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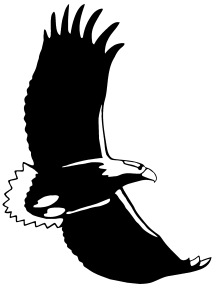

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Bean Goose migration shows a long-term temporal shift to earlier spring, but not to later autumn migration in Finland

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Climate change can challenge the inherited or learned behavioural patterns that were useful in the past. In particular, it may change the spatio-temporal dynamics of migratory behaviour in birds. Here, we explored a 40-year-long time series of Bean Goose (*Anser fabalis*) observations using a citizen science database (tiira.fi – BirdLife Finland) to link the timing of the migration across last forty years and with the large-scale temporal weather fluctuation described by an index of North Atlantic Oscillation (NAO). During 1978–2018, the peak of spring migration of the Bean Goose has advanced approximately a month, whereas the timing of autumn migration has remained more similar across the years. The NAO index was associated only with spring migration. Strong temporal changes of the Bean Goose migration are evident as they adjust their migratory behaviour to changing spring conditions.

1. Introduction

Migration is an adaptation to a seasonally changing environment (Herrera 1978). It is a widespread phenomenon throughout animal kingdom and is known to occur among many taxa such as birds, fish, insects, and mammals (Shaw & Couzin 2013). Migratory birds move between breeding and wintering grounds following availability of recourses (Cox 2010). In the northern hemisphere, where winter weather conditions limit the availability of resources, birds move to lower latitudes in autumn and return when the resources in the north become available again (Newton & Brockie 2008). Spring migration back to breeding areas may increase the breeding success of migrants due to more resources (*i.e.*, food and nest sites) available and possibly less competition in north (Newton & Dale 1996). Generally, similar resource-seeking migratory behaviour among birds is globally widespread and exists in all continents (Newton & Brockie 2008).

Climate change can challenge the inherited or learned behavioural patterns that were useful in the past, such as spatial as well as temporal dynamics of migratory behaviour in birds (Mayor *et al*. 2017). Global warming has shortened the period with cold temperatures in the northern hemisphere (IPCC 2018) and as a consequence, many birds return to their breeding sites earlier and leave to the south later (Saino *et al*. 2011, Kolářová *et al*. 2017, Mayor *et al*. 2017, Usui *et al*. 2017, Nuijten *et al*. 2020). Temperature affects the timing of migration by influencing the availability of resources such as food and water (Newton & Brockie 2008). Also, local weather conditions (*e.g.*, wind, precipitation) impact the timing of migration in birds (Erni *et al*. 2002) and as many species use local weather as a cue to migrate, migration is broadly affected by dynamic high- and low-pressure weather systems along the migration route (Dokter *et al*. 2011).

The ability to respond to changing environmental conditions, however, varies between species (Usui *et al*. 2017). Previous studies have reported the connection between climate change and the migratory behaviour of birds (Saino *et al*. 2011, Usui *et al*. 2017), and especially a trend of advancing spring migration has been recorded in many species (Kolářová *et al*. 2017). Short-distance migrants are usually more responsive to climate change than long-distance migrants (Kolářová *et al*. 2017) because short-distance migrants can follow the changing temperatures while long-distance migrants use more endogenous cues such as circadian rhythm to time their migration (Mayor *et al*. 2017, Usui *et al*. 2017). Population declines have been observed, particularly in migratory birds that do not adapt to increasing spring temperature and advancing phenology (Møller *et al*. 2010). Therefore, information on how well species adapt their migration behaviour on long-term is important for understanding species' adaptability to large-scale environmental changes.

Here, we examined the Bean Goose (*Anser fabalis*) migration timing in Finland using observation data collected in southern Finland over the last 40 years. Bean geese observed in Finland belong to two subspecies, the Taiga Bean Goose (*Anser fabalis fabalis*) and the Tundra Bean Goose (*Anser fabalis rossicus*). Both were included in the study and were not separated in the analysis (as separating them may be unreliable, refer to methods).

The Taiga Bean Goose starts its spring migration in February from the western Baltic Sea region, where most of them winter (Heinicke *et al*. 2018). The birds arrive in Finland between March and May. The Taiga Bean Goose breeds mostly in north-west Russia, northern Sweden, and central and northern areas of Finland (Piironen *et al*. 2022a). The birds coming to breed in Finland or passing through the country migrate across entire Finland. The autumn migration of the Taiga Bean Goose occurs between late August and October.

The Tundra Bean Goose migrates across Finland later than the Taiga Bean Goose both in spring and autumn (Piironen *et al*. 2022b). The spring migration occurs between April and May when the birds migrate through southeast Finland to their main breeding grounds in northern Russia. The autumn migration occurs between late September and October. As migrants of the Bean Goose pass through southern Finland annually, long-term migration observations are valuable to be studied from a temporal perspective from this location.

We set out to answer two questions. Our first research question was whether the timing of the Bean Goose migration has changed between the years 1978–2018. We hypothesized that due to warming climate, the spring migration of the Bean Goose has advanced (*i.e.*, masses arriving earlier) and the timing of the autumn migration delayed, as short-distance migrants have been shown to be able to respond to the prevailing climate conditions (Saino *et al*. 2011). The second research question was whether the large-scale weather conditions, described by North Atlantic Oscillation (NAO), during the migration period are linked to the timing of migration. NAO dictates the climatic conditions in Europe (see further methods; Hurrell 1995) where wintering and breeding grounds of the Bean Goose are mostly located (Piironen *et al*. 2022a, Piironen *et al*. 2022b). Thus, it may indirectly influence the timing of migration (Newton & Dale 1996, Erni *et al*. 2002).

