*), for which the Corsican Pine forest represents the unique suitable habitat (Thibault *et al.* 2006). Thus, its strict protection constitutes a conservation priority in Corsica where this tree species is currently more at risk to anthropogenic activities than to climate change towing to its wide ecological range (Barbet-Massin & Jiguet 2011).

Utbredning och habitat för den Trädkryparen på Korsika

Trädkryparen (*Certhia familiaris*) är en skogsfågel med utbredning från sydvästra Europa till Nordliga delar av Asien. Två fylogenetiska grupper har nyligen identifierats inom arten, en som hittas på Korsika i Medelhavet och i Kaukasus, och en annan som utbreder sig över största delen av Eurasien och nordliga Asien. Det finns begränsat med information om populationen på Korsika. Här presenterar vi nya omfattande data om dess utbredning och habitat. Trädkryparen hittas från havsnivån till den övre trädgränsen men saknas i det trädlösa macchia området, som dominerar vegetationen på Korsika. Häckningar förekommer i varierande trädarter med en stark preferens för äldre bestånd av stora träd, såsom svarttall och äkta kastanj som inte är de vanligaste trädslagen på Korsika. Det minskande antalet trädgårdar med äkta kastanj innebär att bevarandet av mogna svarttallbestånd blir allt viktigare för trädkryparen och andra endemiska arter.

Acknowledgments. We thank Martin Billard, Laurent Chevallier, Samuel Ortion (Faune-France), Gilles Faggio, Isabelle Guyot, Nidal Issa, Cécile Jolin, Philippe Jourde, Nathalie Legrand, Antoine-Marie Pastinelli, Bernard Recorbet, Joseph Piacentini, Antoine Rossi, and Valentin Spampani for providing data. We are very grateful to MSc. Mira Kajanus and an anonymous referee for their useful comments on a first version of the manuscript.

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Ornis Fennica 100: 17–26. 2023

Chick survival in a high-density Northern Lapwing (*Vanellus vanellus*) population on the river islets of the middle Pripyat River, Belarus

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Received 26 March 2021, accepted 28 October 2022

The field studies were conducted in three ephemeral river islets of the middle Pripyat River, southern Belarus in 2006–2007. Nestlings of the Northern Lapwing (*Vanellus vanellus*) were ringed soon after hatching, and reencountered during subsequent visits. Post-hatching survival was estimated by capture-mark-recapture models. Daily survival rates of the Northern Lapwing chicks were very high, varying between 0.90 and 0.99, and the cumulative survival rates over 35 days between hatching and fledging were 0.54 and 0.70 in 2006 and 2007, respectively. Survival rate was lower in the first ten days of life, which is similar to that reported in other precocial species. The key factor supporting this high breeding success is low predation due to nesting of lapwings on periodic river islets that naturally restrict access by mammalian predators and apparent scarcity of terrestrial and avian predators. River islet habitats with co-occurrence of dry and wet fertile microhabitats provide optimum feeding conditions for the Lapwing chicks with a wide range of aquatic, ground and surface invertebrates. Moreover, semicolonial breeding of the Northern Lapwing (about 30 nests/ha) with other waders, terns and gulls increases the effectiveness of anti-predator behaviour. Consequently as a result of low predation pressure and good foraging conditions, in 2006 and 2007, productivity was 2.1 and 2.8 fledged young per single nest with four chicks respectively, a value hardly reported in Europe, except in managed sites.

1. Introduction

In recent decades the Northern Lapwing *Vanellus vanellus*, (hereafter: lapwing) has, along with many other European ground-nesting waders, experienced a strong decline across Europe (Milsom 2005, Donald *et al.* 2006, Roodbergen *et al.* 2012, Plard *et al.* 2020), including the central and eastern lowlands, which are traditionally known to support strong grassland wader populations (Žídková *et al.* 2007, Ławicki *et al.* 2011, Shydlovskyy & Kuzyo 2016, Mischenko 2020). The European lapwing population is currently estimated at about 1.59–2.58 million pairs, with a substantial decreasing trend of 30–49% over the last 27 years (BirdLife International 2021). The lapwing is therefore listed as near threatened (NT) in the IUCN Red List (IUCN 2020). A vast majority of studies report predation as the main, direct cause of the lapwing nest losses (Baines 1990, Blomqvist & Johansson 1995, MacDonald & Bolton 2008, Bellebaum & Bock 2009) and chicks' mortality (Schekkerman *et al.* 2009, Mason & Smart 2015, Mason *et al.* 2018) and low breeding productivity is considered as the main driver of the decline in the number of breeding pairs of this species (Milsom 2005, Bolton *et al.* 2007, MacDonald & Bolton 2008, Roodbergen *et al.* 2012). Predation pressure may be so high that even in favourable habitat conditions, it may effectively limit breeding success and affect population stability (Milsom 2005, MacDonald & Bolton 2008, Mason & Smart 2015).

Survival estimates for the lapwing mostly refer to nest (Šálek & Šmilauer 2002, Bolton *et al.* 2007, Teunissen *et al.* 2008, Królikowska *et al.* 2016, Berthold *et al.* 2017) or post-fledging survival (Bak & Ettrup 1982, Peach *et al.* 1994), whereas survival during the critical post-hatching period remains poorly known in this and other wader species (*e.g.* Berg 1992, Cohen *et al.* 2009, Schekkerman *et al.* 2009). Estimation of post-hatching mortality in ground-nesting avian precocial species, such as waders, is difficult since chick detectability is low and broods are difficult to track (Lukas *et al.* 2004, McGowan *et al.* 2009). Moreover, the numbers of ringed nestlings are frequently too low to allow modelling of survival with a capture-mark-recapture (CMR) approach, which is the best way to achieve reliable estimates of survival rates (Lukas *et al.* 2004, Colwell *et al.* 2007, Rickenbach *et al.* 2011).

The seasonally flooded lowland valley of the middle Pripyat River is the best preserved part of the Pripyat river valley, under law protection as the Mid-Pripyat State Landscape Zakaznik Ramsar site (Kozulin *et al.* 2002). It is known as an Important Bird Area in semi-natural conditions offering supreme habitats for waders and wildfowl either during breeding or migration (Pinchuk *et al.* 2005, Meissner *et al.* 2011, Pinchuk & Karlionova 2011, Pinchuk *et al.* 2016). Each year up to 13 species of waders and more than 20 species of other waterbirds breed in this area (Luchik *et al.* 2017a,b, 2019) with *ca.* 1200–1500 breeding pairs of lapwings found in a 420 km long middle section of the river (Luchik *et al.* 2017b). The highest abundance of waders was in Turov meadow, where the number of the lapwing remained high and quite stable between 2005 and 2008 with about 200–350 nests (Luchik *et al.* 2017b, authors unpublished data). We investigated the post-hatching survival of lapwing chicks at Turov and hypothesized that due to unique breeding habitat conditions, *i.e.*, ephemeral river islets, and semi-colonial breeding of a group of waders, gulls and terns, the post-hatching lapwing chick survival should be high.

2. Methods

2.1. Study area

The studies were conducted in the middle part of the Pripyat river valley in the vicinity of Turov city, southern Belarus (52°04'N, 27°44'E) from late April until mid-June in 2006 and 2007. The study area covered natural, riparian meadows on the right bank of the Pripyat river. Every spring this river valley is flooded (Mongin & Pinchuk 1999, Meissner *et al.* 2011) and the highest parts of the flooded meadows form the islets. In April–May a single islet typically covers an area of about 0.5–2 ha. These periodic islets consist of a mosaic of microhabitats from neutral, fertile aquatic and wetland habitats, fertile and slightly acidic mesic to poor and acidic dry land. The islets are covered by dense and low vegetation of fresh and wet meadow plant species represented mostly by grasses (Afranowicz-Cieślak *et al.* 2014) reaching a maximum height of 0.5 m in some parts. The occurrence of dry and wet habitats with a wide spectrum of plants provides optimum conditions for aquatic and terrestrial invertebrates (Afranowicz-Cieślak *et al.* 2014, Hajdamowicz *et al.* 2015). Due to spring floods and high water levels islets remain inaccessible from the main land until the end of May or beginning of June and therefore, human and mammalian predators' pressure in this area is negligible.

2.2. Field study

The fieldwork was carried out on three islets of which a total area of 3–5 ha in the beginning of May (A. Szurlej-Kielańska, pers. comm.). Despite seasonal variation in water level, similar area remains available for breeding waders and is quite constant each year. The number of the lapwing nests on these three islets was 117 and 122 in 2006 and 2007, respectively. In April, when the highest water level limited the size of the islets to its minimum, lapwing breeding density was extremely high, reaching about 30 nests/ha. Also about 50 pairs of Black-headed Gulls (*Chroicocephalus ridibundus*), 50 pairs of Common Terns (*Sterna hirundo*), and 10 pairs of Little Terns (*Sternula albifrons*) nested on those islets. Due to the limited area of the islets, the nests were located close to each other, which resembled the conditions of a bird colony including typical antipredator behaviour, like simultaneous reaction of most birds to the potential danger.

We monitored lapwing nests and chicks twice a week by carefully inspecting the entire area. Nests with eggs were marked with numbered sticks that according to Galbraith (1987) and Zámečník *et al.* (2018) does not significantly increase nest predation risk. The dates of clutch initiation and hatching were estimated by egg flotation method (Hays & Le Croy 1971). Chicks were ringed with a metal ring. Only chicks with known date of hatching were included in this study. In the second part of the season the field inspections were carried out every 1–4 days. Both the frequency of inspections and their extent (entire or part of the area) depended mainly on weather conditions and availability of volunteers. Each control was carried out by at least 3–4 experienced volunteers to minimize the time and disturbance to birds. During subsequent visits, newly hatched chicks were ringed and all recaptures were noted. Mobility of chicks was limited and did not affect the effectiveness of field checks since chicks were not able to leave the islets.

2.3. Statistical analysis

We initially tested daily survival models on raw data, but none of the models passed goodness of fit tests (nonparametric bootstrap in MARK, White & Burnham 1999). For this reason, raw data were pooled into five- and six-day long periods covering 38 and 43 days in total, in 2006 and 2007, respectively, depending on the numbers of controls and the time intervals between them to maximize regular distribution of controls (*i.e.*, shorter pooling periods, while desirable, would result in no controls in some of them). After pooling, the final datasets included eight recapture 'occasions'. Due to the differences in breeding phenology, they covered periods from 8th May to 15th June 2006 and from 24th April to 6th June 2007; the extremes represent the dates when the earliest chick was ringed and the last survey was performed. Uneven intervals between successive occasions were accounted for in the model in MARK (White & Burnham 1999) by setting interval lengths to the desired number of days to get reliable daily survival estimates.

We used standard Cormack-Jolly-Seber models (CJS models), in which two types of parameters were estimated: the survival probability Φ and recapture probability p. In the first step, the model with both parameters, fully time-dependent model $\{\Phi_t, p_t\}$ (a global model) and its reduced versions were fitted, with constant parameters $\{\Phi_t, p.\}$, $\{\Phi., p_t\}$ and $\{\Phi., p.\}$. Then to address possible dependence of the survival rate on the age of chicks, we implemented age-structure in the survival parameter, fitting models with 2 and 3 age classes. An age class spans one occasion, so a model with two age classes estimates two survival parameters: one for chicks aged 1–5 (6) days and the second one for all older chicks. A model with three age classes is similar, but estimates three separate parameters: for chicks aged 1–5, 6–10 and all older. These models reflect the scenario in which the survival rate is different (most likely lower, as expected for most precocial species) in the youngest chicks (age 1–5 and 6–10 days) and then stabilizes (at a different, most likely higher value) at older age (≥11 days). We do not have reliable data on the mean clutch size in the studied lapwing population and, in assessing the number of young surviving to fledging, we assumed that three or four eggs hatched in the nest. The recapture probability in our models was treated as time-dependent, constant or had a linear (on a logit scale) trend imposed, assuming that it could constantly decline (or increase) with time (*e.g.*, due to vegetation growth). We calculated the cumulative survival, simulating daily model-averaged parameter estimates (considering age-structure) for the period of 35 days, roughly between hatching and fledging.

The goodness of fit tests were performed by parametric bootstrapping procedure in MARK with 1,000 simulations and assessed by the quasi-likelihood parameter, $\hat{c}$, based on deviance). In this approach, the observed $\hat{c}$ from the global models is divided by the $\hat{c}$ from simulations (White & Burnham 1999). In both years, $\hat{c}$ indicated moderate to slight overdispersion in the data (2006: mean $\hat{c}$=1.53, min-max range: 1.23−2.31, 2007: mean $\hat{c}$=1.36, min-max range: 0.81−2.20) and thus model ranking was adjusted by these mean values. Then these adjusted models were ranked by the Akaike's information criterion (AIC) corrected for small sample sizes (AICc). As model rankings were relatively balanced in these two years, averaged parameters were used for inference (Burnham & Anderson 2002).

The effect of multiple visits in the field that potentially may increase the chance of an individual not surviving (*e.g.*, chick being predated) was assessed by TEST 3, which is a part of the goodness of fit tests performed in RELEASE run under MARK (White & Burnham 1999). This test checks for violations of one of the CJS model assumptions, saying that all individuals marked at an occasion *i* have the same probability of surviving to occasion *i*+1, regardless of whether they were marked at occasion *i* or before. This test contrasts groups of individuals caught for the first time to those which were caught before, thus testing for the effect of previous catching on the probability of survival. There was no evidence for violations of this assumption and, thus, for the effect of previous catching on survival, as the overall results of this test were not significant (2006: χ^2=3.035, df=6, p=0.804, 2007: χ^2=11.547, df=6, p=0.07). Model construction and fitting, as well as GOF tests were all performed in MARK 7.2 (White & Burnham 1999).

3. Results

In the two study years, a total of 403 chicks were ringed, mainly during the first two days of their life: 250 chicks (62%) on the day of hatching and 43 (11%) on the next day. Of these, 182 were recaptured at least once before fledging. The oldest chicks recaptured were 36 days old, and there were several cases of ringed chicks recaptured at the age of 25 days or more (16 in 2006 and 26 in 2007).

Models including age-structure in survival had the highest support in both seasons (Table 1). The relative importance of age structure (*i.e.*, the cumulative weight of models including any age-structure) was ω=1.0 in 2006 and ω=0.98 in 2007, strongly indicating that the survival rate of the lapwing chicks is related to age. Survival rate was lowest in the youngest chicks (1–10 days of age). Model-averaged daily survival probabilities in both years ranged from 0.91 to 0.99 (Table 2). Over 35 days between hatching and fledging, the cumulative daily survival rate was 0.54 (CI: 0.28–0.72) in 2006 and 0.70 (CI: 0.42–0.82) in 2007. Model-averaged recapture probabilities varied greatly (0.17–0.99 and 0.04–0.44 in 2006 and 2007, respectively) and were generally higher earlier in the season (Table 2). The number of young surviving to fledging time was estimated at 2.1 and 1.6 fledglings per nest in 2006 and 2.8 and 2.1 in 2007 for the four and three chicks hatched in the lapwing nest respectively (Table 3).

4. Discussion

The breeding density of the lapwing on river islets in the middle Pripyat river was much higher than maximum densities reported in other areas, *i.e.*, in England and Wales in 1995–1997 (0.8 nest/ha,

Table 1. Models fitted to the lapwing chicks capture-recapture data from Turov, Prypyat river, Belarus, 2006–2007. Models are ranked according to the Akaike Information Criterion corrected for small sample size (AICc). Δ AICc – difference in AIC units between the best-supported model and a given model, ω AICc – model weight, NPar – number of parameters in a model. (.) – parameter constant in time, (t) – parameter time-dependent, (trend) – parameter with a linear trend. (a2) and (a3) denote for 2 and 3 age-classes in the survival parameter.