2. Materials and methods

2.1. Long-term migration data

We used data from a citizen science bird observation database Tiira of BirdLife Finland (tiira.fi). Tiira is an online portal where anyone can report their observations. We used all the Bean Goose observations (*i.e.*, *A. f. fabalis* and *A. f. rossicus* were pooled, as identifying them from distance is unreliable) that were made in southern Finland (Kymenlaakso, Southwest Finland, Satakunta, and Uusimaa) between 1.1.1978 and 31.12.2018. We used all the information that is mandatory to report on each observation: date of observation, number of birds observed, location and species. The status of observed birds, *e.g.*, migrating or local, can also be reported but this information is voluntary and not included in all observations. We used all observations, disregarding their status. We assumed the observed birds in our study area in southern Finland to be mostly migrating as their breeding grounds are located further north. This might, however, cause some inaccuracies. If a large group stays in the area for a longer time, it might be observed and counted several times.

Spring and autumn migration periods were processed as separate datasets. Timespan was chosen as 1.1.–30.5. for spring migration and 1.8.–31.12. for autumn migration. We converted calendar dates to Julian dates (DOY, day of year) to make data easier to handle statistically. We decided to include the observations only from southern Finland to reduce the possibility of counting the same individuals more than once along their migration route as they move through Finland. Also, including only the observations from southern Finland prevents counting the birds that have already arrived at their breeding grounds in central or northern Finland. The number of observations was 34,269 in the spring and 13,877 in the autumn. The sum of the birds observed was 3,613,619 in the spring and 678,150 in the autumn. The mean flock size (number of geese in one observation) was 89.1 (SD ± 320). We studied the change in the timing of early, middle, and late phases of migration using dates when 5%, 50%, and 95% of the cumulative sum of migrants was reached (*i.e.*, temporal distribution of masses, rather than early or late observations, Fig. 1).

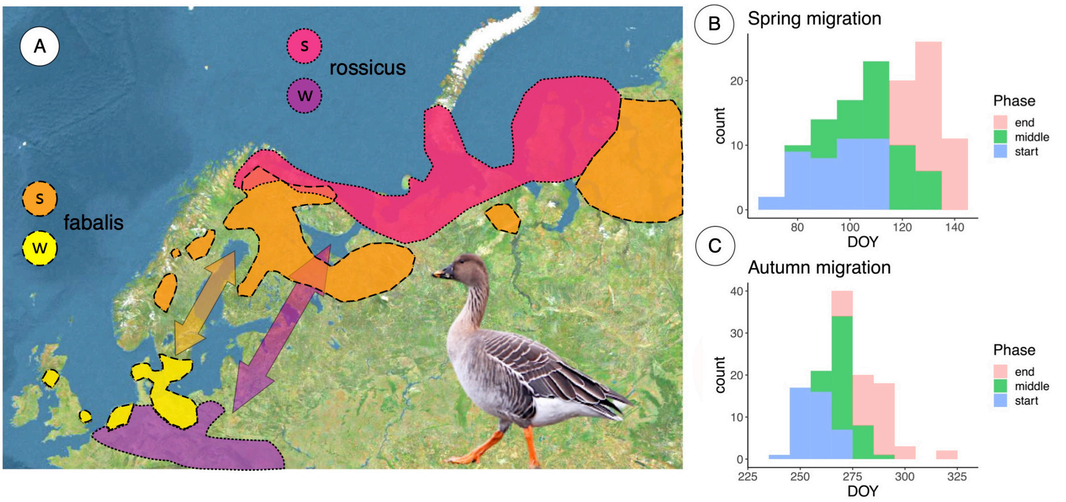

Fig. 1. The western distribution of Bean Goose populations (A). The map is modified for illustrative purposes from Heinicke *et al.* 2018 and should only be considered to highlight the main distribution of the Taiga Bean Goose (*Anser fabalis fabalis*) in comparison to Tundra Bean Goose (*Anser fabalis rossicus*). The map shows summer (s) and winter (w) distributions for *A. f. fabalis* (orange, yellow) and *A. f. rossicus* (pink, purple). Noteworthily, the location of Finland is central to bean goose migration routes (in between the two arrows). In our study however, we focused on both sub-species together, because their separation is not reliable from migrating individuals in our dataset as majority migrates through north Europe. The timing of migration in the data characterized by histogram plots for spring (B) and autumn (C). Analysis included observations from southern Finland (regions Kymenlaakso, Southwest Finland, Satakunta and Uusimaa). The change in the timing of early, middle, and late phases of migration was observed using 5th (start), 50th (middle), and 95th (end) percentiles of the observed migrants, respectively. DOY (here: day of year) refers to Julian days (1.1.= 1). The Taiga Bean Goose (Photo taken on Lista, Norway by Marton Bernsten) image was modified from Wikimedia Commons and used under CC BY-SA 3.0 licence.

Citizen data typically contains weaknesses that may reduce its reliability (Callaghan *et al.* 2019). Data is not collected systematically, and observation effort is usually spatially and temporally unevenly distributed. We studied the timing of migration, and therefore temporal shifts in observation efforts may affect our results. In our analysis, we assumed that the activity of birdwatchers has not changed considerably across the years so that it would have resulted in differential detectability of a large waterfowl, which birdwatchers have been traditionally used to identify. Another weakness in this data is the impossibility of controlling the expertise of the birdwatchers and therefore all the identifications may not be correct. Due to large number of data points, we estimated that the patterns of migration were not substantially impacted by the incorrect observations.

2.2. Large-scale weather conditions

North Atlantic Oscillation (NAO) is a large-scale atmospheric circulation pattern that describes the weather oscillation (*i.e.*, atmospheric pressures, wind directions, precipitation) on the Northern Atlantic Ocean (Hurrell 1995). It is measured by an index that describes the monthly difference in atmospheric pressure at sea level between the Icelandic Low and the Azores High. For example, positive NAO correlates with warm and moist winters in Europe, and negative NAO correlates with cold and dry winters.

We studied the effect of large-scale weather phenomena on long-term migration dynamics by examining the relationships between the timing of migration and the NAO index. We used the daily NAO index to calculate the average NAO for the spring and autumn migration periods for each year. Average NAO between January and May was used for spring migration and average NAO between August and December for autumn migration. Several studies have found a connection between the average NAO index during the migration period and the timing of the migration (Gunnarsson *et al.* 2006, Van Buskirk *et al.* 2009, Kim *et al.* 2015). NAO index we used was provided by the Climate Analysis Section, NCAR, Boulder, USA. Measuring points are in Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland.

2.3. Statistical analyses

We used Pearson product-moment correlation to study the temporal trend in the timing of migration during the last 40 years. We studied the year and early, middle, and late phases of the migration. We used observation date as a response variable and year as a predictor variable.

To study the relation between NAO index and the migratory behaviour of the Bean Goose, we used linear regression. We built models separately for the early, middle, and late phases of migration. We used observation day as a response variable, and year and average NAO as predictor variables.

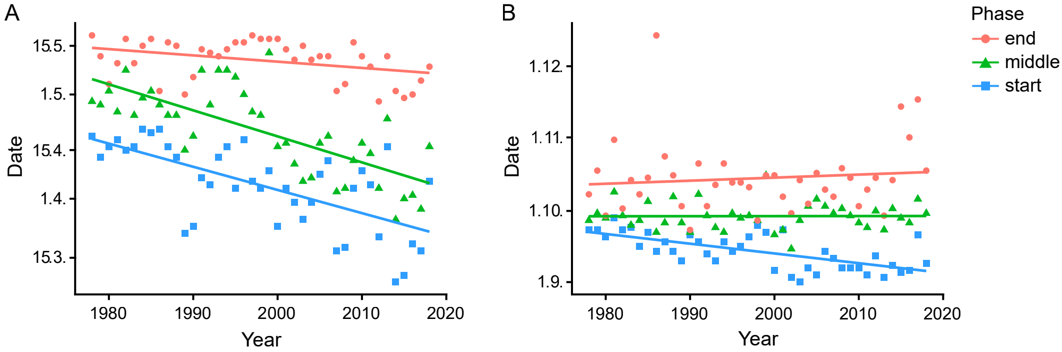

Fig. 2. Bean goose migration shows a long-term shift to earlier spring migration but not to later autumn migration. Relationship of spring (A) and autumn (B) migration dates to the observation year when 5% (start), 50% (middle), and 95% (end) of the cumulative sum of birds had been reached for that year.

We included the year to account for the temporal change in the timing of migration using the regression analysis. All analyses were performed with R program version 4.1.2 (R Core Team 2021).

3. Results

Over the 40-year-long research period the Bean Goose spring migration has advanced in all the phases of migration (Fig. 2A). The change, *i.e.*, days per year, was strongest in the early (r=–0.66, n=41, p<0.001) and middle (r=–0.72, n=41, p<0.001) phases. The timing of migration has also advanced in the latest phase of the migration (r=–0.37, n=41, p=0.02), although much less so. Specifically, the early phase of spring migration has advanced 26 days (p<0.001, SD±4.5), the middle phase has advanced 30 days (p<0.001, SD±4.9) and the late phase has advanced 7 days (p=0.02, SD±2.9). In the spring, NAO index correlated with the early phases of migration (Table 1).

Regarding the autumn migration (Fig. 2B), the timing of autumn migrants had only changed in the early phase (r=–0.66, n=41, p<0.001), by advancing by 17 days (p<0.001, SD±3.3) for the entire 40-year period. A temporal trend of later (or earlier) migration was non-significant for the middle and late phases. In the autumn, NAO index was not found to be associated with the timing of migration (Table 1).

4. Discussion

We show that during the past 40 years the spring migration of the Bean Goose has advanced by nearly a month. The beginning of autumn migration has advanced by two weeks. In spring, the timing of migration was also affected by NAO index in the early phase of migration.

Table 1. Relationship of spring and autumn migration dates to the observation year and the average NAO index. The connection was tested separately on days when 5%, 50%, or 95% of the cumulative sum of birds had been reached. We used a linear regression analysis as a statistical model.

			Estimate	Std. Error	t-value	p-value
Spring	5%	Intercept	1363	227	5.99	<0.001
		NAO	–14.7	5.27	–2.78	<0.01
		Year	–0.63	0.11	–5.56	<0.001
	50%	Intercept	1589	236	6.74	<0.001
		NAO	–3.99	5.47	–0.73	0.47
		Year	–0.74	0.12	–6.26	<0.001
	95%	Intercept	466	140	3.32	<0.01
		NAO	–5.68	3.26	–1.74	0.09
		Year	–0.17	0.07	–2.38	0.02
Autumn	5%	Intercept	1082	153	7.07	<0.001
		NAO	–0.57	3.48	–0.16	0.87
		Year	–0.41	0.08	–5.39	<0.001
	50%	Intercept	262	158	1.66	0.11
		NAO	0.64	3.59	0.18	0.86
		Year	0.01	0.08	0.06	0.95
	95%	Intercept	–36.4	401	–0.09	0.93
		NAO	9.69	9.12	1.06	0.30
		Year	0.16	0.20	0.81	0.42

Such correlation was not observed in autumn migration.

Our data shows that migrants are arriving earlier in our study area in southern Finland, but we were not able to track the progression of migration along the migration route. This means that while arrival on southern staging grounds has advanced, this does not necessarily mean that arrival on the breeding grounds has also advanced.

The change in spring migration might be the result of the elevated winter and spring temperatures (IPCC 2018, Ruosteenoja *et al.* 2016). As a short-distance migrant, the Bean Goose can possibly react to local weather conditions and follow the progressing spring as they move towards their breeding grounds in higher latitudes. Subspecies Taiga Bean Goose and Tundra Bean Goose differ in their timing as the Taiga Bean Goose starts to arrive in Finland earlier than the Tundra Bean Goose. Yet, all the phases of spring migration have advanced by one to four weeks, and thus, it is likely that there has been a change in the timing of both subspecies.

Migratory birds may shorten their migratory journey in warm winters (Usui *et al.* 2017), and the wintering grounds of the Bean Goose have partly moved closer to its nesting areas (Nilsson 2011). However, there is variation between years as the Bean Goose might migrate further south on cold winters, as shown in a study by Nilsson (2013) where the number of wintering Bean Geese correlates negatively with January temperatures in southern Sweden. The shortening of the migration journey may have some connection to the progressively earlier arrival in Finland. However, in this study, we were not able to determine the migration distance and in previous studies, migration distance has not been shown to explain the advancing arrival on breeding grounds (Gunnarsson *et al.* 2006, Nuijten *et al.* 2020). This could indicate that the advanced arrival in Finland is most likely caused by a shortening stay on wintering grounds.