Model	AICc	Δ AICc	ω AICc	Model likelihood	NPar	Deviance
2006						
Phi(a3) p(trend)	651.612	0.000	0.977	1.000	4	129.934
Phi(a3) p(t)	659.224	7.613	0.022	0.022	10	124.908
Phi(a2) p(t)	665.693	14.082	0.001	0.001	8	135.649
Phi(.) p(t)	665.805	14.193	0.001	0.001	8	135.760
Phi(.) p(trend)	676.277	24.666	0.000	0.000	3	156.655
Phi(a2) p(trend)	678.075	26.464	0.000	0.000	4	156.398
Phi(a3) p(.)	683.600	31.988	0.000	0.000	4	161.922
Phi(.) p(.)	690.792	39.181	0.000	0.000	2	173.212
Phi(a2) p(.)	692.170	40.558	0.000	0.000	3	172.548
2007						
Phi(a2) p(t)	843.913	0.000	0.603	1.000	9	96.011
Phi(a3) p(t)	846.026	2.113	0.210	0.348	10	96.011
Phi(a2) p(trend)	847.236	3.323	0.115	0.190	3	111.771
Phi(a3) p(trend)	848.962	5.049	0.048	0.080	4	111.452
Phi(.) p(t)	850.536	6.623	0.022	0.037	8	104.735
Phi(.) p(trend)	855.425	11.512	0.002	0.003	3	119.959
Phi(.) p(.)	880.984	37.071	0.000	0.000	2	147.552
Phi(a2) p(.)	882.288	38.375	0.000	0.000	3	146.823
Phi(a3) p(.)	884.333	40.420	0.000	0.000	4	146.823

Hart *et al.* 2002), in South Bohemia, Czech Republic in 1988–1998 (0.2 nest/ha, Šálek & Šmilauer 2002) or in the Lviv region, western Ukraine in 2008–2014 (2.5 nest/ha, Shydlovskyy & Kuzyo 2016). A very high number of breeding pairs along with the mobility of chicks limited to islets provided very good conditions for the study on the post-hatching survival using CJS models. To our best knowledge, no similar studies have been carried out in such a dense lapwing population before.

We also documented a very high survival of the lapwing chicks in the Pripyat river floodplain. Cumulative survival probability from hatching to fledging varied between years, 0.54 in 2006 and 0.70 in 2007, and these are exceptionally high values, hardly reported in Europe, except at managed sites (Roodbergen *et al.* 2012, Plard *et al.* 2020). In the studies considering the lapwing chicks' survival, none have reported survival rate prior to fledging reaching or exceeding 35% without predator removal or applying electric fences as a ground predator exclusion method (Schekkerman *et al.* 2009, Fletcher *et al.* 2010, Rickenbach *et al.* 2011, Roodbergen *et al.* 2012, Malpas *et al.* 2013). The approximate minimum productivity threshold needed to maintain a stable population of Northern Lapwings is estimated at 0.6–0.8 chicks per pair per year in Central and Western Europe (MacDonald & Bolton 2008). In comparison, the productivity of 2.1 and 2.8 fledged young per nest found in this study in

Table 2. Model-averaged daily survival rates (A) and recapture probabilities (B) (± SE) of the lapwing chicks near Turov, Prypyat river, Belarus in 2006 and 2007.

A	Parameter	Age		
	Daily survival	1–5 days	6–10 days	11 days and older
	2006	0.973 ± 0.014	0.907 ± 0.024	0.999 ± 0.001
	2007	0.935 ± 0.017	0.998 ± 0.007	0.999 ± 0.004

B	Parameter	Occasion						
	Recapture rate	2	3	4	5	6	7	8
	2006	0.99 ± 0.01	0.42 ± 0.06	0.36 ± 0.04	0.31 ± 0.03	0.26 ± 0.03	0.21 ± 0.03	0.17 ± 0.04
	2007	0.44 ± 0.07	0.25 ± 0.04	0.20 ± 0.04	0.09 ± 0.03	0.14 ± 0.04	0.04 ± 0.02	0.04 ± 0.02

2006 and 2007 largely exceeds this threshold and indicates that the population at Turov is highly productive. The high survival rate of chicks seems to be the main factor resulting in high recruitment to the breeding population and stable, abundant breeding population in this area.

We found that the survival rate of lapwing chicks was lowest in their first ten days of life. This age-dependent survival supports the results of previous studies on the lapwing and other precocial species (*e.g.*, Flint *et al.* 1995, Chouinard & Arnold 2007, Colwell *et al.* 2007, Schekkerman *et al.* 2009). However, an exception with relatively high survival rate during the first days post-hatching was noted in southwest Norway (Grønstøl *et al.* 2013). The survival of precocial chicks is related to the development of thermal independence from adults, and the capability of evading predators. Younger chicks tend to lie motionless when approached by humans or terrestrial predators, whereas older chicks respond by running to evade danger (Colwell *et al.* 2007, authors' unpublished data), which might also contribute to a higher chance of survival in the latter. The predation pressure in the study area was low, but small lapwing chicks seem to be more vulnerable to trampling by horses and cows than larger chicks. Moreover, as they age, chicks become more proficient in thermoregulation and foraging (Kersten & Brenninkmeijer 1995, Schekkermann & Visser 2001).

Table 3. Estimated number of lapwing chicks surviving to fledging near Turov, Prypyat river, Belarus in 2006 and 2007.

Number of chicks hatched	Mean	95% confidence interval
2006		
3	1.6	0.83–2.15
4	2.1	1.12–2.87
2007		
3	2.1	1.25–2.47
4	2.8	1.67–3.29

Nesting on periodic river islets naturally restricts access by mammalian predators and this is likely the key factor supporting such high breeding success of the studied species. Although there were no studies on the populations of main predators, their numbers in the study area seem to be very low. The only species of terrestrial predator observed during intensive field studies was the red fox (*Vulpes vulpes*), but we found no signs of its presence on the islets. The red fox avoids crossing water, and this limits its distribution (Mullins *et al.* 2014, but see Storm *et al.* 1976). Among avian predators, the Hooded Crow (*Corvus cornix*) and the Marsh Harrier (*Circus aeruginosus*) were observed, but only occasionally. Moreover, foxes and crows were significantly limited by Turov inhabitants as domestic ducks and geese are raised free-range without cages there. As foxes and crows steal chickens, locals try to get rid of crows' nests or chicks at an early stage of incubation and kill adult foxes using traps around fox dens. As a result, during the field study, there were only about five nests of the Carrion Crow in the area and, in early spring, one fox den within a distance of 1 km from the study site.

Waders and terns that breed close to each other exhibit communal nest defence against predators (Göransson *et al.* 1975, Dyrcz *et al.* 1981, Houde 1983, Elliot 1985). In the study area, chicks hatched in high numbers on river islets remained in that area and none of them have ever been observed out of the islet areas, even when the islets were partially connected to the mainland in late May and early June. Every time appearance of a predator or human caused a strong anti-predator reaction of numerous adult lapwings, gulls and terns, which we observed also in the pre-hatching period. Such collective nest defence usually results in lower predation rate in the areas with the highest densities of breeding waders (Houde 1983, Elliot 1985, Kis *et al.* 2000, Seymour *et al.* 2003). Furthermore, in the Lapwing, brood survival is negatively correlated with the distance between the natal and feeding sites (Blomqvist & Johansson 1995). In our study area, chicks moved only within the relatively small area of the islet and this may have contributed to the observed high survival rate. In addition, the islets were connected to the mainland only after the water level in the river got lower, which was in the turn of May and June, *i.e.*, just before or after fledging in most chicks. Hence, predation might not be an important factor limiting breeding success of the Lapwing in this area. The highest losses were recorded during the egg laying and incubation periods due to trampling by livestock (mainly horses) that sometimes crossed the river and entered the islets, or due to flooding by the river (authors' unpublished data).

Survival of precocial chicks depends also on suitable habitat with patches of vegetation enabling them to hide and patches of invertebrate-rich foraging habitats (Johansson & Blomqvist 1996). The gradual lowering of the water level in spring creates a mosaic of unflooded and flooded small patches of grassland with higher vegetation in the centre of the islet, suitable for hiding, and bare soil with low grass on the outskirts, allowing chicks to access food easily. Hence, river islet habitats composed of dry and wet fertile microhabitats provide optimum feeding conditions with a wide range of aquatic and terrestrial invertebrates and co-occurrence of various microhabitats (Afranowicz-Cieślak *et al.* 2014, Hajdamowicz *et al.* 2015). The combination of a low predation pressure and optimal habitats for chick rearing results in high chick survival rate that is likely to maintain the stability of the local Lapwing breeding population.

Ungöverlevnad i en tät population av tofsvipor (*Vanellus vanellus*) på flodholmar vid mellersta delen av floden Pripyat i Belarus

Fältstudierna gjordes vid tre efemära flodholmar i mellersta delarna av floden Pripyat i södra Belarus åren 2006–2007. Tofsvipeungar ringmärktes efter att de kläckts och observerades därefter med jämna mellanrum under återkommande besök. Vi uppskattade överlevnaden efter kläckning med märknings-återfångst modeller. De dagliga överlevnadsuppskattningarna hos tofsvipeungarna var väldigt höga, mellan 0.90 och 0.99 och den kumulativa överlevnaden till 35 dagars ålder, från kläckning till flygfärdighet, var 0.54 under 2006 och 0.70 under 2007. Överlevnaden var lägre de 10 första levnadsdagarna, vilket motsvarar uppskattningar hos andra precociala arter. Nyckelfaktorn till den observerade höga häckningsframgången är låg predationsrisk vid dessa periodiska flodholmar som på ett naturligt sätt begränsar tillgängligheten för rovdäggdjur och minskar tätheten av rovfåglar. Flodholmarnas habitat med både torra och fuktiga mikrohabitat utgör optimala furageringsomständigheter för tofsvipeungarna med ett brett utbud av akvatiska, jordlevande och ytlevande evertebrater. Dessutom utgör det semikoloniala häckningsbeteendet hos tofsvipan (*ca.* 30 häckningar / ha) tillsammans med andra vadare, tärnor och måsfåglar ett effektivt skydd mot rovdjur. Tack vare ett lågt predationstryck och goda furageringsomständigheter under studien var antalet flygga ungar per häckning 2.1 under 2006 och 2.8 under 2007, vilket är ovanligt höga värden i Europa.

Acknowledgements. We are grateful to all volunteers taking part in this study, particularly to Ivan Bogdanovich and Dmitry Zhuravliou for their help in the field work and to Agnieszka Ożarowska for language correction. Aleksandra Szurlej-Kielańska kindly provided data on the size of the river islets and supported the field work. This study was a part of L.P. PhD project at the University of Gdańsk, financially supported by the grant of the State Committee for Scientific Research KBN 3395/PO1/2008/34 and grant of the University of Gdańsk for young scientists BW 1440-5-0405-6.

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Estimating the onset of natal dispersal for a large diurnal raptor: A methodological comparison

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Received 23 March 2022, accepted 20 December 2022

We estimated the onset of natal dispersal for a large diurnal raptor with high propensity towards large-scaled exploratory movements during the post-fledging period, the White-tailed Sea Eagle (*Haliaeetus albicilla*). We analysed GPS tracking data of 21 juveniles with respect to the onset of natal dispersal comparing six methods available from the recent literature. While none of the methods significantly differed from the visual method, the Distance Threshold method underestimated the dispersal onset for some individuals. Likewise, coefficient of variation methods overestimated the dispersal onset in few cases, presumably because the temporal scale of available GPS fixes did not correspond to the scale of discrete dispersal movements. We conclude that all tested methods are generally suitable to estimate the dispersal onset, specifically if the research question does not depend on an exact but rather a rough estimate. A visual determination might increase flexibility to account for individual behavior and yields consistent results across individuals, but highly reduces the comparability across observers and studies. For research questions relying on exact estimates, we propose using a combination of an automated method and a visual determination as a back-up method for single individuals with clear under- or overestimation. An exploratory comparison showed that the temporal resolution of the GPS may further affect the accuracy of natal dispersal estimates. For individuals with clear movement patterns, high-resolution movement data could increase the accuracy of Coefficient of Variation methods. We underline the necessity for further investigation on the effects of temporal resolution on dispersal onset estimates.

1. Introduction

In many raptor species, the onset of natal dispersal generally forms the end point of the post-fledging period and marks the start of a long and complex dispersal phase (Greenwood & Harvey 1982). Late in the post-fledging period, juveniles are still dependent on their parents for prey deliveries while at the same time exhibiting exploratory behavior in the form of excursions from the nest (Engler & Krone 2021; Soutullo *et al.* 2006b). This way, juveniles can assess the habitat conditions outside the natal territory and potentially lower associated risks or costs of their dispersal.

As juveniles usually become independent from their parents during dispersal, natal dispersal forms a key phase for individuals with respect to their survival, reproduction and adaptations to environmental changes (Morrison & Wood 2009). Thus, the behavioral decision-making process of the individual throughout its dispersal can ultimately not only affect its survival and reproductive success, but also have an impact on population dynamics (Bonte *et al.* 2012; Bowler & Benton 2005).

Accurately describing and analyzing related movement decisions forms the base for understanding the biology of the study species (Serrano 2018). Some research questions address movements throughout the natal dispersal process over large time periods or with large-scaled spatial reference, *e.g.* activity range size over multiple months (Walls & Kenward 2020). While in such cases, accurately determining the time point of the onset of natal dispersal might not always be strictly necessary, other research questions rely specifically on such information. For example, the quality of the natal environment can shape early dispersal movements, and identifying related long-term developments (*e.g.* premature dispersal onset due to habitat degradation) relies on exact and reliable estimates for the onset of natal dispersal (Balbontín & Ferrer 2005; Engler & Krone 2021). Additionally, such information can be crucially important for developing species-specific conservation strategies of raptor species (Balotari-Chiebao *et al.* 2016, Weston *et al.* 2013), *e.g.* by contributing to appropriate spatial and temporal planning of nest protection guidelines in relation to potential anthropogenic disturbance (Engler & Krone 2021).

Accurately estimating the time point of natal dispersal onset is challenging, as assessment methods are not suitable for all raptor species due to complex movement behavior and high levels of individual variation in the time point of natal dispersal (Weston *et al.* 2013, Cadahía *et al.* 2010, Soutullo *et al.* 2006a, Engler & Krone 2021). Different approaches have been used in the recent literature and on different raptor species to estimate the time point of natal dispersal, including Distance Threshold (DT) methods and Coefficient of Variation (CV) methods and visual inspection. DT methods incorporate territory metrics such as home range sizes derived at the population level (Weston *et al.* 2013, Soutullo *et al.* 2006a 2006b, Walls & Kenward 1995, Ferrer 1993a) and rely on the assumption that the defined distance thresholds robustly reflect both an appropriate distance and duration to distinguish dispersal from other movement types (Weston *et al.* 2013). CV methods, on the contrary, use a mathematically based approach by integrating coefficients of variation to determine rates of increase in the distance from the nest over given time periods (Weston *et al.* 2013, Cadahía *et al.* 2008, Soutullo *et al.* 2006b, Walls & Kenward 1995, Ferrer 1993b). They hence compute a metric that describes the variability of movement and are based on the assumption that dispersal from the parental territory forms the most distinctive phase by means of an increased variability in distance from the nest of origin during the exploratory stage (Cadahía *et al.* 2008, Soutullo *et al.* 2006a). Accordingly, the onset of dispersal should be represented by the highest variation in distance over a certain time period (Weston *et al.* 2013).