The early phase of the spring migration was connected to NAO index. Positive NAO index during winter months correlates with warm winter weather in Europe (Hurrell 1995). As the timing of spring migration and NAO index are connected, early spring migration is plausibly a result of warm winters. A similar connection between positive NAO index and spring migration was observed in a study of Icelandic migrants when several species advanced their migration after mild winters (Gunnarsson & Tómasson 2011).

In the autumn, the Bean Goose showed advanced timing of migration. However, only the start of their autumn has shifted forward. The early migrants are most likely successful breeders from the subspecies Taiga Bean Goose and their offspring, who have advanced the start of their migration from their breeding grounds on boreal zone. Non-breeding and unsuccessfully breeding taiga Bean Geese migrate to moult on Novaya Zemlya in the Arctic Ocean (Piironen *et al.* 2021). Moult migrants stay on Novaya Zemlya for approximately three months and start their autumn migration later than successful breeders. Moult migrants form a large part of the population and thus, their movement has a major effect on the observed timing of the autumn migration (Piironen *et al.* 2021). Noteworthily, we must acknowledge that we cannot reliably separate the contribution of the Tundra Bean Goose in our data, and it is possible that their later timing compared to the Taiga Bean Goose (Piironen *et al.* 2022b) may complicate the interpretation of the autumn migration.

Because of climate change, also autumns in Finland are getting warmer, though the trend is not as strong as in spring (Ruosteenoja *et al.* 2016, IPCC 2018). Contrary to our prediction, the Bean Goose has not delayed the main timing of the autumn migration, which could indicate slower autumn migration and stopping to feed in suitable sites across the migration route. Migratory birds' responses to climate change are more versatile in the autumn than in the spring, but many short-distance migrants have delayed their autumn migration significantly (Jenni & Kéry 2003).

In autumn, the timing of migration was not connected to NAO index. The breeding grounds of the Tundra Bean Goose reach outside the area that is affected by NAO, which may partly explain this result. The effect of NAO is greatest in winter months (Hurrell 1995), which may also explain why spring migration follows the index more closely. Start of the autumn migration is probably more linked to local weather conditions on breeding grounds.

In spring, advancing the migration to follow the progressing spring is important as the young plants are important food for birds because of the high nutrition quality (Lepage *et al*. 1998). High-nutrient food is especially important for the survival of goslings (Doiron *et al*. 2015). Autumn migration, on the other hand, is not subjected to a similar selection pressure which may partly explain why the change in the timing of migration is greater in spring than in autumn (Kölzsch *et al.* 2016). The Bean Goose is a single-brooded species and a longer stay on the breeding grounds would probably not improve its breeding success.

Our results are in line with the short-distance migrants' ability to adapt to climate change by adjusting their migration behaviour (Kolářová *et al.* 2017). The ability to change the timing of migration suggests that the Bean Goose has the potential to adapt to environmental changes through its migratory behaviour. A four-week advancement in spring migration is a major shift in a species' migratory behaviour and one of the largest shifts documented so far (see also, Nuijten *et al.* 2020).

Metsähanhen muutto Suomessa on aikaistunut keväällä, mutta ei syksyllä

Ilmastonmuutos vaatii eliöitä mukauttamaan perinnöllisiä tai opittuja käyttäytymismallejaan muuttuviin ympäristöolosuhteisiin. Erityisen alttiita muutoksille voi olla erilaisten habitaattien välillä muuttavat linnut, joiden selviytyminen on yhteydessä muuton onnistuneeseen ajoittamiseen. Tässä tutkimuksessa käytimme metsähanhesta (*Anser fabalis*) avoimeen lintutietopalveluun, Tiiraan (tiira.fi – BirdLife Suomi), kerättyjä havaintoja selvittääksemme, onko lajin muuton ajoituksessa tapahtunut muutosta viimeisten 40 vuoden aikana. Lisäksi selvitimme ajoituksen yhteyttä muuton aikaiseen suursäätilaan käyttämällä Pohjois-Atlantin suursäätilaa kuvaavaa NAO-indeksiä. Tutkitulla ajanjaksolla 1978–2018 kevään päämuutto on aikaistunut kuukaudella. Syysmuuton kohdalla muutos oli vähäistä. NAO-indeksi oli yhteydessä vain kevään ensimmäisten muuttajien ajoitukseen. Kevätmuuton voimakas aikaistuminen osoittaa metsähanhen sopeuttaneen muuttokäyttäytymistään vastaamaan kevään muuttuvia olosuhteita.

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Breeding biology of Red-backed Shrikes (*Lanius collurio*): distribution, performance and post-fledging survival in Denmark

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Agricultural intensification and habitat degradation across Europe have caused declines since the 20th century in populations of birds adapted to open landscapes, such as the Red-backed Shrike (*Lanius collurio*). Effective conservation strategies require knowledge on species' breeding biology. To understand the status of the Danish breeding population better, we investigate which factors affect their breeding parameter (*i.e.* distribution, performance, post-fledging survival and behaviour). Our focus on the post-fledging period addresses present knowledge gaps due to the importance of this, yet under-studied, phase of passerines' breeding cycle. We studied breeding pairs on different habitat types with Denmark-wide Citizen Science data, complemented by data of local projects in Northern Zealand and Northern Jutland (Denmark). Significantly fewer pairs were found in agricultural habitats and more in forests, semi-natural open habitats and synanthropic habitats. Pairs in forests had a significantly higher breeding productivity compared to agricultural or semi-natural open habitats for data from the years 2000 to 2021. Some project sites showed significantly higher number of fledglings compared to others, indicating that these sites are potential core areas for breeding productivity. Over the last two decades, the mean breeding productivity across Denmark was stable with 2.3 fledglings per successful pair. The survival rate of ringed fledglings increased during the post-fledging period, likely due to their increase in more active and independent behaviour. The relatively low breeding productivity found in this study calls for further studies including detailed data from potentially secondary habitats like agricultural areas to understand the effects of habitat on population fluctuations.

1. Introduction

Birds adapted to open landscapes inhabit nowadays mostly anthropogenic managed areas, in which intensified agricultural practices have caused degradation of suitable habitats and subsequent severe declines of these bird populations since the 20th century (Krebs *et al.* 1999, Tryjanowski *et al.* 2011, Bowler *et al*. 2021). Implementations of effective conservation strategies are crucial to prevent further population losses (Donald *et al.* 2001), which requires thorough knowledge on species biology, including detailed information on species specific environmental preferences (Titeux *et al*. 2007, Tryjanowski *et al.* 2011). Knowledge on breeding performance as well as post-fledging survival is important to fully understand mortality, dispersal and trends in avian populations (Anders & Marshall 2005, Hušek *et al*. 2012, Cox *et al.* 2014). Despite its importance for the first-year survival and consequently for the breeding performance (Marcum & Yosef 1998), the post-fledging period is under-studied across most passerines (Anders & Marshall 2005, Cox *et al.* 2014). Especially birds with short nestling periods depend on prolonged parental care during the post-fledging period (Grüebler & Naef-Daenzer 2010). The Red-backed Shrike (*Lanius collurio*, family Laniidae) stays only for a relatively short period of approximately two weeks in the nest. Hereafter follows the post-fledging period with prolonged parental care of the fledglings for approximately three to four weeks (Cramp & Perrins 1993). This study will pay particular attention to the post-fledging period to address knowledge gaps on this key period (Marcum & Yosef 1998).

The Red-backed Shrike is adapted to breed in open and semi-open habitats, with shrubs as perches for its hunting strategy as well as nest-site (Cramp & Perrins 1993). It mainly feeds on large invertebrates, which it catches and tears apart with a hooked bill and tomial tooth that all member of the Laniidae family developed (Yosef *et al.* 2020). In the anthropogenically altered landscape, it depends on the high abundance of invertebrates promoted by extensive land use and landscape heterogeneity (Brambilla *et al*. 2007, Titeux *et al.* 2007, Bakx *et al*. 2020). Therefore, Red-backed Shrikes can be considered as a good indicator species to evaluate landscape changes and nature management (Latus *et al*. 2004, Tryjanowski *et al.* 2011, Bech *et al.* 2020). Although the species is a long-distance migratory bird which only spends a relatively short period of its annual life cycle in the European breeding ground (Tøttrup *et al*. 2012), conditions in their breeding grounds seem to affect population developments strongly (Marcum & Yosef 1998). The populations of Red-backed Shrikes in Europe – as with most other members of the Laniidae family worldwide – have declined drastically due to landscape changes and increased mortality in their breeding range, along migration routes and in their wintering grounds (Marcum & Yosef 1998). The breeding distribution ranges across most parts of Europe and Western Siberia (Keller *et al*. 2020, Yosef *et al*. 2020), with the Danish population located on the north-western edge (Yosef *et al*. 2020). The species has become more widespread across Denmark since the 1970s (Vikstrøm & Moshøj 2020). However, it cannot be explained by an increasing Danish breeding population because during the same time the breeding population has not shown a positive trend (Grell 1998) and the numbers in point-count data have even declined (Heldbjerg & Fox 2008). Thus, changes in the habitat selection might explain better why Red-backed Shrikes became more widespread, which stresses the need to study differences in their breeding performance across habitat types.

The Red-backed Shrike is listed in the EU Birds Directive (EU 2009), emphasising conservation responsibilities in the European Union (EU). To implement effective conservation measures, a better understanding of its breeding biology, life history parameters and population trends is crucial (Greenwood 2007, Cox *et al.* 2014, Pedersen *et al*. 2018b). This study aims to address present knowledge gaps regarding major parts of the breeding biology of Red-backed Shrikes, focussing on the post-fledging period. In order to study this poorly understood phase of their breeding cycle, we combine Denmark-wide Citizen Science data from the ornithological web-portal DOFbasen (DOF 2020) with detailed studies from different sites in the region of Northern Zealand and Northern Jutland (Denmark) on breeding parameters, such as the distribution, performance (*i.e.* success and productivity), post-fledging survival and behaviour. We expect to deepen the knowledge on Red-backed Shrikes breeding biology in Denmark with these three objectives: 1) On a national scale we analyse the distribution of breeding pairs in different habitat types. Furthermore, we test on a local scale whether habitat type, breeding phenology or predation pressure effect their breeding performance. 2) In addition to analysing the mean breeding productivity between different sites and across Denmark, we give novel insights on the post-fledging survival of young Red-backed Shrikes. 3) During the post-fledging period, we describe the survival rate of fledglings and their behavioural activity. Knowledge gained from this study helps to improve our understanding of the status and trends of the Danish population of Red-backed Shrikes and can contribute to further develop effective conservation strategies to achieve objectives of passerine bird conservation within anthropogenically altered landscapes (Latus *et al*. 2004, Cox *et al*. 2014).

2. Materials and methods

2.1. Study area

This study combines data from two ecological scales in order to answer questions on Red-backed Shrikes breeding biology. On a national scale, we used Citizen Science data on breeding distribution and productivity across Denmark. On local scale, we used data on the breeding performance from various study site with different habitat types. Hulsig Hede (57°41′00″N, 10°28′00″E) in the northernmost part of Jutland and Melby Overdrev (56°01′00″N, 11°99′00″E) at the northern coast of Northern Zealand are both heathland-dune habitats surrounded by coniferous plantations. They differ in size and are respectively 35 km^2 and 2 km^2 large. Rørvig (55°97′00″N, 11°77′00″E) is a 6 km^2 large area in the north-western coast of Northern Zealand with heathland-dune habitats in the North and extensively managed pastures in the South. Gribskov (55°99′00″N, 12°29′00″E) is a 56 km^2 mixed forest area in Northern Zealand, consisting of several forest clearings. In the north-east part of Northern Zealand (55°87′00″N, 12°30′00″E), we studied breeding pairs using sites within the agriculture, which is with approximately 812 km^2 the dominant land cover type in this area.