Inconsistent estimates are the dominant outcome from the majority of available dispersal methods and very few studies have compared their applicability and accuracy (Weston *et al.* 2013, Cadahía *et al.* 2008, Soutullo *et al.* 2006b). Further, as such methodological comparisons have only been made for Golden Eagles *Aquila chrysaetos* (Weston *et al.* 2013, Soutullo *et al.* 2006b) and Bonelli's Eagles *Hieraaetus fasciatus* (Cadahía *et al.* 2008), comparisons for additional raptor species are necessary to develop suitable and reliable methods for identifying the onset of natal dispersal of species that exhibit complex movement patterns during the post-fledging period.

Over the last decades, the ongoing technical development of tracking devices has led to an exponential increase in tracking data, thus expanding the spatio-temporal scale at which movement patterns can be analysed (Hooten *et al.* 2017; Kays *et al.* 2015). The value of high resolution tracking data for studying animal movements with the goal to infer an understanding as the base for conservation strategies has been demonstrated by multiple studies on raptor species, including the Montagu's Harrier (*Circus pygargus*, Schaub *et al.* 2020) and the Northern Goshawk (*Accipiter* *gentilis*, Blakey *et al.* 2020). However, the effect of temporal resolution of tracking data on the outcome of analyses is still scarcely addressed and likely depends on the movement scale and behavior of the animal (Gunner *et al.* 2021, Ryan *et al.* 2004).

Therefore, the focus of this study was to compare DT methods, CV methods and a visual determination with regards to their accuracy in estimating the onset of natal dispersal using a raptor species that displays large-scaled exploratory movements with high individual variability during the post-fledging period, the White-tailed Sea Eagle (WTSE, *Haliaeetus albicilla*, Engler & Krone 2021). The WTSE is a large diurnal raptor that inhabits undisturbed areas in forests, on islands and along coastal areas, with access to fish-rich freshwater lakes that offer perching possibilities along the shoreline to increase foraging success (Fischer 1984, Krone *et al.* 2013, Nadjafzadeh *et al.* 2016). Additionally, we aimed to examine whether the temporal resolution of data affected dispersal onset estimates, using a small sample size of two exemplary individuals.

2. Methods

2.1. GPS tracking

We analysed tracking data from 21 WTSE fledglings that were equipped with Global Positioning System (GPS) or Global System for Mobile Communications (GSM) satellite transmitters between 2004 and 2016 in North-East Germany. Nestlings were fitted using a backpack-style harness system (Krone *et al.* 2013) at an age of 42 to 66 days. The transmitters' weight accounted for 3% of the eagles' body weight on average (3.3 ± 0.6%, n = 21, range: 1.7–4.2%). We determined the individual date of fledging by visually by mapping GPS positions using the distance to the center of the nest, while taking individual positioning errors into account (Engler & Krone 2021). Locations were recorded at different intervals from every 30 minutes to once per day between hours 06:00 and 20:00 (UTC+2). For a uniform temporal scale, GPS fixes were filtered to one location per day closest to 12:00 (Engler & Krone 2021). Additionally, data at 30-minute intervals was available for two individuals (4876, 4877) and we used data from these individuals for a separate investigation with higher resolution. Additional information on transmitter models and data preparation are reported by Engler and Krone (2021). Originally, 31 nestlings were tagged, ten of which were removed from the analysis due to early technical failure or large data gaps (Engler & Krone 2021). The animal permits were issued by the following authorities with the permit numbers indicated in parentheses: State Veterinary and Food Inspection Office Mecklenburg-Western Pomerania (LVL M-V/3104), Lower Saxony State Office for Consumer Protection and Food Safety (33.42502-080/06) and Brandenburg State Office for Consumer Protection, Agriculture and Land Consolidation (23-2347-3-2009).

2.2. Estimation of natal dispersal onset

We used the number of days since fledging as the metric for onset of natal dispersal, using a DT method, CV methods and a visual approach (Table 1): For method 1, we defined circular and temporally fixed parental home-range (HR) sizes for breeding pairs as the mean of available HR sizes from the literature. We used averaged HR sizes of 13.48 km² (radius of 2.07 km, n = 20) for breeding pairs from the two core areas of the study region and 53.25 km² (radius of 3.90 km, n = 11) for all other breeding pairs, as described by Engler and Krone (2021). To avoid underestimation of the onset of dispersal caused by pre-dispersal excursions we used a threshold of spending at least five days outside the parental territory. Based on recommendations by Walls and Kenward (1995), we chose this particular time period as we considered it to reflect the time period at which juveniles would be capable of returning from an excursion without serious impact to their health, at a life stage when they are still not capable of foraging on their own (authors' pers. observation.).

Among the CV methods (Table 1, methods 2–4), we calculated the coefficient of variation in distance (CV_D) as the ratio of standard deviation to the mean distance for consecutive time periods of the respective length in days. For example, method 2 calculated CV_D as the standard deviation

Table 1. Applied methods to estimate the time point of natal dispersal of juvenile White-tailed Sea Eagles. DT = Distance Threshold method. CV = Coefficient of Variation method. Visual = Visual determination method.

Method	Type	Description	Reference
1	DT	First day of five consecutive locations beyond the radius of respective circular parental territory.	Soutullo *et al.* (2006b), Walls and Kenward (1995)
2	CV	Highest coefficient of variation (3-day period)	Weston *et al.* (2013), Cadahía *et al.* (2008), Soutullo *et al.* (2006b)
3	CV	Highest coefficient of variation (5-day period)	See references in method 2
4	CV	Highest coefficient of variation (10-day period)	See references in method 2
5	CV	Maximum change in proportion of locations inside the fixed circular parental territory between –30 days and +30 days, per day.	Weston *et al.* (2013)
6	Visual	Observed location pattern, subjective assessment	Walls and Kenward (1995)

of distance to the nest over a rolling 3-day period divided by the mean of distance to the nest over the same time period. We defined the dispersal date as the day midway between the first and last location of the time period for which CV_D was highest. We only considered CV_Ds of relocations with a distance >1 km from the nest for >3 consecutive days, to make sure that estimates are biologically relevant. By choosing a distance of only 1 km, we aimed to maintain the character of a mathematical computation rather than adding the approach of detection based on distance thresholds as in method 1.

For method 5, we similarly tried to identify time periods with maximum rates of change while accounting for the large temporal scale at which dispersal can occur (Weston *et al.* 2013). Here, the proportion of locations inside the fixed, circular parental territory was determined for 30 days before (T_1) and 30 days after (T_2) each relocation and the difference in proportions ($T_{diff} = T_1 – T_2$) was calculated for a 60-d time period. In daily time steps, this window was shifted forward, resulting in T_{diff} for multiple consecutive time periods. The time point of dispersal was then defined as the date for which T_{diff} was maximal (Weston *et al.* 2013).

Thirdly, a visual determination of the onset of dispersal from visual exploration of movement trajectories served as a base reference (method 6), for which we mapped relocations for each individual using the fixed circular parental territory sizes reported in Engler and Krone (2021) as boundary thresholds for each bird. We then closely inspected movement paths individually to identify the most likely time point at which the onset of natal dispersal took place.

2.3. Effect of temporal resolution of GPS time intervals

To preliminarily investigate whether the temporal resolution of GPS time interval affected estimates of dispersal onset compared to the visual determination method, we additionally calculated differences in estimates ($|\Delta_{days}|$) based on the high-resolution data set for each method in comparison to the visual determination method. Additionally, we compared low-resolution estimates to high-resolution estimates. We used a very limited sample size of two individuals for this investigation.

2.4. Statistical analysis

Differences in estimates of dispersal onset between methods were tested using a non-parametric Quade-test for repeated measures, due to the comparatively small sample size and preliminary diagnostics of the distribution of the data. We performed a post-hoc Quade multiple-comparison test with BH correction (Benjamini & Hochberg 1995) to further identify between-group differences. The significance level α was set at $p<0.05$ for all statistical tests. Summarizing group values are presented as mean ± standard deviation (SD), if not stated otherwise. Data processing and statistical analyses were performed in software R, version 3.5.1 (R Core Team 2018).

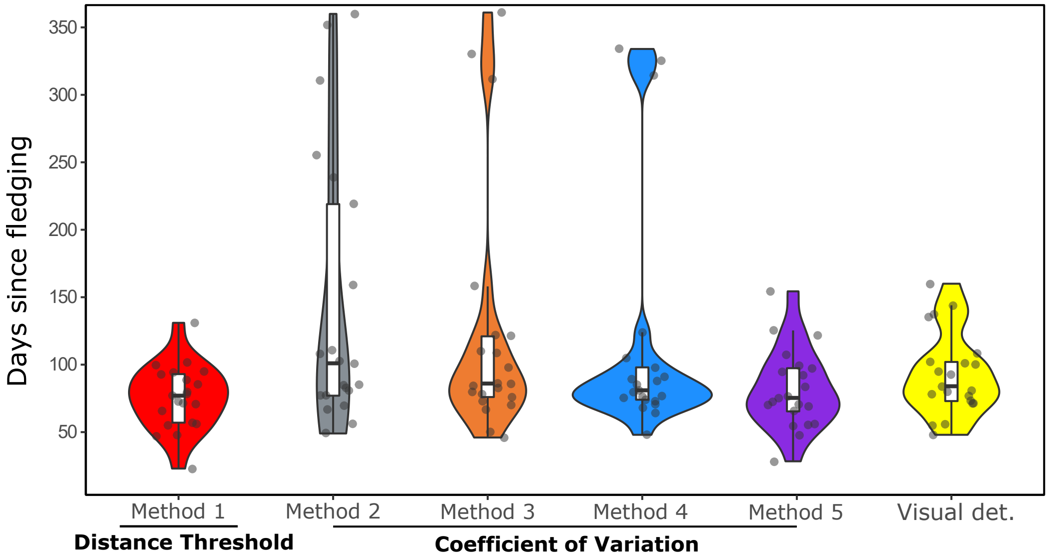
3. Results

3.1 Estimation of natal dispersal onset

Across methods, mean estimates of the time point of dispersal ranged from 82.4 to 145.1 days after fledging and showed large variability within methods (between individual eagles) but little between methods (Fig. 1). While estimations based on a visual determination averaged 92.8 (±30.2) days after fledging, the DT method yielded the lowest mean estimates (75.8±23.8 days) as well as the lowest within-method variation among all methods. Within CV methods, methods 2–4 showed the highest means and standard deviations (Fig. 1). The differences in mean estimates and standard deviations in CV methods compared to the visual determination method reduced with increasing length of the time period over which the coefficient of variation was calculated. For multiple individuals, the time point of emigration was estimated long after the time point of emigration measured by the visual determination (Fig. S1).

In contrast, the variability in estimates was roughly three times lower for method 5 compared to CV methods 2–4 (Fig. 1) and it yielded the closest estimates (82.4±29.3 days) to the visual approach among all methods.

Overall, the choice of method significantly affected the outcome of estimates for the onset of natal dispersal (Quade's test, F(5, 100)=3.15, $p<0.02$). Among all group combinations, only



mean	75.8	145.1	123.8	116.2	82.4	92.8
sd	23.8	100.7	91.9	88.5	29.3	30.2

Fig. 1. Estimations of dispersal onset in White-tailed Sea Eagles (n=21) by a Distance Threshold method, Coefficient of Variation methods and visual determination represented as violin and boxplots with whiskers to 1.5 Inter-Quartile Range (IQR). Points indicate time of dispersal (days since fledging) of individuals.

estimates of the DT method and method 2 (Pairwise Quade's test, p=0.014) as well as method 2 compared to method 4 (Pairwise Quade's test, p=0.037) and method 5 (Pairwise Quade's test, p=0.024) differed from each other, as shown by a post-hoc analysis. None of the methods significantly over- or underestimated the dispersal onset compared to the visual determination.

3.2. Effect of temporal resolution of tracking data

The comparison of dispersal onset estimates between two levels of temporal resolution of two individuals yielded widely different results (Fig. 2). For individual no. 4876, which went on multiple excursions (n=9) up to 28.6 km distance from the nest prior to onset of natal dispersal (Fig. S1), estimates of all methods based on a higher resolution data set generally underestimated the onset of dispersal. $|\Delta_{days}|$ ranged from 34 days (method 4) to 75 days (method 1), averaging at 35.7 (±15.3) days for estimates of CV methods 2–4 (Fig. 2). Estimates based on the low-resolution data set were generally higher and closer to a visual determination than those based on higher resolution data, with a difference of 46 days for method 1 and an average of 29.8 (±12.4) days across all methods.

In contrast, for individual no. 4877, which undertook fewer excursions (n=6) with shorter maximum distance (2.9 km) and a single event of rapid increase in distance from the nest site (Fig. S1), $|\Delta_{days}|$ was highest for method 1 with a premature detection of dispersal onset by 37 days (Fig. 2). All CV methods (methods 2–5) yielded highly consistent estimates when calculated with the high-resolution data set, differing by only 1.0 days (±0) on average compared to the visual determination method. Additionally, while low resolution estimates were lower for methods 3 and 4 (24 days ±0) in comparison to the high-resolution estimates, method 2 overestimated the dispersal onset by 148 days for low resolution data with reference to the visual determination estimate.

For both individuals, estimates of dispersal onset for the visual determination were identical between the high- and the low-resolution data set.

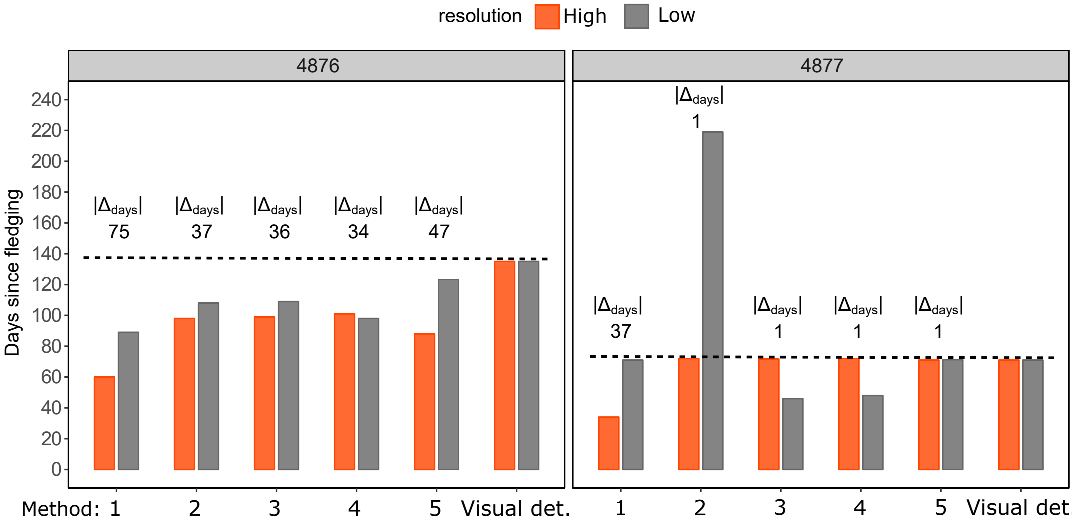


Fig. 2. Comparison of estimates in dispersal onset for two individuals (no. 4876 and 4877) with two levels of temporal resolution. Orange bars represent the days since fledging based on a data set with 48 GPS fixes per day, grey bars are based on the low-resolution data set with a resolution of a single GPS fix per day. $|\Delta_{days}|$ represents the absolute difference in days between estimates of the high-resolution data set with the visual determination. The horizontal, dashed lines mark estimates of the onset of dispersal using visual determination.

4. Discussion

4.1. Estimation of natal dispersal onset

To our knowledge, our study is one of few that compares different methods of estimating dispersal time of young raptors from the nest. Overall, none of the tested methods significantly over- or underestimated the onset of natal dispersal compared to the visual determination method. The DT method, using methodological adaptations to account for pre-dispersal excursions of WTSE on a biologically meaningful level (Walls & Kenward 1995), yielded precise estimates for most individuals. However, for some individuals the method wrongly detected clear events of exploratory excursions during the pre-emigration phase as the onset of natal dispersal. This result was mainly linked to individuals with extensive exploratory behavior regarding the number, distance and the duration of excursions (Engler & Krone 2021). The results highlight, that accounting for individual variation and complexity in post-fledging movement patterns remains the major challenge for such methods, particularly for species with high propensities towards excursive behavior (Weston *et al.* 2013, Cadahía *et al.* 2008, 2005, Kenward *et al.* 1993). We conclude, however, that universally applied measurements of distance thresholds might form an alternative to a rather subjective visual determination of dispersal. The methodological drawbacks of risking underestimation due to using fixed biological parameters could be tolerated compared to the disadvantages of a highly subjective approach of a visual determination and makes results more comparable between studies.

Although not significantly different from the visual method, CV methods 2–4 yielded the highest variation in dispersal estimates and the variance of estimates decreased with an increasing time interval, over which the estimate was calculated. In several cases, rapid small-scaled movements over short time periods caused an overestimation of dispersal onset due to delayed detection. These results for rate-based methods are consistent with findings reported for two other large raptor species, the Bonelli's Eagle *Hieraaetus fasciatus* (Cadahía *et al.* 2010, 2008) and the Golden Eagle *Aquila chrysaetos* (Weston *et al.* 2013, Soutullo *et al.* 2006a, 2006b), which show similar (pre-) dispersal behavior. In these cases, the results highlight the disadvantages of solely rate-based estimation methods reported in the recent literature, as they do not take the spatial scale of movements into account (Weston *et al.* 2013).

Method 5, however, yielded the lowest within-method variation and resulted in estimates closest to the visual determination. By operating on a larger temporal scale while taking a presence/absence ratio within the parental HR into account, method 5 seemed to integrate the scale of natal dispersal movements the best, hence coping with individual variation and movement patterns acting on similar spatio-temporal scales. Compared to the DT method and the other CV methods, method 5 did not show signs of under- or overestimation for outlier individuals with either strong exploratory behavior or rapid small-scaled movements. Therefore, we rate this method as an accurate alternative to a visual estimation.

We used a visual determination as the reference, because it is a direct approach, offers the highest levels of flexibility for scientists and lets them integrate their personal experience on the study species the most. Equally, this represents a major drawback for the method, as estimates are highly subjective and inter-observer comparability is therefore strongly compromised (Cadahía *et al.* 2008). Accordingly, estimates based on visual determination need to be presented as transparently as possible and conclusions should be drawn with caution, particularly when comparing results between species with different dispersal behavior.

Ultimately, both DT and CV methods generally appear to form suitable alternatives to a subjective visual estimation of the time point of dispersal for WTSE. However, in multiple cases only a visual determination coped with the irregular movement patterns during the post-fledging period. These results are highly consistent with a respective comparison for Golden Eagles, which showed similarly complex movement patterns prior to emigration (Weston *et al.* 2013). We highlight that the choice of method should also be made based on the respective research question and the purpose of calculating the date of dispersal onset in the first place. If the main research goal does not rely on an exact date, and aims for larger temporal time periods, *e.g.* when calculating and comparing temporal activity ranges (Murphy *et al.* 2017), both DT and CV methods might be suitable options. In such situations, the advantages of producing automated, objective estimates without the risk of reduced comparability due to subjective estimation could justify the risk of premature or delayed estimates for few individuals (Cadahía *et al.* 2008).

On the contrary, if the research question requires precise estimates of the natal dispersal onset, specifically method 5 appears to be a suitable alternative to a visual estimation, as it appears to cope well with outlier individuals. Precise estimations become increasingly important, *e.g.* when identifying effects of the natal environment on the dispersal onset (*e.g.* premature dispersal onset due to habitat degradation; Balbontín & Ferrer 2005; Engler & Krone 2021). In the same context, researchers rely on exact estimates for the onset of natal dispersal, when the main goal is to develop species-specific conservation strategies such as planning of temporal nest protection guidelines for raptor species (Balotari-Chiebao *et al.* 2016, Engler & Krone 2021, Weston *et al.* 2013).

In general, we propose to use a combination of a) an automated method such as method 5 as the primary choice and b) a visual determination as the backup method specifically for raptor species with high propensities towards rapid movements on large spatio-temporal scales and strong excursive behavior. The latter could be used only on individuals, where both DT and CV methods clearly yielded under- or overestimated time points of dispersal onset.

Although we were not able to incorporate precise, individual-based yet data-intensive representations of the parental HR as described and proposed by McLeod *et al.* (2002) and Weston *et al.* (2013), they could additionally form a promising alternative to adequately estimate the onset of dispersal for raptor species with strong excursive behavior.

We highlight that accurately determining the onset of natal dispersal and differentiating between pre-dispersal movements is not solely important for raptor species, but also for other bird groups and even mammals that display excursive behaviour. For example, studies on seabirds (*e.g.* frigatebirds *Fregata minor,* Collet *et al.* 2020) and mammals such as flying squirrels *Pteromys volans* (Selonen & Hanski 2006) and roe deer *Capreolus capreolus* (Ducros *et al.* 2020) frequently applied spatial metrics such as parental home range boundaries similar to method 1 in order to account for and discriminate between excursions and natal dispersal.

4.2. Effect of temporal resolution of tracking data

The exploratory comparison of low and high temporal resolutions indicated that an interaction between excursive behavior, method and temporal resolution may further influence the outcome of dispersal onset estimates for raptor species.

For the individual with strong excursive behavior (no. 4876), all methods yielded better estimates on low- rather than on high-resolution data, as high-resolution based estimates generally underestimated the onset of dispersal compared to the visual method.

We assume that the higher resolution of GPS fixes increased the chances of premature detection of dispersal onset due to the frequent small-scaled movements in the form of excursions. In these cases, the temporal scale of available GPS fixes and hence the scale on which methods are applied might not correspond to the temporal scale on which discrete dispersal movements take place. The results could indicate that the compared methods do not necessarily perform better on high-resolution tracking data, if the propensity of the individual or species towards large-scaled exploratory movements during the post-fledging period is high.

On the contrary, CV methods based on high-resolution data yielded particularly highly consistent and precise estimates for the individual (no. 4877) with a distinct event of emigration and a rapid increase in distance from the natal territory. Similar effects for different temporal resolutions have already been demonstrated, for example, in inferential models or when calculating travel distances (Postlethwaite & Dennis 2013; Rowcliffe *et al.* 2012). In line with the comparison between methods, this further indicates that for single individuals, CV methods based on low-resolution data could not accurately detect the singular event of dispersal. Possibly, the temporal scale over which the coefficient of variation was calculated was too small to account for the distance covered during natal dispersal onset (method 2).

We conclude that for raptor species with rather clear movement patterns the availability of high-resolution movement data could additionally increase accuracy and consistency of estimates when using methods based on coefficients of variation. Although these findings are only exploratory, we underline that in future studies special consideration should be given to the effect of temporal resolution on estimates of natal dispersal characteristics, particularly for target parameters with high individual variability and species with strong excursive behavior.

Due to the increasing number of GPS tagged animals and an increasing temporal resolution of the data, automatized pattern detection methods and the need for validation of their reliability will become increasingly relevant for wildlife research.

En jämförelse av metoder för att uppskatta påbörjandet av spridningsfasen hos en stor dagrovfågelart

Vi undersökte tidpunkten för när havsörnens (*Haliaeetus albicilla*) ungar påbörjar sin spridningsfas. Havsörnens flygga ungar utför relativt långa utforskande flygturer innan de beger sig iväg, vilket försvårar uppskattningarna. Vi analyserade GPS spårningsdata från 21 juvenila havsörnar där vi jämförde den uppskattade tidpunkten för påbörjandet av spridningsfasen med hjälp av sex metoder som nyligen beskrivits i litteraturen. Ingen av metoderna skiljde sig från metoden att visuellt bestämma tidpunkten, men 'Distance Threshold' metoden underskattade tidpunkten för spridningsfasens början. Däremot överskattade varianskoefficient-metoden påbörjandet av spridningsfasen, antagligen på grund av att datapunkterna från GPS spårningen inte tillräckligt exakt sammanföll med informationen från de separata spridningshändelserna. Vi sammanfattar att alla metoder som testades generellt sett är ändamålsenliga för att uppskatta påbörjandet av spridningsfasen, speciellt ifall forskningsfrågan inte kräver en väldigt exakt uppskattning. En visuell uppskattning ökar flexibiliteten att ta i beaktande individuell variation och ger överensstämmande resultat mellan örnindivider, men försvårar jämförandet mellan observatörer och studier. För studier som kräver exakt information om påbörjan av spridningen rekommenderar vi att kombinera en automatiserad metod med visuella metoder som stöd ifall uppskattningarna av vissa individer är tydligt över- eller underskattade. Våra data tyder även på att den temporala upplösningen i data påverkar uppskattningarna av påbörjandet av spridningsfasen. För de individer som har tydliga rörelsemönster kunde data med hög upplösning förbättra noggrannheten i varianskoefficient-metoden. Vi understryker att det behövs mera studier i effekten av temporal upplösning vid studier av tidpunkten för påbörjan av spridningsfaser.

Competing interests. The authors declare that they have no competing interests.

Data availability statement. We will make individual-wise dispersal onset estimates publicly available by adding a table to the supporting information (Table S1). As underlying raw movement data contains highly sensitive information on nest location of White-tailed Sea Eagles, we will not make such information available.

Acknowledgements. We would like to thank the administrations of the nature park Nossentiner Schwintzer Heide and of the nature park Usedom for their cooperation, support and confidence. Without the help of W. Mewes and T. Lauth monitoring the breeding places and the tree climbers B. Ortscheid, A. Laubner, N. Kenntner and P. Sömmer our study would not have been possible. We are very grateful to H. and T. Dornbusch for logistical and financial support of the Sea Eagle project. We also would like to thank all reviewers and associate editors for their valuable efforts and comments, as they have significantly contributed to improving this paper.

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Online supplementary material

Supplementary material available in the online version includes Figure S1 ana Tables S1–S2.

Ornis Fennica 100: 38–50. 2023

Foraging behaviour of the Great Spotted Woodpecker (*Dendrocopos major*) in the Białowieża National Park: Comparison of breeding and non-breeding seasons

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Received 5 August 2021, accepted 16 January 2023

Although the Great Spotted Woodpecker (*Dendrocopos major*) is the most common of the European woodpecker species, there are no studies detailing its foraging behaviour in the breeding and non-breeding seasons. Our research, conducted in the primeval oak-lime-hornbeam forest of the Białowieża National Park in 1999–2011, compared foraging sites and foraging techniques used by this species in these two seasons. Great Spotted Woodpecker predominantly foraged on standing trees, while lying trees and the ground were occasionally used as foraging sites, but almost exclusively in the breeding season. European hornbeam (*Carpinus betulus*) and small-leaved lime (*Tilia cordata*) were the most frequently used for foraging in the breeding season, whereas Norway spruce (*Picea abies*) and pedunculate oak (*Quercus robur*) were used in the non-breeding season. Great Spotted Woodpecker foraged more frequently on dead and large trees in the non-breeding season. In the breeding season, Great Spotted Woodpecker collected food mainly from living substrates, predominantly sites on large diameter trunks and at low height, while in the non-breeding season it collected food from thin, dead and upper branches. Searching for food and gleaning it from the tree surface was the most common foraging technique used in the breeding season, whereas seed extraction from cones dominated in the non-breeding season. The percentage of foraging time spent on this type of food was positively correlated with the index of Norway spruce seed production. Our study showed that the foraging behaviour of the Great Spotted Woodpecker in the two seasons differs significantly due to changes in food resources.

1. Introduction

The Great Spotted Woodpecker (*Dendrocopos major*) is the most omnivorous of all European woodpecker species with diverse foraging techniques and feeding sites (Michalek & Miettinen 2003). In the breeding season and later in summer its diet consists of invertebrates collected from the surface of trees, while in autumn and winter it feeds on invertebrates living in the wood and seeds of coniferous tree species, mostly Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) (Osiejuk 1994, 1998, Pavlík 1997, Jiao *et al.* 2008, Michalek & Miettinen 2003). Conifer seeds are an important component of the Great Spotted Woodpecker's diet, especially in periods when food of animal origin is limited, for example in winter (Hogstad 1971, Osiejuk 1998). In early spring, this woodpecker may enrich its diet by ringing trees (making holes around the trunk) and drinking the leaking sap or eating invertebrates attracted to it (Turček 1954, Kruszyk 2003). Moreover, it may also depredate bird nests (Kuitunen & Aleknonis 1992, Skwarska *et al.* 2009).

Seasonal changes in the foraging behaviour of woodpeckers are mainly due to changing food types and their amounts, which in a temperate climate is closely correlated with the occurrence of the four seasons. In addition, severe weather conditions such as thick snow cover, can make access to food difficult, forcing woodpeckers to change their foraging techniques or sites where they can find it (Rolstad & Rolstad 2000, Czeszczewik 2009). Moreover, the need to feed nestlings during the breeding season may cause a change in foraging behaviour because food eaten by nestlings may be different from that of adult birds. For example, Pavlík (1997) revealed that the diet of *D. major* nestlings consisted mainly of leaf-eating Lepidoptera larvae, while these larvae constituted only a small part of the diet of adult woodpeckers.

Although the Great Spotted Woodpecker shows large variation in its diet throughout the year, research on seasonal differences in foraging behaviour of this species has rarely been conducted with the same methods in the same site (Jenni 1983, Székely & Moskát 1991). Indeed, studies usually addressed a specific period of the year, such as the breeding season (Török 1990, Pavlík 1997), summer (Osiejuk 1991) or winter (Hogstad 1971, Vanicsek 1988, Osiejuk 1994, 1996, 1998). The foraging behaviour of this woodpecker species in primeval forests is also poorly known. Previous work from the Białowieża Forest focused exclusively on dead trees used by different woodpecker species in deciduous stands, but the characteristics of feeding sites presented in that paper were limited to the species, condition and diameter of the tree trunk (Walankiewicz *et al.* 2002). A more detailed characterisation of foraging sites of *D. major*, in relation to sex, was presented by Stański *et al.* (2020). Another paper by Stański *et al.* (2021a) described anvil placement sites of this woodpecker species. However, none of the above-mentioned papers analysed foraging behaviour in relation to the seasons.

The primary objective of our study was to identify the parameters of trees and sites located therein used by the Great Spotted Woodpecker as feeding grounds with respect to seasons (breeding and non-breeding). We predicted clear preference of foraging on certain tree species and the sites within these trees because they provide more food than others. These include large trees (*i.e.* those with a large trunk diameter at breast height), as they are inhabited by more invertebrates compared to trees with thinner trunks (Lõhmus *et al.* 2010, Sukovata & Jaworski 2010). We hypothesised that the foraging techniques and foraging sites would differ between the two seasons analysed. It was expected that in the breeding season *D. major* is more likely to collect food from the surface of trees, whereas in the non-breeding season it is more likely to extract food from dead parts of trees, as many invertebrates overwinter in dead wood (Lõhmus *et al.* 2010). Moreover, we expected the species to feed primarily on Norway spruce seeds during the non-breeding season, as food of animal origin is limited at this time.