2.2. Breeding distribution on different habitat types

To describe which habitat types are used by Red-backed Shrikes, breeding distribution across Denmark from data of the Third Danish Breeding Bird Atlas Survey for the years 2014 to 2017 (n = 1534 pairs, Vikstrøm & Moshøj 2020) was analysed. Classes of the Corine Land Cover (CLC) from 2012 in 100-metre resolution (CLC 2012) were grouped into the three main habitat types used in this study – forests (CLC classes: forests, woodland-shrubs), agricultural habitats (CLC classes: agriculture and natural vegetation, arable land, complex cultivation pattern, pastures, fruit trees) and semi-natural open habitats (CLC classes: beach and dunes, moors and heathlands, natural grasslands, wetlands) – as well as into synanthropic habitats (CLC class: artificial surfaces). A random distribution pattern was created by simulating 1534 random points 1000-times across Denmark. The percentage of the random and observed breeding pair points in each habitat type were calculated by spatial analyses and compared by conducting a Chi-square test.

2.3. Potential factors affecting breeding success and productivity

During the breeding season from May to August 2021, detailed data on the breeding biology of Red-backed Shrikes was collected. To find territories of breeding pairs, forest clearings in Gribskov and the heathland-dune area at Melby Overdrev were visited and locations of observed breeding pairs were collected to later search for their nest. In the agricultural landscape matrix of Northern Zealand, we used old breeding sites from Citizen Science data and revisited these sites to search for breeding pairs and later for their nest. To reveal differences in breeding success, we compared the percentage of pairs observed with fledglings from the total number of breeding pairs found with established territories at each study site (n = 72 pairs). Unsuccessful pairs which either lost or abandoned their brood, did not show any behaviour indicating the presence of fledglings for at least two subsequent visits.

In order to test which factors can explain the variation in number of fledglings, we used a Generalized Linear Model (GLM) of the Poisson family to test three factors: (1) The main breeding habitat type. (2) The breeding start, indicated by the hatching date which was estimated based on the age of the ringed nestlings (n = 34 individuals, Olsson 1995, Van den Burg 2011). For individuals that were found after fledging (n = 16 individuals), their age was estimated in an approximate interval (three to seven days), following a guide based on morphological changes in fledglings with known age (Bloche 2023, in prep.). (3) The predation risks at each site, calculated as observation per hour of the main avian predators for their young – Eurasian Magpie (*Pica pica*), Eurasian Jay (*Garrulus glandarius*), Hooded Crow (*Corvus cornix*) and Eurasian Sparrowhawk (*Accipiter nisus*, Matyjasiak 1995, Söderström & Karlsson 2011, Van den Burg 2011).

Additionally, we combined this detailed field study with data on the breeding productivity from other project sites, Rørvig (n = 55 pairs for the years 2016 to 2021) and Mols Bjerge (n = 20 pairs for the years 2010 to 2011), as well as previous study years at Gribskov (n = 553 pairs for the years 2006 to 2011 and 2018 to 2021). We included also long-term Citizen Science data in form of breeding bird observations ("Ynglepar Observationer") with comments on the number of fledglings collected from DOFbasen for the years 2000 to 2021 (n = 351 pairs, DOF 2020). We identified the main habitat types for the breeding bird observations from DOFbasen using their reported location and recent aerial images in 0.6-metre resolution (Esri Inc. 2021). With this larger data set we tested three factors: (1) The main breeding habitat type. (2) The variation in mean breeding productivity between years. (3) The mean breeding productivity for each area (Gribskov, Rørvig, Mols Bjerge and Denmark-wide) and its variation between the years from 2018 to 2021.

2.4. Post-fledging survival

To study post-fledging survival, nestlings were ringed with metal- and colour-ring combinations below their tarsi at the age of approximately eight days to allow individual recognition of birds in the field after fledging (Van den Burg 2011). At the age of two weeks, the young fledge but stay together in family groups for around four more weeks until they disperse or initiate autumn migration (Cramp & Perrins 1993). During that post-fledging period, fledglings were resighted every second to fourth day, using binoculars, telescope and camera. Detection probability and apparent survival rate were calculated by running "Young Survival for marked adults" models, an extension to the Cormack-Jolly-Seber model, with encounter histories for each pair (Cooch 2008). The detection probability describes the likelihood of observing an individual at each visit. We used a constant detection probability to study the variation in apparent survival rate, the probability that an individual is still alive at each age stage. From the apparent survival rate for each age, we calculated the survival over the study period (8 to 44 days after hatching) which indicates the post-fledging survival.

2.5. Post-fledging behavioural activity

Fledgling activity during the post-fledging period was studied by collecting different behavioural traits during the post-fledging period: non-familiar mixing between fledglings, maximum flying distances and different types of hunting attempts. Flying and hunting behaviour were used to create an activity score from 0 (no activity) to 5 (Table 1). The relationship between fledglings' activity score and their age in days was tested with a GLM. ANOVA and further Tukey's post-hoc tests analysed the significance of the regression. The frequency of the observed values for each behavioural trait was analysed along different age. For flying behaviour, natural groups of 15- to 30- and 31- to 44-day-old birds were observed within the data, and therefore tested for significant differences by using a Chi-square test. For the non-familiar mixing of fledglings, the percentage of pairs with mixing fledglings was calculated for each age in days after hatching of the young. We did a GLM and ANOVA test for significance of the regression. To additionally describe behavioural changes in a spatial context, the maximal distance to the nest-site of each fledgling was calculated and compared between the nest visits.

All statistical analyses were performed in R (R Core Team 2021) and $p < 0.05$ was set as the significance level. Survival analyses from the resighting data of ringed fledglings were performed in the program MARK 9.0 (White 2021) and spatial analyses in ArcGIS 10.6.1 (Esri Inc. 2021).

Table 1. Values in the activity score from flying and hunting behaviour for the ringed fledglings at the project sites Gribskov, Melby Overdrev and agricultural habitats in Northern Zealand for the year 2021 (n = 74 observation visits).