2. Material and methods

2.1. Study area

The Białowieża Forest is located on the border between Poland and Belarus. It is a remnant of the vast lowland forests that covered Europe hundreds of years ago. The Białowieża National Park (BNP), established in 1921, is located in the Polish part and covers 105 km^2. BNP forest stands, most of which can be classified as primeval forests, are characterised by diverse tree communities of large trees and large amounts of dead wood, including standing snags and fallen, uprooted trees (Tomiałojć 1991, Tomiałojć & Wesołowski 2004). The study plot (about 10 km^2), located in the southern part of the Strictly Protected Area (the best protected zone of the BNP), was covered by an oak-lime-hornbeam stand (*Tilio-Carpinetum*), which is the dominant forest type in the area. It is the most structurally diverse stand, which can be subdivided into five to six layers including three canopy layers. The main tree species growing in the area are small-leaved lime (*Tilia cordata*), European hornbeam (*Carpinus betulus*), Norway spruce, pedunculate oak (*Quercus robur*) and Norway maple (*Acer platanoides*). They are accompanied by many other tree species, such as European ash (*Fraxinus excelsior*), common aspen (*Populus tremula*) and elms (*Ulmus* spp.). The Great Spotted Woodpecker is the most common woodpecker in this area, with up to 2.0 pairs/10 ha (Wesołowski *et al.* 2015a).

2.2. Data collection

Data were collected from 1999 to 2011. Observations were conducted only on days without strong wind (not exceeding 4 on the Beaufort scale), rain or snow to minimise the impact of weather. Observations were usually started one or two hours after sunrise and finished at noon. Great Spotted Woodpecker foraging behaviours were sampled during slow walks in the study area and birds were located using sound (*e.g.* alarm call, drumming) and visual cues. To avoid the observer's influence on the woodpecker's behaviour, we conducted observations from a distance and only when the bird did not show restless behaviour. In addition, to minimise the number of observations of the same individuals in the collected data, after completing a given observation, the researcher started searching for a new foraging woodpecker in a new location several hundred meters away.

Once a foraging woodpecker was located, we recorded the time duration of foraging, foraging substrate, and foraging technique. The time duration of foraging (to the nearest 5 seconds) was measured from the moment the foraging woodpecker was located until the moment it finished foraging (usually leaving the tree). Foraging substrates were classified as a standing tree, fallen tree, or ground. Foraging techniques were classified as: searching and gleaning, wood pecking, bark pecking/scaling, ringing and sap sucking, extracting hornbeam seeds, extracting Norway spruce seeds from cones. If foraging took place on a standing tree, we additionally recorded the following parameters: tree species, tree condition (alive or dead), tree diameter at breast height (DBH), part of a tree (trunk or branch), condition of a foraging spot (alive or dead), diameter at a foraging spot, and height of a foraging spot above the ground. DBH was calculated based on the circumference of the tree trunk, which was measured using a tape measure, whereas the diameter of a foraging spot was estimated from the woodpecker body size as a reference. The height of foraging was assessed using Suunto Height Meter PM-5/1520 or the height of an observer as a reference.

To determine tree preference, we measured tree availability on 82 plots between 1999 and 2003. These plots (0.25 ha each) were randomly selected in the study area, where foraging woodpeckers were observed. For each tree, we recorded its species, condition (alive or dead) and DBH.

2.3. Data analysis

Data from different years were pooled and then analysed by two seasons: breeding and non-breeding. We considered the months of April, May and June as the breeding season, with the remaining months as the non-breeding season (Wesołowski *et al.* 2020). We collected 1001 records of foraging Great Spotted Woodpeckers in total, 507 of which were in the breeding season and 494 in the non-breeding season. The total time of observations of foraging woodpeckers was 993 min in the breeding season and 3602 min in the non-breeding season. However, all analyses involving the determination of the parameters of trees and sites on these trees used by the Great Spotted Woodpecker included only observations of foraging on standing trees, as foraging on fallen trees was rarely observed. Furthermore, observations where trees were used as anvils (*i.e.* where conifer and hornbeam seeds were extracted by woodpeckers) were excluded from this analysis because time spent hammering hornbeam nuts and conifer cones does not indicate the attractiveness of a given tree or site as a place of food storage, but only its suitability as an anvil. Characteristics of the sites preferred by the Great Spotted Woodpecker as anvil placement sites were presented in Stański *et al.* (2021a). After excluding the above-mentioned observations, 382 records remained in the breeding season and 123 records in the non-breeding season.

To analyse the preference for trees selected as foraging sites, selection indices were calculated according to their species and condition. For this purpose, the proportion of trees representing a specific species and condition status (dead or alive) visited during foraging was divided by the proportion of available trees from a given group in the resources (Manly *et al.* 2002). Available trees were considered those with a DBH of at least 6 cm (the minimum DBH of a tree used for foraging by the Great Spotted Woodpecker). For each selection index, 95% confidence limits were calculated (assuming 0 for results with a negative value) according to the formula given by Manly *et al.* (2002). A selection index was statistically significant if the confidence limits did not contain the value of 1. A tree was considered “preferred” when its selection index was significantly greater than 1, and “avoided” when its selection index was significantly lower than 1 (Manly *et al.* 2002).

The G-tests were used to compare the parameters of foraging sites and foraging techniques between the breeding and non-breeding season. To perform these analyses, the foraging time was converted into percentages, *i.e.* the percentage of foraging time spent on a given tree species, a given height category, etc. was calculated. For the purpose of these analyses trees were categorized according to their DBH into one of the following four classes: <20 cm, 20–40 cm, 40–60 cm, and >60 cm, while the exact foraging spot was divided both according to its diameter (into one of the three classes: <15 cm, 15–30 cm, >30 cm) and its height above the ground (into one of the five classes: <5 m, 5–10 m, 10–15 m, 15–20 m, >20 m).

To check whether the DBH of trees selected for foraging differs between the breeding and non-breeding seasons, a general linear model (GLM) was used. Prior to the analysis the dependent variable - DBH was log-transformed to approach the normality and homoscedasticity of the data. The analysis was performed only for the most frequently used tree species: European hornbeam, small-leaved lime, pedunculate oak, Norway spruce and Norway maple. Tree species (five mentioned above tree species) and season (breeding vs. nonbreeding) were included in the analysis as fixed categorical explanatory variables. Moreover, we also included interactions between variables to find potential differences between DBH in breeding and non-breeding seasons in relation to tree species.

Since foraging on Norway spruce seeds was the dominant method of obtaining food in the non-breeding season, we checked whether the level of seed production by this tree species in a given year affected the percentage contribution of foraging on spruce seeds to the total foraging time of the studied woodpecker. Spearman’s rank correlation was used for this purpose. The index of Norway spruce seed production in particular years was correlated with the percentage contribution of foraging on this type of food to the total foraging time in the period from July of a given year to March of the following year (*i.e.* in the non-breeding season). This analysis was conducted for data collected from 2002 to 2010. Data on Norway spruce seed production was derived from the paper by Wesołowski *et al.* (2015b). To assess the level of seed production, the authors of the above-mentioned publication counted cones in the uppermost 5-metre section of the surveyed trees on their southern side in autumn of the current season. Next, based on the number of cones, they determined a crop index from 0 (no cones) to 4 (heavy seed yield). For detailed methodology see Wesołowski *et al.* (2015b). G-tests and calculations of selection indices were carried out using formulas prepared in Excel. Other statistical analyses were performed using Statistica version 12.0.

3. Results

3.1. Trees used for foraging

Great Spotted Woodpecker foraged mainly on standing trees. It used fallen trees very rarely and almost exclusively in the breeding season, and foraging on the ground was observed only during this season (Table 1). The use of foraging sites (ground, fallen trees, standing trees), expressed as a percentage of foraging time, differed significantly between the seasons (G=9.57, df=2, p=0.008).

The Great Spotted Woodpecker collected food on trees representing 11 species during the breeding season and nine species during the non-breeding season. The distribution of the recorded foraging time per specific tree species differed between the seasons (G=47.65, df=10, p<0.001). In the breeding season, woodpeckers foraged mostly on European hornbeams and small-leaved limes, whereas during the non-breeding season – on Norway spruces and pedunculate oaks (Fig. 1). The selection indices showed statistically significant preferences for oaks, maples and aspens in the breeding season and for oaks, maples and spruces in the non-breeding season. Lime and hornbeam, although the most abundant in the study area, were used below the levels predicted based on their availability (Table 2).

Live trees were used more often during foraging than dead trees, but selection indices indicated a preference for the latter in both analysed seasons (Table 2). The proportion of foraging time spent on live and dead trees differed in both seasons (G=8.82, df=1, p=0.003). In the non-breeding season, the use of dead trees increased more than twice compared to the breeding season (Table 3). The use of trees in each thickness class differed between the seasons (G=30.33, df=3, p<0.001). The foraging time on trees in all thickness classes, except the thinnest one, was similar in the breeding season,

Type of foraging site	Breeding season		Non-breeding season	
	n	% time	n	% time
Standing trees	472	93.05	493	99.97
Fallen trees	18	3.75	1	0.03
Ground	17	3.20	0	0

Table 1. Percentage distribution of foraging time in particular foraging sites in the breeding and the non-breeding seasons. All observations were included. N = number of sample size.

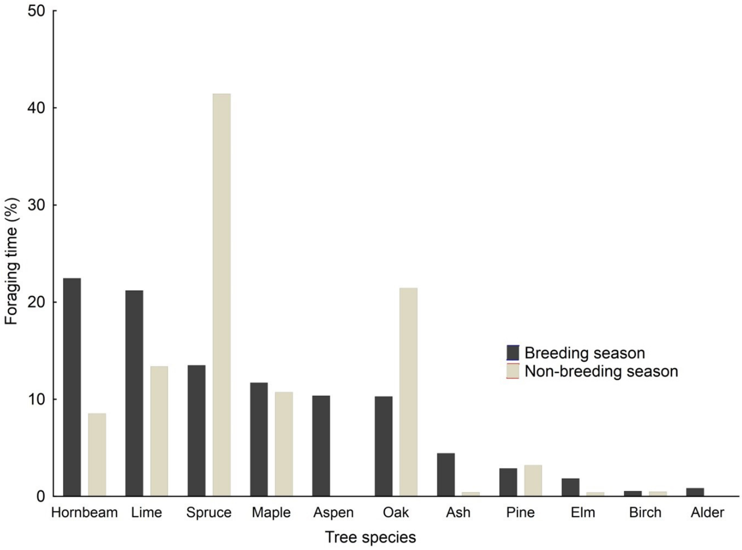

Fig. 1. Percentage of foraging time of the Great Spotted Woodpecker on particular tree species in breeding and non-breeding seasons. Sample size is 382 for breeding season and 123 for non-breeding season. Only observations on standing trees were included whereas observations of foraging on hornbeam and conifer seeds were excluded.

Table 2. Tree species used during foraging by the Great Spotted Woodpecker in relation to their availability. Only observations on standing trees were included whereas observations of foraging on hornbeam seeds and conifer seeds were excluded. A tree is "preferred" when its selection index is significantly greater than 1, and "avoided" when its selection index is significantly lower than 1. A selection index is statistically significant if the confidence limits (CL) do not contain the value of 1.

Tree species	Resources (no. of trees)	Breeding season		Non-breeding season	
		No. of visits	Selection index with 95% CL	No. of visits	Selection index with 95% CL
Hornbeam	4004	101	0.73 (0.57–0.90)	23	0.52 (0.27–0.77)
Lime	4299	86	0.58 (0.44–0.73)	10	0.21 (0.05–0.37)
Spruce	1270	48	1.10 (0.71–1.49)	42	2.99 (2.04–3.94)
Oak	208	42	5.88 (3.65–8.12)	27	11.74 (6.67–16.82)
Maple	342	45	3.83 (2.43–5.23)	13	3.44 (1.15–5.73)
Ash	93	5	1.57 (0.00–3.38)	2	1.95 (0.00–5.41)
Elm	298	17	1.66 (0.63–2.69)	2	0.61 (0.00–1.69)
Aspen	54	30	16.19 (8.78–23.59)	–	
Birch	24	2	2.43 (0.00–6.90)	1	3.77 (0.00–13.31)
Alder	7	4	16.65 (0.00–38.26)	–	
Pine	43	2	1.36 (0.00–3.85)	3	6.31 (0.00–15.46)
Other	487				
Alive	10439	327	0.91 (0.88–0.95)	79	0.68 (0.59–0.78)
Dead	690	55	2.32 (1.75–2.89)	44	5.77 (4.40–7.14)

whereas in the non-breeding season the woodpecker foraged most of the time on the thickest trees (Table 3). Generally, trees selected during foraging in the non-breeding season had a larger DBH compared to trees used in the breeding season, however, no differences were found between both seasons in the case of individual tree species (Table 4, Fig. 2).

3.2. Foraging spots on trees

In the breeding season, live parts of trees were used about twice as often as dead parts, while the result was the opposite for the non-breeding season (Table 3), and the difference between the seasons was significant (G=34.55, df=1, p<0.001). During the breeding season, *D. major* used tree trunks more often than branches, in contrast to the non-breeding season when branches were the dominant foraging sites (Table 3). The seasons differed significantly in this respect (G=57.35, df=1, p<0.001). In the breeding season, foraging sites on different thickness classes were used with similar intensity, whereas in the non-breeding season, more than 75% of the foraging time was spent on sites of <15 cm thick, and the thickest spot was used for a very short time (Table 3). The distribution of the observed foraging time across diameter classes differed between the seasons (G=35.44, df=2, p<0.001). The foraging time of *D. major* was quite evenly distributed among the sites in different height classes in the breeding season, whereas the percentage of foraging time in the non-breeding season increased with increasing height of foraging sites (Table 3). The difference between the seasons was significant in this respect (G=68.29, df=4, p<0.001).

3.3. Foraging techniques

Searching for food and gleaning it from the tree surface or ground was the most common foraging technique in the breeding season. However, the most time-consuming foraging technique of woodpeckers was the extraction of seeds from Norway spruce cones (about 36% of their total foraging time). In the non-breeding season, these seeds became the primary food and the foraging time spent on them doubled. Hornbeam seeds were another important component of the woodpecker's diet in the non-breeding season (Table 5). Foraging techniques significantly differed between the seasons (G=60.62, df=5, p<0.001).

We also found that the percentage of foraging time spent on Norway spruce seeds in the non-breeding season was significantly positively correlated with the index of spruce seed production (Spearman rank correlation r=0.93, p<0.001, n=9). During periods when spruce trees produced many cones, the woodpecker foraged exclusively or almost exclusively on seeds of this tree species (Fig. 3).

4. Discussion

Our results showed that both foraging sites as well as foraging techniques of the Great Spotted Woodpecker differed during the breeding and non-breeding seasons. In the breeding season, this woodpecker mainly collected food of animal origin, however, food of plant origin also contributed to its diet. In the non-breeding season, however, the proportion of time spent collecting food of plant origin more than doubled, with the woodpecker feeding mainly on Norway spruce seeds. It is well documented in the literature that seeds of coniferous trees, mainly Scots pine and Norway spruce are an important component of this woodpecker's diet in winter (Hogstad 1971, Alatalo 1978, Osiejuk 1994, Michalek & Miettinen 2003). Our research showed that the spruce seeds

Table 3. Percentage distribution of foraging time in relation to tree condition, its DBH, condition of used site, part of tree, diameter of used site, and height of foraging above the ground. N = number of sample size. Only observations on standing trees were included whereas observations of foraging on hornbeam seeds and conifer seeds were excluded.

Variable	Breeding season (n=382)	Non-breeding season (n=123)
Tree condition		
Alive	82.20	63.69
Dead	17.80	36.31
Tree size class (DBH)		
<20 cm	7.16	0.59
20-40 cm	33.96	10.19
40-60 cm	28.56	28.66
>60 cm	30.32	60.56
Condition of foraging site		
Alive	67.65	26.77
Dead	32.35	73.23
Part of tree		
Trunk	62.57	12.41
Branch	37.43	87.59
Diameter of foraging site		
<15 cm	39.08	75.14
15-30 cm	33.31	21.35
>30 cm	27.60	3.51
Height of foraging		
<5 m	22.27	0.59
5-10 m	22.16	3.88
10-15 m	20.98	17.40
15-20 m	22.64	25.79
>20 m	11.94	52.33

Table 4. Results of general linear model assessing the effect of tree species (European hornbeam, small-leaved lime, pedunculate oak, Norway spruce and Norway maple) and season (breeding vs. nonbreeding) on the DBH trees used during foraging by the Great Spotted Woodpecker.

Effect	df	F	p
Intercept	1	18383.68	<0.001
Tree species	4	34.71	<0.001
Season	1	29.65	<0.001
Tree species x season	4	1.96	0.100
Error	427		

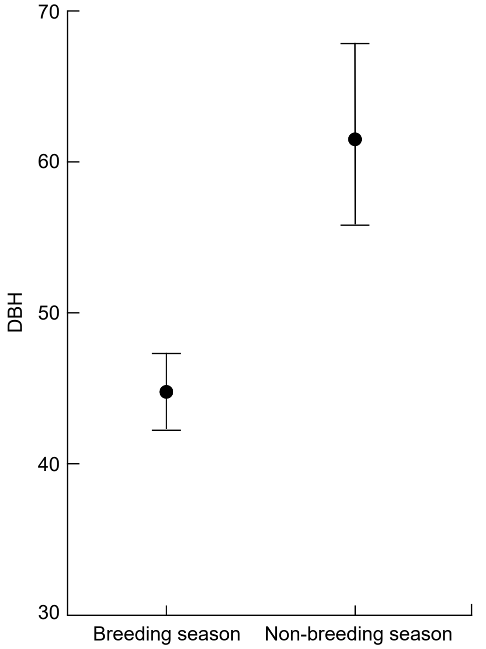

Fig. 2. Diameter at breast height (DBH) of trees used by the Great Spotted Woodpecker during foraging in breeding and non-breeding seasons. Whiskers indicate 95% confidence limits. Only observations on standing trees were included whereas observations of foraging on hornbeam and conifer seeds were excluded.

play a key role for the Great Spotted Woodpecker also in the primeval oak-lime-hornbeam stand of the Białowieża National Park, despite the fact that potential food resources are very diverse due to the high diversity of tree species in this area, supporting a rich invertebrate fauna (Gutowski & Jaroszewicz 2001). In contrast, seeds of Scots pine are rare food of this woodpecker in the study area due to the low abundance of this tree species in oak-lime-hornbeam forest (see Table 2).

Our results further revealed that Norway spruce are also important foraging sites for food of animal origin. Dead wood of Norway spruce is inhabited by many organisms, mainly insects (*e.g.* beetles), which also overwinter in it (Hilszczański 2008, Lõhmus *et al.* 2010). This is the reason why some woodpecker species, such as Three-toed Woodpecker (*Picoides tridactylus*) (Hogstad 1970, Pechacek 2006) or White-backed Woodpecker (*Dendrocopos leucotos*) (Czeszczewik 2009), frequently forage on spruce, but such information is rarely reported for the Great Spotted Woodpecker (Alatalo 1978, Stański 2020).

Searching and gleaning, which were common in the breeding season, were replaced in the non-breeding season by pecking at wood or bark, which resulted in a change of foraging sites. In some periods of the year, usually the colder ones, the number of invertebrates living on the surface of trees becomes low or access to them is difficult (Nicolai 1986, Rolstad & Rolstad 2000, Stańska *et al.* 2018). This forces woodpeckers to change their foraging technique and to search for new sites to collect food. Searching and gleaning are the most effective techniques on parts of trees with cracks and crevices, which provide a suitable habitat for a rich invertebrate fauna (Nicolai 1986). This may explain why, in the breeding season, woodpeckers foraged more frequently on trunks, at low height and at sites with a large diameter. In the non-breeding season, woodpeckers searched for food on higher and mostly dead, not very thick branches, suggesting that such places are rich in invertebrates that live inside the wood. The attractiveness of dead branches for the Great Spotted Woodpecker as foraging sites was also demonstrated by Smith (2007) in forests of England. The significant preference for oak trees by woodpeckers throughout the year can also be explained by the presence of many dead branches, which, combined with their large size and rough bark, makes them an excellent habitat for invertebrates that live both on their surface and inside them (Southwood 1961, Nicolai 1986, Izdebska 2010).

European hornbeam was the most frequently visited tree species by the Great Spotted Woodpecker in the breeding season, which suggests its important role as a site providing food. The low selection index, indicating avoidance of hornbeams, resulted mainly from the high availability of small DBH hornbeam trees. Young, thin hornbeams in BNP oak-lime-hornbeam stands are very abundant, but their smooth bark and hard wood do not make them suitable foraging sites. Older trees, on the other hand, are characterised by thick bark, full of cracks and the presence of branches that break quite easily, resulting in damaged places where the wood is susceptible to rot and decay (Walankiewicz & Czeszczewik 2006). In addition, the number of dead branches

Table 5. Foraging techniques used by the Great Spotted Woodpecker in the breeding and the non-breeding seasons. All observations were included. N = number of sample size.

Foraging technique	Breeding season		Non-breeding season	
	N	% time	N	% time
Searching and gleaning	238	26.75	20	1.00
Pecking of wood	48	10.68	38	5.65
Pecking and scaling of bark	119	20.98	64	7.29
Ringing and sap sucking	10	2.57	2	0.14
Extracting hornbeam seeds	5	2.61	90	12.22
Extracting seeds from cones	87	36.41	280	73.70

increases with increasing DBH of hornbeam trees (Michałowska 2010). Great Spotted Woodpeckers foraged mostly on old, thick hornbeam trees with an average DBH of more than 40 cm, trees which, although quite common, are not as numerous as young trees in BNP primeval stands. Moreover, we found that hornbeam seeds were an important component of the Great Spotted Woodpecker’s diet in the non-breeding season, which is rarely reported from other areas (Löhrl 1972, Jenni 1983). The comparison of trees selected for foraging with trees selected for cavity excavation in the BNP oak-lime-hornbeam forest showed some similarity. *D. major* most often excavated nesting holes in aspen, hornbeam and pedunculated oak (Hebda *et al.* 2017). Two of the latter tree species were also frequently used during foraging, while foraging on aspen was less frequent, but given its low abundance in the stand it was a species strongly preferred as a foraging site. On the other hand, nesting holes were rarely found in Norway spruce and small-leaved lime, which are frequent foraging sites (Hebda *et al.* 2017).

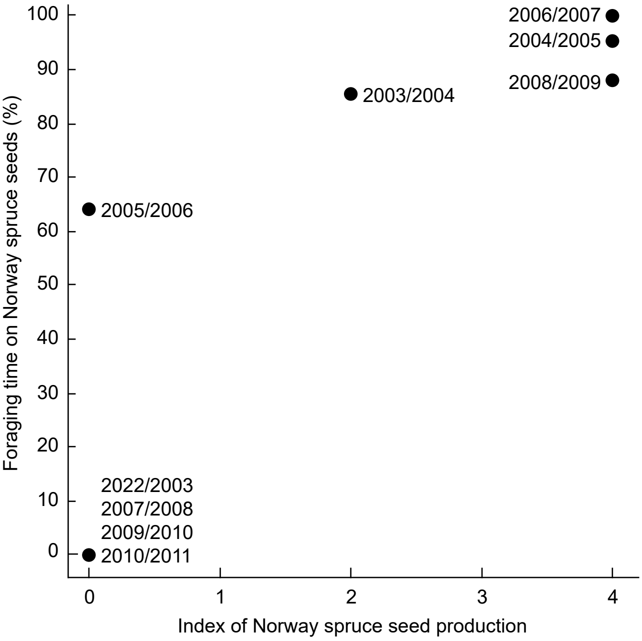

Fig. 3. Percentage of foraging time of the Great Spotted Woodpecker on Norway spruce seeds in non-breeding seasons in relation to index of Norway spruce seeds production. The numbers next to the points represent particular non-breeding seasons. Indices of Norway spruce seeds production based on Wesołowski *et al.* (2015b).

Our results largely agree with those obtained by Jenni (1983), who conducted his study in oak-hornbeam forest near Basel in Switzerland. He found that in winter, the Great Spotted Woodpecker foraged mainly on dead parts of trees (70% of the foraging time) and in upper tree strata, whereas in April, May and June it foraged on lower levels and the use of dead substrates decreased to 40%. The similarity also applied to the foraging techniques used – pecking was used throughout the year, while gleaning was used only in warmer months. The author also revealed a strong preference by woodpeckers for oaks in winter. However, in contrast to our results, tree seeds in his research were not important to *D. major* in winter.

In the same area, Stański *et al.* (2021b) conducted analogous studies on the Middle Spotted Woodpecker (*Leiopicus medius*), which allows us to compare the foraging sites selected by both woodpecker species. In general, they foraged on specific tree species with similar intensity – hornbeam was the most visited tree species in the breeding season, but in the non-breeding season the use of this tree species decreased, while the use of Norway spruce increased. Moreover, the most preferred tree species by both woodpecker species as foraging sites in both seasons was pedunculate oak. In addition, both the Middle- and the Great Spotted Woodpecker in the non-breeding season clearly preferred foraging on trees with a large diameter. However, unlike *D. major*, parameters of foraging spots and foraging techniques used by *L. medius* were similar in both seasons (Stański *et al.* 2021b).

Our study had some limitations. Firstly, data from the whole study period were pooled and analysed only in the seasonal aspect (breeding and non-breeding seasons). The aspect of year-to-year variation in foraging sites and techniques used was omitted from the analysis due to the small number of records collected in some years. The availability of food that the Great Spotted Woodpecker feeds on varies considerably from year to year (Wesołowski & Rowiński 2006, Wesołowski *et al.* 2015b), so both preferred sites and foraging techniques can differ every year. In addition, weather conditions can also vary from year to year which can affect how and where woodpeckers forage (*e.g.* snow cover can make access to food difficult). We suggest that future studies should include the aspect of year-to-year variation in *D. major* foraging, taking both food abundance and weather conditions into account.

Many previous studies have shown the strict positive relationship between dead wood resources and the abundance of bird communities including woodpeckers (Kouki & Väänänen 2000, Walankiewicz *et al.* 2002, Lõhmus *et al.* 2010, Czeszczewik *et al.* 2013). However, intensive forest management, including the removal of dead or decaying trees caused dead wood to become a highly limited resource, which translated to the decline both in the number of woodpeckers and their species richness in many areas (Angelstam & Mikusiński 1994, Bütler *et al.* 2004, Czeszczewik & Walankiewicz 2006). In spite of the great role of dead trees and dead branches, studies highlighting their role as foraging sites usually involve specialized woodpecker species such as the White-backed woodpecker and the Three-toed woodpecker (*e.g.* Pechacek 2006, Czeszczewik 2009). In contrast, our finding clearly showed that dead wood is important as a foraging site even for such a common and omnivorous species as the Great Spotted Woodpecker, which proves the necessity of maintaining sufficient amounts of dead wood in commercial forests rather than removing it, as is usually done. Furthermore, the seasonal variation in foraging sites and foraging techniques of *D. major* suggests that a diverse stand structure may be potentially beneficial not only for the species studied, but also for other woodpecker species. The results of our study can be applied in forest management carried out both in the Białowieża Forest and other forests.

In conclusion, our study showed, that the foraging behaviour of the Great Spotted Woodpecker differed significantly between the two seasons in all the analysed aspects. Although the food of animal origin dominated in the woodpeckers' diet in the breeding season, food of plant origin also had a substantial share. In the non-breeding season, Norway spruce was the most important tree species, where *D. major* obtained food, mainly in the form of seeds, extracted from cones. When considering food of animal origin, large-diameter sites located on trunks and at low height were used most frequently in the breeding season. In the non-breeding season, on the other hand, the studied woodpecker most often collected food on upper dead branches.

Födosöksbeteende hos större hackspett (*Dendrocopos major*) i Białowieża National Park under och mellan häckningssäsongerna

Trots att den större hackspetten är den vanligaste hackspetten i Europa finns det inga studier om dess födosöksbeteende under och mellan häckningssäsongerna. I vår undersökning, som utfördes i en orörd ek-lind-avenbok skog i Bialowieża nationalpark under 1999–2011, studerade vi födosöksplatser och -tekniker som arten använder under och mellan häckningssäsongerna. Större hackspetten sökte sin föda främst i stående träd medan de använde liggande träd endast sporadiskt och uteslutande under häckningssäsongen. Avenbok (*Carpinus betulus*) och lind (*Tilia cordata*) användes mest vid födosök under häckningssäsongen, medan gran (*Picea abies*) och ek (*Quescus robur*) användes mest mellan häckningssäsongerna. Hackspettarna sökte oftare föda i stora döda träd utanför häckningssäsongen. Under häckningssäsongen samlade hackspettarna föda främst från levande substrat på grova stammar på låg höjd, medan de främst använde kvistar högre upp på tunnare, döda träd mellan häckningssäsongerna. Födosökande och samlande av föda från trädens ytor användes främst som teknik under häckningssäsongen, medan dissekering av kottar dominerade mellan häckningssäsongerna. Födosökstiden som hackspettarna använde för att dissekera kottar korrelerade positivt med granens fröproduktionsindex. Vår undersökning visar att födosöksbeteende hos större hackspett skiljer sig märkbart på grund av förändringar i födoresursernas tillgänglighet.

Acknowledgements. We would like to thank the late Dr. hab. Wiesław Walankiewicz, for his considerable help in data collection and inspiration, that made this work possible.

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The Mistle Thrush (*Turdus viscivorus*) in a production forestry context: A territory mapping study

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Received 14 July 2022, accepted 25 January 2023

In Northern Europe, the Mistle Thrush (*Turdus viscivorus*) is a relatively poorly studied species inhabiting forested landscapes where it has historically experienced population declines. Those declines have been attributed to the spread of intensive forest management; yet, the populations have stabilized or increased in recent decades. To distinguish the main forestry impacts on its breeding numbers and distribution, a multiple-visit territory-mapping study was carried out over 15 km^2 of production forest landscape in Estonia. At the landscape scale, the breeding distribution was concentrated to conifer forests on bog peat where the densities were five times higher than in other conifer forests and (at least) ten times higher than in non-conifer forests. This reveals a broad distribution pattern where high-density (core) habitats only host a small fraction of the total population; their relative contribution to the recruitment remains unknown. At the breeding territory scale (within 150 m from a nest), Mistle Thrushes avoided recent clear-cuts and preferred larger areas of old stands more than expected from the distribution of suitable stands for nesting. This indicated that, in a short term, clear-cutting reduces nesting habitats of this species disproportionately more than expected from the cut area alone; this is in accordance with the documented 20th century declines of the species in Fennoscandia. The relationship with forestry drainage is more complicated, however, due to delayed effects and covariation with the main breeding habitat. The basic ecology of the species in conifer forest-wetland landscapes, which are subjected to management pressures, warrants future studies and might provide general insights into the dynamics and functioning of these ecosystems.