Activity score	Flying behaviour	Hunting behaviour
0	No	No
1	< 2 metres	No
2	> 2 metres	No
3	> 2 metres	Unsuccesful try
4	> 2 metres	Succesful try
5	> 2 metres	Contant over longer periods

3. Results

3.1. Breeding distribution on different habitat types

Compared to expected by a random distribution, significantly fewer breeding pairs of Red-backed Shrike used agricultural habitats whereas more pairs used forests, semi-natural open habitats ($p < 0.001$ for the three habitat types) and synanthropic habitats ($p < 0.01$, Fig. 1, Table S2). However, most breeding sites were located in agricultural dominated areas, 44%, as this is the dominating available habitat type. Whereas, 30% of the breeding sites were in forests and less than 20% in semi-natural open habitats.

3.2. Potential factors affecting breeding success and productivity

We found a significantly ($p < 0.001$) higher breeding site fidelity in the forest areas compared to agricultural habitats between the year 2021 and previous years. Whereas 82% of the forest clearings with breeding pairs in the last years also had pairs during the territory search in this study, previous breeding sites within agricultural habitats only contained in 17% of the sites still breeding pairs this year. Furthermore, breeding pairs in forest areas had a significantly ($p < 0.05$) higher breeding success compared to agricultural and semi-natural open habitats, where more than half of the breeding pairs abandoned or lost their brood (Table 2).

Table 2. Success of finding possible breeding birds during the territory search in different habitat types: Agricultural habitat includes sites visited in agricultural habitats of Northern Zealand (n = 29), forest clearing includes the sites in Gribskov (n = 33) and heathland and dune only the one site Melby Overdrev (n = 10). All sites visited from May to August 2021. Chi-square test to calculate p-value with significance values (0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ').

Habitat type	Sites with possible breeding birds	Successful breeding pairs
Agricultural habitat	17%	40%
Forest clearing	82%	63%
Heathland and dune	–	44%
p-value (Chi-square test)	<0.0001 ***	0.046 *

The breeding productivity (*i.e.* number of fledglings) of successful pairs differed significantly between habitat types and years (respectively $p < 0.001$, Table S3). Pairs in forest clearings produced significantly more fledglings compared to pairs in agricultural habitats and semi-natural open habitats ($p < 0.001$), but no difference was found between the latter two habitat types (Fig. 2, Table S4). However, when analysing only data from the 1-year study in the year 2021, none of the three factors explained variations in the number of fledglings significantly (habitat type: $p = 0.83$, hatching date: $p = 0.99$, potential avian predators per hour: $p = 0.78$, Table S5). The mean hatching date was 5.5 days earlier in Gribskov than in the agricultural and semi-natural open habitats, however, the difference was not significant ($p = 0.39$, Table S6).

Denmark-wide Citizen Science data and local project data for the years 2018 to 2021 showed significant differences in the mean number of fledglings of successful pairs between areas ($p < 0.001$). Pairs in Gribskov had with 3.6 fledglings (se = 0.36) a significantly ($p < 0.001$) higher

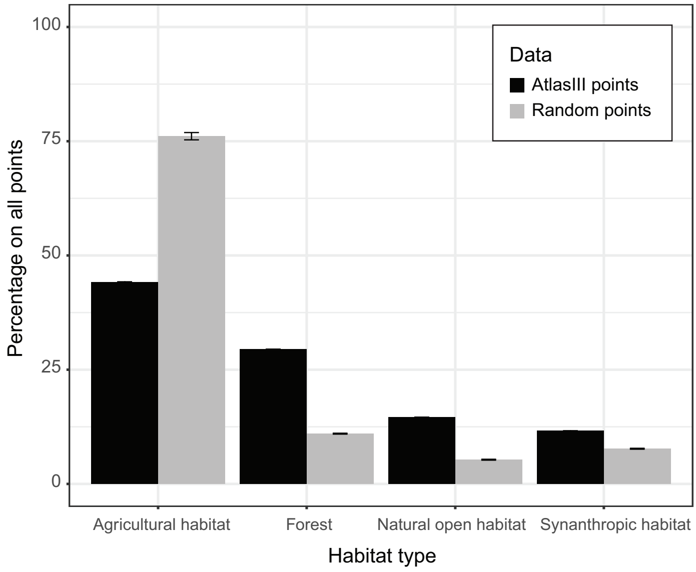

Fig. 1. Bar plot, comparing the percentage of points from breeding pairs of Red-backed Shrikes in the Third Danish Breeding Atlas Survey for the years 2014 to 2017 (AltasIII, black bars, n = 1534 pairs, Vikstrøm & Moshøj 2020) and mean of the 1000 times simulated random points (grey bars with standard error, n per simulation = 1534) in different habitat types of the Corine Land Cover data from the year 2012 (Table S1, CLC 2012).

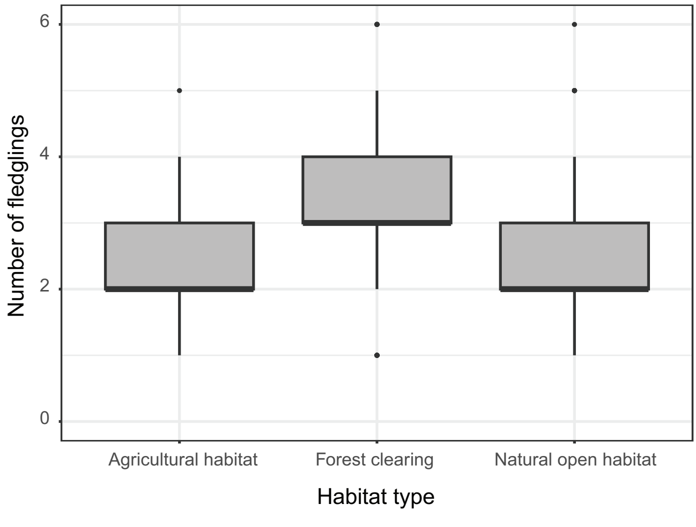

Fig. 2. Number of Red-backed Shrike fledglings in different habitat types for the years 2000 to 2021. Boxplot showing median (bold black line), 25th to 75th percentile interquartile range (grey box), largest values within 1,5 times interquartile range (vertical black line) and residuals outside this range (black dot) for the number of fledglings in agriculture, forest clearings and semi-natural open habitats from DOFbasen data from the years 2000 to 2021 (n = 351 pairs, DOF 2020), as well as project data from Rørvig for the years 2016 to 2021 (n = 55 pairs), Gribskov for the years 2006 to 2011 and 2018 to 2021 (n = 553 pairs), Melby Overdrev for the year 2021 (n = 4 pairs) and the agricultural landscape in Northern Zealand for the year 2021 (n = 2 pairs).