1. Introduction

Among the Palaearctic thrush species, the Mistle Thrush (*Turdus viscivorus*) has remained relatively poorly studied, although its status has repeatedly raised broader ecological questions. Thus, while it was formerly known as an elusive bird of old conifer forests, it spread to the West-European countryside and urban settlements in the 19th to 20th century (*e.g.*, Peus 1958, Snow 1969). That spread has recently reversed to a partial decline, at least in the British countryside where the Mistle Thrush is becoming confined to urban areas (Mason 2000). During approximately the same time period, the populations in boreal forests declined – but then partly recovered – along with the transformation of near-natural landscapes into production forest. For example, the Finnish Mistle Thrush population declined 2.5-fold between 1945 and 1975, which was attributed to the extensive logging of old stands (Järvinen *et al.* 1977). It has not been explained why this decline was followed by an increase and stabilization (Fraixedas *et al.* 2015).

Despite such intriguing trends and a general understanding of the breeding biology of the Mistle Thrush, its actual breeding densities and their variation across landscape gradients and transformation have been rarely measured. At least in Northern Europe, a challenge is posed by the mobility of the species within its home range, so that single-detection based counts in small plots or narrow strips (*i.e.*, point counts and transect counts) are of uncertain reliability (*e.g.*, Kuus 2018). In turn, multiple-visit territory mapping techniques are laborious at the landscape scale; in European forest birds, these have been used mostly for plot-scale assessment (Mikusiński *et al.* 2018). Thus, actual landscape distributions of breeding Mistle Thrushes based on comprehensive surveys are better documented for the West-European countryside (*e.g.*, Mason 2000, Vowinkel 2009) than in the North-European forest landscapes.

In this paper, I describe a breeding population of Mistle Thrushes in a production forest landscape in Eastern Estonia. The Estonian forests constitute a heterogeneous transition between the boreal (conifer) and temperate (broad-leaved) forest zones, with a strong ecological imprint of clear-cutting based forestry since the 19th century (*e.g.*, Lõhmus *et al.* 2004, 2016). In the second half of the 20th century, this was accompanied by an ecologically controversial expansion of forest land due to broad-scale draining of mires. In these landscape mixtures, Mistle Thrushes are mostly found in Scots pine (*Pinus sylvestris*) dominated stands, but reliable density estimates and an understanding of the forestry pressures are missing (Kuus 2018).

To fill these gaps, I mapped breeding Mistle Thrushes on a large transformed forest landscape, which included drained mires increasingly integrated into the even-aged silvicultural system. I specifically ask how the Mistle Thrushes are distributed in relation to clear-cutting and drainage, which are changing the age structure, landscape pattern, and tree-species composition of the forests.

2. Material and methods

2.1. Study area and field methods

The analyses are based on territory centres (ideally, nests) mapped at the landscape scale using multiple-visit surveys. All the field work, data interpretation and analysis were performed by the author.

The study area was situated in East Estonia, along River Ahja (Fig. 1). The total area was 1473 ha, including 1197 (81%) of forest land that was almost entirely managed for timber production using clear-cutting based approaches. The management exceptions were *ca.* 10 ha of key habitats recently protected in state forests, and some private forests, the owners of which were not focused on timber-related income. In Estonia, typical timber harvest rotations range from *ca.* 60 years in deciduous or mixed stands on the most productive sites to *ca*. 120 years in pine forests on the poorest soils; this produces an unbalanced site type representation within stand age classes.

The landscape included several bog areas embedded in the forest (Fig. 1), which had been densely ditched in the 1960s; the drainage systems were renovated again in the 2010s. The total area of those bogs (ombrotrophic and mixotrophic combined) was 353 ha (23% of the total) and no open bog remained at the time of the study: 273 ha was categorized as 'forest' on the Estonian base map and the rest was transitional wooded bog. The woodland cover of the bogs was mostly Scots pine; the pine was also more common than Norway spruce (*Picea abies*) in other conifer forests outside the bogs (824 ha). In contrast, the spruce was more common in mixtures with deciduous trees on productive soils.

The study area was surveyed in three adjacent parts (Fig. 1). The central part (413 ha) was mapped in each year, 2020–2022; an analysis of its total breeding bird assemblage in 2020 has been published (Lõhmus 2020). The northern area

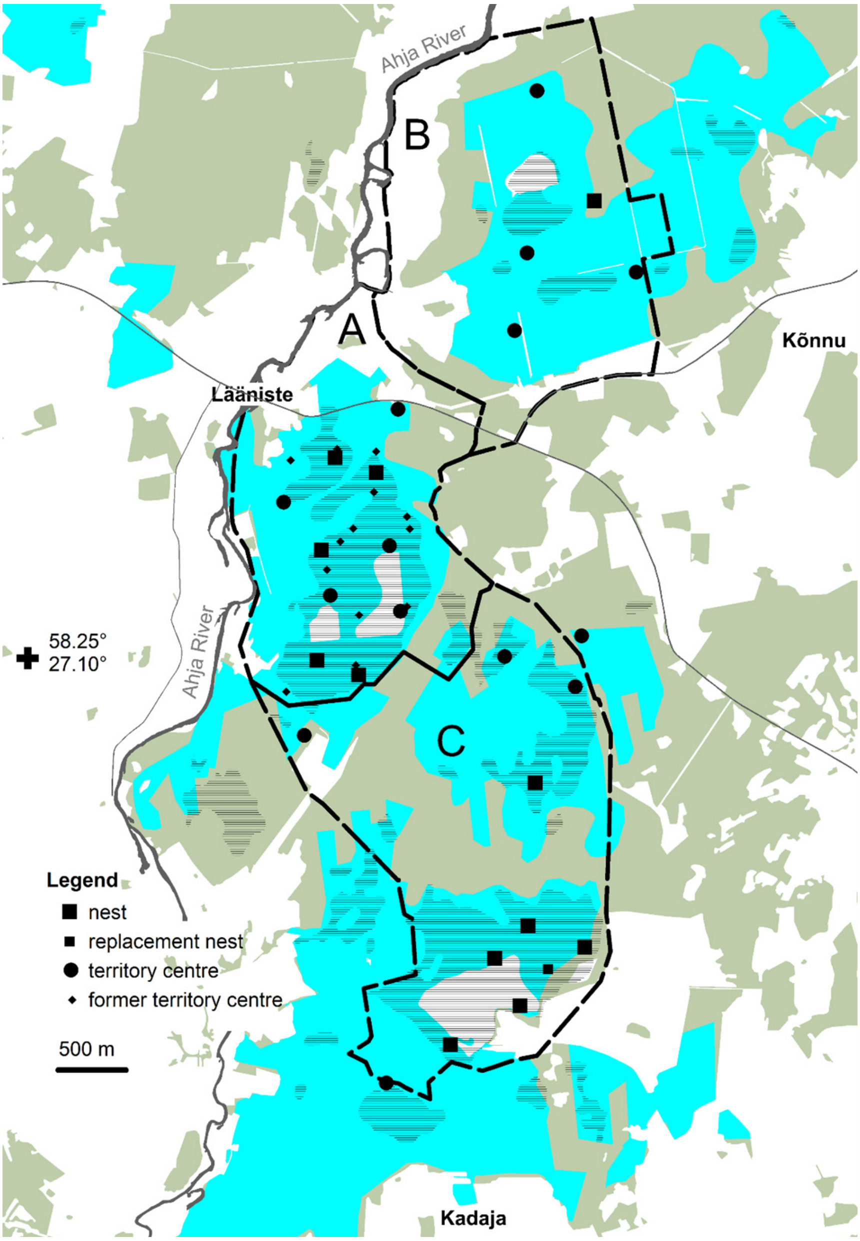

Fig. 1. The study areas and breeding territory distribution of *Turdus viscivorus* in three adjacent East-Estonian landscapes. For the area A, the large symbols depict 2022 results; the small symbols are from 2020–2021. For the areas B and C, the symbols refer to years 2021 and 2022, respectively. The coloured areas are forests, with conifer forests (source: CORINE 2018 land cover) distinguished in blue colour and bog areas shaded (Fibric and Hemic Histosols; source: Estonian soil map).

(483 ha) was only mapped in 2021 and the southern area (576 ha) in 2022. The basic method was a multiple-survey mapping of all breeding birds based on conventional techniques (Tomiałojć 1980) with an average 7–8 visits from mid-April to late June. Specifically, in the Mistle Thrush, this was accompanied by nest searching also after the nesting season, which allowed to roughly

establish survey effectiveness. Thus, in two years in the central area, six pairs were detected in the basic surveys and one pair was added after re-interpretation of the nests found (Lõhmus 2022a). Also, each landscape was briefly visited in late March and early April to detect early presence of singing birds. For the paper, those additional observations and nest records have been included, and I consider total survey errors exceeding 10% unlikely in any landscape.

I followed conservative rules when assigning territories because Mistle Thrushes can be highly mobile even during a single survey, its spring migration partly overlaps with the early breeding season, and there is uncertainty about the presence of second clutches in Estonia (see below). Thus, without nests or simultaneous observations, I did not consider inter-observation distances <300 m sufficient for distinguishing territories even if these seemed to form separate clusters. Most recorded territories were eventually based on at least 4–5 observations, the type and spatial arrangement of which was used to assign a territory (activity) centre when no nest was found.

2.2. Data processing

All the observations and territory delineations were digitalized in a geographical information system. The subsequent map analysis was performed at two spatial scales, using MapInfo Professional version 10.5 (Pitney Bowes Software Inc. 2010) and publicly available data sources. In the case of recent forest management operations, the latter were updated based on my field records.

2.2.1. Landscape-scale distribution

A landscape-scale assessment was based on breeding densities (no. of nests and territory centres) among some major land cover types, replicated among the three study area parts (Fig. 1). For the central part, I only used the last (2022) field mapping. The aim of the assessment was to characterize broad density variation of the species by land cover classes across the landscape. Based on the species' biology, I distinguished: (i) 'forests' based on the Estonian 1:10,000 basic map provided by the Land Board (accessible at https://geoportaal.maaamet.ee); on this map, clear-cuts, forest rides and small forest roads are included in the forest area; (ii) 'coniferous forests' as the overlap of forests and the relevant land cover type (312) of the CORINE Land Cover 2018 map (accessible at https://land.copernicus.eu); (iii) bog areas based on the Estonian soil map (provided by the Land Board) as Fibric Histosol (ombrotrophic bog) or Hemic Histosol areas (mixotrophic bog). This assessment was obviously constrained by the actual areas mapped (sample sizes; presence and configuration of certain land cover types). Thus it could not be fully formalized beforehand – it is rather a post-hoc interpretation of the distribution map, which should be tested elsewhere.

2.2.2. Nest-site preferences

At a smaller scale, I compared clearcutting- and drainage-related variables within 150 m radius around 22 Mistle Thrush nests and accompanying background points. The analysis was based on nests only because of the uncertainty of the locations of those territory centres, which are based solely on observations of singing or calling birds (Lõhmus 2022a). Also, although repeated observations can roughly indicate territory borders, such delineation is unreliable due to multiple sources of error. The 150-m radius approaches half of the shortest observed nearest neighbour distances as recorded in the central and southern areas where I had multiple nest founds. From the nests of different years in the same area, I also included only those that were at least 150 m apart or in another forest stand.

Because the nest-site analysis aimed at complementing the landscape analysis, each background point location was restricted to a site similar to the nest in terms of its broad habitat type. The locations were established through the same procedure: the point closest to 300 m (but no less) and to a cardinal direction in a potentially suitable stand and at least 300 m away from any other nest or background point. 'Potentially suitable stand' was defined as of the same broad land cover class (conifer on peatland; other conifer; non-conifer; wooded mire) and at least

90% of the age of the actual nest stand. In the case of multiple options, I selected the location away from the plots selected for other nests. Overall, it was a conservative approach to habitat selectivity, since at least two background points were situated close to probable territory centres where the nests had not been found.

In a 150-m circle (7 ha) surrounding each nest or background point, I analyzed the age structure of surrounding forest stands, the total length of the ditch network (including straightened streams) and distance to the nearest ditch using SQL queries and the Distance Calculator tool of the MapInfo software. The age structure was expressed as the relative area of four stand-age classes, with post-clearcut open areas (0–15 years of age) and stands above minimum rotation age (>80 years) as extremes, and approximate end of self-thinning (*ca.* 40 years) distinguishing the two classes in between. Area of wooded mire was initially considered, but omitted from multi-factor analysis due to its strong relationship with the distance to the nearest ditch ($r = 0.71$, $n = 44$, $p < 0.001$). I updated the original stand age data (age of the dominant tree layer in the breeding year) provided by the Estonian Forest Registry with fresh logging data. The ditches were analyzed as revealed on the Estonian base map.

After checking for the collinearity of the measurements (factor variables), I looked for the best logistic model (factor variable subset) for explaining nesting probability, *i.e.*, difference between the nest plots and background plots (binomial dependent variable). The prioritization was based on AICc values of alternative models, which were calculated using the function dredge (MuMIn package; Barton & Barton 2019); factor significance was estimated based on the likelihood ratios. The relationship between the nesting probability and the best explanatory factor variable was plotted using visreg (Breheny & Burchett 2017).

3. Results

3.1. Landscape-scale distribution

In total, I registered 24 Mistle Thrush breeding territories in the landscapes in 2021 (northern part) and 2022 (central and southern part) (Fig. 1). Based on territory centres, the landscape-scale density variation was more than ten-fold in forests: from 0.5 territories km^{-2} in non-conifer forests to 5.5 territories km^{-2} in conifer forests in bogs (Table 1). In the central and southern parts of the area, where the latter (optimal) habitat covered >100 ha, the density estimates were consistent: 6.6 and 5.4 territories km^{-2}, respectively. Outside forests, the Mistle Thrush only inhabited wooded bogs for which my sample was very small – the two pairs recorded in a total of 80 ha provided a tentative estimate 2.5 pairs km^{-2}.

Three shortest nearest-neighbour distances,

Table 1. Recorded breeding densities of the Mistle Thrush by land cover classes and study area part (not shown for <100 ha areas marked with asterisks). See Fig. 1 for the distribution of the pairs on the landscape.

		Territories/km^2 (total no. of territories)				Total area (ha)
	Land cover class	Central	Northern	Southern	Total	
	Total area	2.4 (10)	1.0 (5)	1.6 (9)	1.6 (24)	1472.6
1	Forest land	2.8 (9)	1.4 (5)	1.6 (8)	1.8 (22)	1197.4
1a	Conifer forest	3.4 (9)	1.7 (4)	2.1 (7)	2.4 (20)	824.3
	Non-bog conifer forest	0.7 (1)	1.9 (4)	0 (0)	0.9 (5)	551.4
1b	Non-conifer forest	(0)*	0.8 (1)	0.5 (1)	0.5 (2)	373.1
2	Area on bog soils	6.2 (9)	(0)*	4.5 (8)	4.8 (17)	353.0
2a	Conifer bog forest (1a∩2)	6.6 (8)	(0)*	5.4 (7)	5.5 (15)	272.9
2b	Wooded mire (2–2a)	(1)*	(0)*	(1)*	2.5 (2)	80.1

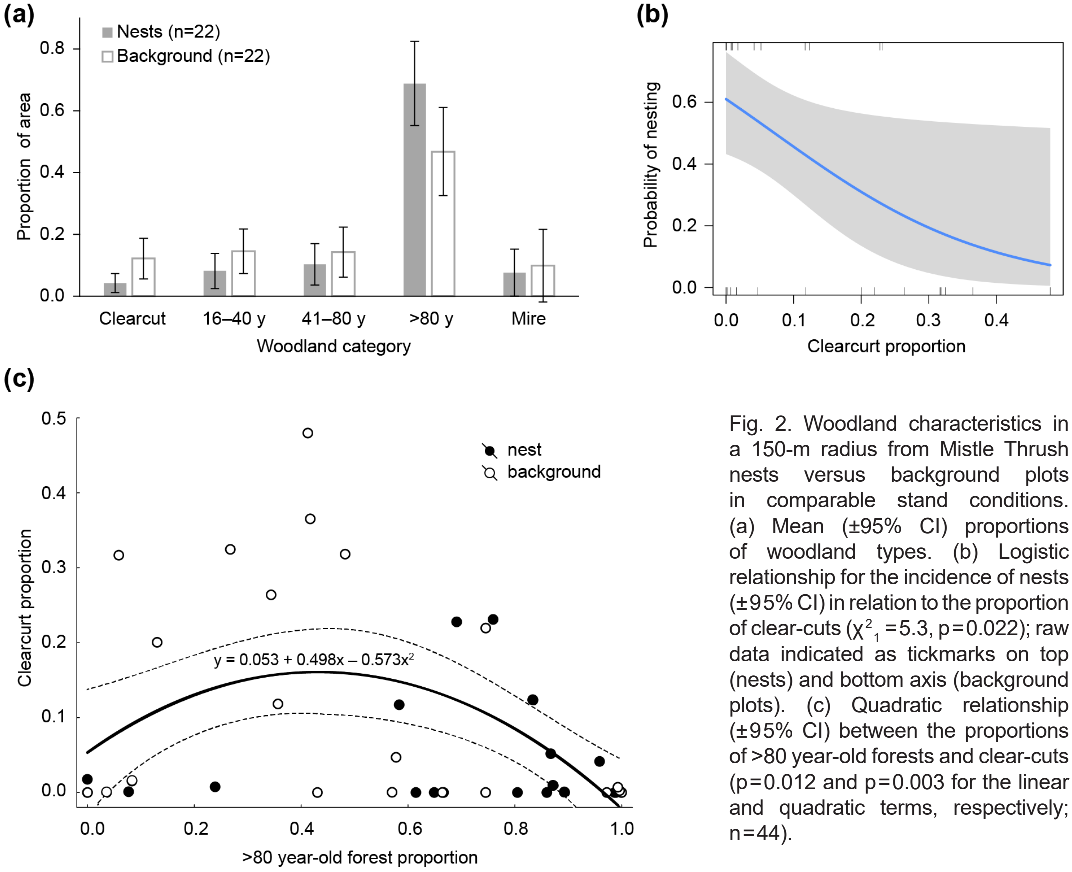

Fig. 2. Woodland characteristics in a 150-m radius from Mistle Thrush nests versus background plots in comparable stand conditions. (a) Mean (±95% CI) proportions of woodland types. (b) Logistic relationship for the incidence of nests (±95% CI) in relation to the proportion of clear-cuts ($\chi^2_1 = 5.3$, $p = 0.022$); raw data indicated as tickmarks on top (nests) and bottom axis (background plots). (c) Quadratic relationship (±95% CI) between the proportions of >80 year-old forests and clear-cuts ($p = 0.012$ and $p = 0.003$ for the linear and quadratic terms, respectively; $n = 44$).

as measured between nests found, were within a range of 300–350 m. Yet, according to the observations, neither defended territories nor foraging areas were located symmetrically around nests.

3.2. Nest sites

Of the 22 found nests that were considered spatially independent data points, only two were situated in non-bog sites. These two were also the only nests in mid-aged stands: a 28 year-old *Vaccinium myrtillus*-type pure pine stand and a 41 year-old drained *Filipendula*-type spruce-pine mixture; both of high productivity (estimated annual increment 10–12 m^3 ha^{-1}; the Estonian site productivity index Ia–I). Among the 20 bog sites, 17 nests were located in drained mixotrophic bog forests, with a mean age 98 ±13 (SD) years (range 83–128 years). Those sites were of variable timber productivity: seven were poor sites (annual increment 1.5–2.9 m^3 ha^{-1}; productivity index V–Va) and the rest were medium-productivity sites (2.7–4.9 m^3 ha^{-1}; III–IV). Finally, three nests were at the edges of the wooded ombrotrophic bog of the southern area, no more than 50 m from what was categorized as bog forest (age range 106–119 years) on the base map.

There was only one active nest that was apparently a replacement clutch after the first clutch was lost early in the breeding season. I obtained no evidence of 2nd broods but, in some breeding territories, the males were heard actively singing in late June. The nests themselves were distinct from those of the other thrush species in the area, for they were abundantly camouflaged with fruticose and pendulous lichens. Another peculiarity was frequent nesting in drained pine bogs on suppressed (smaller) dead pines and pine stumps, 3.4 ±1.5 (SD) m from the ground

Table 2. The most informative logistic regression models (ΔAICc < 2; no. 1–5) distinguishing Mistle Thrush nest plots (n=22) from otherwise similar background stands (n=22). Model p-values are based on log-likelihood (LL) differences from the null model (0; no fixed variables).

Model no.	Parameter estimates					Model performance		
	Intercept	Relative forest area within 150 m			Distance to ditch (m)	LL (df)	AIC$_c$	p
		Clearcut	>80 yr	16–40 yr				
0	0.00					–30.5 (1)	63.1	
1	–0.59	–5.360	1.679			–26.3 (3)	59.2	0.015
2	0.83	–6.511		–3.231		–26.6 (3)	59.9	0.021
3	0.45	–6.247				–27.9 (2)	60.0	0.022
4	–1.21		2.061			–28.0 (2)	60.3	0.025
5	–2.19		2.950		0.009	–27.0 (3)	60.8	0.033

(nine nests), which were prone to fall either due to heavy lean or partly rotten base (Fig. S1 in the online only supplementary materials). Twelve nests were on live pines, with a mean diameter at breast height 23.6 ±6.2 cm, at height 5.9 ±2.2 m from the ground. One nest was on a live birch and one on a live spruce.

Woodland areas within 150 m from nests contained less clearcut and more old-forest area than background plots in otherwise similar stands (Fig. 2). Their univariate relationships also comprised two of the best five logistic regression models (within ΔAICc<2); the overall top model was based on both of these factors (each contributing at $p<0.1$; likelihood-ratio test); and one of these was alternatively present in each of the two remaining top models (Table 2). Accounting for the (non-linear) relationship between these two main factors revealed that the thrushes tolerated some clear-cut area around nest only at simultaneously high proportion of old forest (Fig. 2c). The only other effects included in the top models, each once, were a negative relationship with the area of 16–40 year-old stands (combined with the area of clear-cuts) and a positive relationship with the distance to the nearest ditch (combined with the area of old stands). The total length of the ditch network did not contribute to the top models.

For the area of >80 year-old stands (the main and preferred nesting habitat), the factor collinearity analysis revealed two ecologically notable patterns. (i) This variable had a stronger negative relationship with the area of mires (omitted from the multi-factor modelling) among the nest plots ($r=-0.53$, $n=22$, $p=0.011$) than among the background plots ($r=-0.38$, $n=22$, $p=0.080$). (ii) The >80 year-old stands were generally situated in more densely drained parts of the landscape, as their areas in background plots were larger where ditches were closer ($r=-0.44$, $n=22$, $p=0.040$). However, that relationship was even clearer in the nest plots ($r=-0.70$, $n=22$, $p<0.001$). A similar contrast was seen for the old-forest correlation with the density of the ditch network ($r=0.12$, p=n.s. and $r=0.50$, $p=0.018$, respectively).

4. Discussion

In the Estonian production forest landscape, Mistle Thrushes were nesting in habitats vulnerable to intensive forest management. The specific patterns detected were: (i) the importance of old pine-dominated bog forests and (ii) avoidance of adjacent clear-cuts, while (iii) no direct negative influence of the forestry drainage was detected. Instead, (iv) the drainage systems co-varied with the nesting areas on the landscape and their vicinity was specifically preferred by the thrush. Thus, the short-term effect of the bog drainage on this species is positive and can create high-density patches (see below). The mechanisms involved may be the functioning of ditch banks as foraging grounds and better shade provided by the denser post-drainage stand. Independent data supporting this hypothesis comes from a Finnish mire restoration study where the species was absent in pristine areas, but several pairs were found in degraded areas, also in a short time perspective after restoration (Alsila *et al.* 2021).

However, those positive forestry drainage impacts are probably partly transient, which introduces instability and uncertainty to the Mistle Thrush population dynamics. First, during the first decades after bog drainage, the overgrown open areas do not yet provide nesting habitat and may lose some value as foraging grounds. This is supported by a Finnish landscape-scale survey where any possible positive drainage effects were far outweighed by negative clear-cutting effects on this species (Väisänen & Rauhala 1983). Also, my study confirmed that the clear-cutting effects extend beyond the area logged and are pronounced within at least the 150 m distance measured. Both these effects are also plausible for explaining the large historical decline of the Fennoscandian populations (Järvinen *et al.* 1977). Secondly, long-drained pine mires on more fertile soils typically undergo an irreversible regime shift after clear-cutting, transforming these into spruce-deciduous mixtures on decayed peat (Lõhmus *et al.* 2015). Such transformation-prone sites formed half of all the nest sites on bog soils in my study. Their perspective is to be lost as nesting habitat for the species during the coming decades.

Such ecological characteristics of the Estonian breeding population of the Mistle Thrush are clearly closer to its conspecifics in Fennoscandia than those in West Europe (see also Introduction). How exactly the coniferous and bog habitats shape its ecology in North Europe is still poorly known. Apparently, the Mistle Thrush has a distinct diet there. A study in different biomes in European Russia distinguished large beetles as the main prey in the breeding season, with minor shares of large moths and other insects (Prokofyeva 2006). In Estonia, pine-dominated production forests on mineral land are not poorer than other forest types in such insect biomass, but calcium availability (snails) may be limiting birds there (Rosenvald *et al.* 2011). However, the food base in (drained) bog forests has not been specifically studied. According to my observations, Mistle Thrushes often forage on ground in clearcuts and thinned forests, particularly since the second half of the breeding period. Its breeding performance in (hemi)boreal bogs and conifer forests may be thus limited by early-season conditions, which may be further linked to why second clutches are rare (not confirmed by me; mentioned as likely by Rootsmäe & Veroman 1974). For comparison, Blackbirds (*Turdus merula*) in the same study landscape (but nesting in much more productive sites) usually had two and, rarely, even three clutches (Lõhmus 2022a).

In terms of population distribution, my key finding was that conifer forests on bog peat had Mistle Thrush densities five times higher than other conifer forests and (at least) ten times higher than non-conifer forests. Such unequal distribution is supported by some other Estonian surveys (unfortunately based on small samples). Thus, my estimate 5.5 pairs/km^2 for drained bog forest is close to the 5 pairs/km^2 in similar forests in south-western Estonia (Kiis 2020). The estimate 0.9 pairs/km^2 for non-bog conifer forests matches a line-transect estimate in Hiiumaa Island (Väli & Laurits 2006). At the landscape scale, a line transect study suggested 2,200 pairs in the forest-rich Pärnu county, Southwest Estonia (Ellermaa 2003), which has 831 km^2 of conifer forest (as defined in the current study). At 2.4 pairs/km^2, the latter implies *ca.* 2,000 pairs in conifer forests (and perhaps 3,000 pairs altogether) – estimates reasonably close to Ellermaa's (2003).

Extrapolating these habitat-specific densities all over Estonia indicates that only a small proportion of Mistle Thrushes currently nest in distinct high-density habitats. Thus, conifer forests on bog peat cover only *ca.* 760 km^2 (*ca.* 4000 pairs), while other conifer forests encompass at least 6,700 km^2 (> 6,000 pairs?) and non-conifer forests *ca.* 16,000 km^2. Adding transitional wooded mires, where local densities probably vary much, supports the current national population assessment, 15,000–25,000 pairs (Kuus 2018). High-density habitats might provide *ca.* 20% of this. It is not clear how common such ratio might be in this species or in other bird species with sparse distributions (Bernstein *et al.* 1991), and what is the share of recruitment of the Mistle Thrush in the high-density habitats (*cf.* Johnson 2007). For example, in Poland, the species remains by far the most fragmentation prone thrush species (minimum forest size needed estimated at 25 ha;

Cieslak 1991), but its breeding densities are much more stable throughout pine-forest succession after 30 years of age (Zawadzka *et al.* 2018) than in my study. Again, the reason of weaker stand-age dependence is unclear but it may be related to a more abundant prey base at southern latitudes. Weaker food limitation, accompanied with higher reproduction rates (multiple clutches), may have also supported the historical adaptation of the southern populations to landscape transformation.

In conclusion, northern populations of the Mistle Thrush constitute an interesting model of species responses to the two regionally dominant forestry-related drivers of the landscape change – logging and artificial drainage. Even in this simple system, their impacts on populations are not independent and straightforward, particularly over longer (decadal) time frames. While peatland drainage can support high-density habitats for the Mistle Thrush for many decades, these can be irreversibly lost later. In contrast, logging may cause rapid habitat loss, but the dynamics may reveal alternative outcomes after 30–40 years depending on the silvicultural focus on conifer species, rotation lengths, and the set-aside system. Understanding the mechanisms and rates of such population responses can significantly improve the current assemblage-scale models of those changes (Lõhmus 2022b).

Kartläggning av dubbeltrastens (*Turdus viscivorus*) revir i ett skogsbrukslandskap

I norra Europa är dubbeltrasten (*Turdus viscivorus*) en relativt undermåligt studerad art som bor i skogslandskap och vars populationer historiskt sett har minskat. Populationsminskningarna har kopplats till intensifieringen av skogsbruket, men minskningarna har avtagit eller stabiliserats under de senaste årtiondena. För att urskilja skogsbrukets effekter på dubbeltrastens häckande par och deras distribution har jag gjort en revirkartläggningsstudie i en 15 km^2 stor produktionsskog i Estland. På landskapsnivå var häckningsdistributionen koncentrerad till barrskogar på torvmyrar där tätheterna var fem gånger högre än i andra barrskogar och (minst) tio gånger högre än i andra skogstyper. Detta innebär att häckningsdistributionen är bred men där kärnhabitat med höga densiteter bara utgör en en liten del av hela populationen och deras relativa kontribution till rekrytering av nya häckare är fortfarande oklar. På häckningsrevirnivå (inom 150 m från boet) undviker dubbeltrastar kalhyggen och föredrar större områden med äldre trädbestånd mer än vad som förväntas baserat på distributionen av passande bestånd för häckning. Det här innebär att kalhyggen minskar andelen lämpliga häckningsrevir oproportionerligt mycket mer än vad som förväntas baserat på kalhyggets storlek, i enlighet med dokumenterade populationsminskningar i Fennoskandien under 1900-talet. Kopplingen till skogsdikning är mer komplicerad på grund av fördröjningseffekter och samvariation med habitatet i själva häckningsreviret. Fortsatta studier av dubbeltrastens ekologi i barrskogsvåtmarker under olika typer av användningsgrad kan ge generella insikter om dessa ekosystems funktioner och dynamik.

Acknowledgements. The Estonian Environmental Agency provided access to the National Forest Register. Kadri Runnel helped with the procedures in R. Emma Vatka, Patrik Karell and an anonymous reviewer constructively commented on the manuscript. The Estonian Research Council provided financial support (grant PRG1121).

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