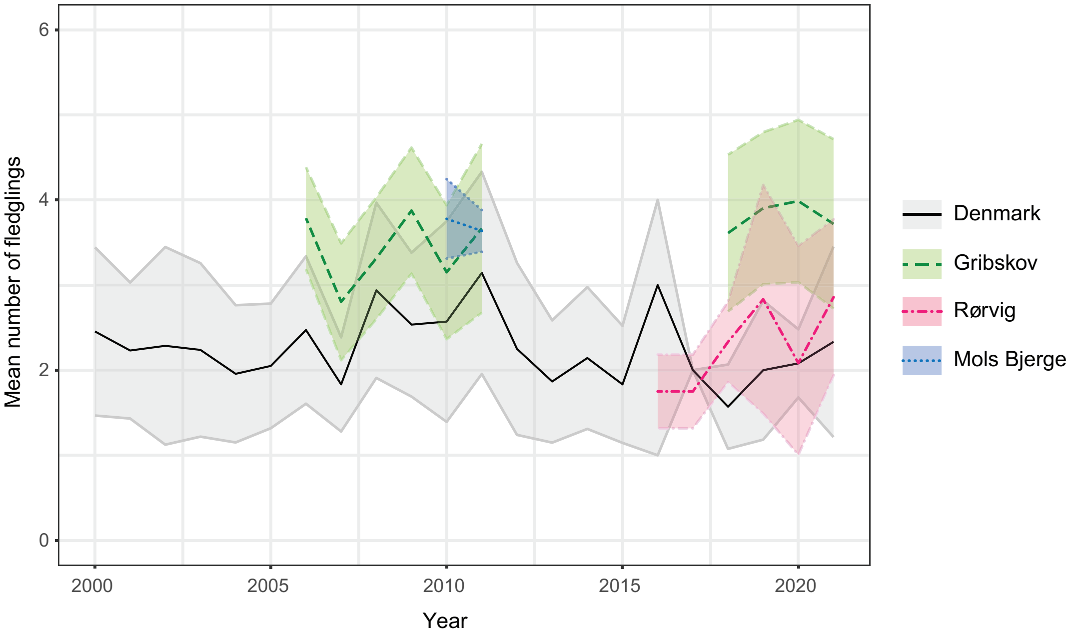

Fig. 3. Changes in mean number of fledglings of Red-backed Shrikes from the years 2000 to 2021 (means shown as lines and standard errors shown as shaded areas). Data of Denmark-wide breeding bird observations from DOFbasen (black solid line and grey area, n = 351 pairs, DOF 2020) are shown for the entire period, data from Rørvig (red dash-dotted line and area, n = 55 pairs) from the years 2016 to 2021, data from Mols Bjerge (blue dotted line and area, n = 20 pairs) from the years 2010 to 2011 and data from Gribskov (green dashed line and area, n = 553 pairs) from the years 2006 to 2011 and 2018 to 2021.

mean breeding productivity compared to pairs from DOFbasen data across Denmark and project data from Rørvig, with respectively 2.3 fledglings (se = 0.39, 0.45, Fig. 3, Tables S7 and S8). Denmark-wide, the mean breeding productivity shows a stable trend over the last two decades, though with some yearly fluctuation.

3.3. Post-fledging survival

All eight pairs with ringed nestlings were successful in producing at least one fledgling. The young survival model calculated a constant detection probability of 0.77 (se = 0.03). The model using this constant detection probability had an AIC value of 237.6, which is 1.8 AIC points better than the AIC value of the model with an age-dependent detection probability (Table S9). Therefore, we calculated the likelihood of surviving each day, the apparent survival rate, with the constant detection probability. The apparent survival rate increased logistically with the age of the young (Fig. 4). Over the study period, the young had a survival rate of 0.73 (se = 0.07).

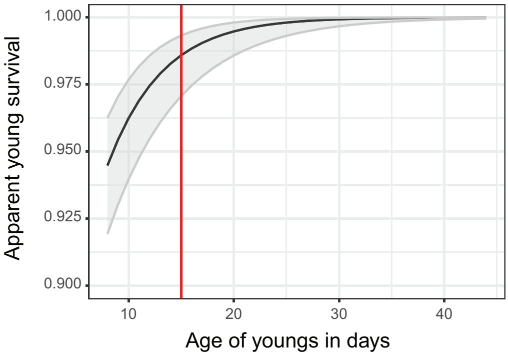

Fig. 4. Apparent survival rate (black line) with limits of lower and upper 95% Confident Interval (grey area) of 8- to 44-day-old Red-backed Shrikes for data from Gribskov, Melby Overdrev and agricultural habitats in Northern Zealand for 2021 (n = 74 pairs). The red vertical line indicates the age they usually fledge (15 days after hatching, Cramp & Perrins 1993).

3.4. Behavioural activity during the post-fledging period

The fledglings' activity increased significantly ($p < 0.001$) during the post-fledging period, with significant ($p < 0.05$) differences between pairs (Fig. 5, Table S10). A significant ($p < 0.001$) increase in long flying distances was found two weeks after fledging (Fig. S1, Table S11). Moreover, fledglings start to forage more independently with days passing since they left the nest: first successful hunting attempts were observed after 22 days and at least 35-day-old birds hunted constantly over longer periods (Fig. S2). Two weeks after leaving the nest, fledglings were observed further than 200 metres away from the nest site, while they stayed within that radius before. At the same time fledglings were observed more often to mix between non-familiar members. The percentage of pairs with fledglings that non-familiar mix increased significantly ($p < 0.001$) over the post-fledging period (Fig. 6, Table S12).

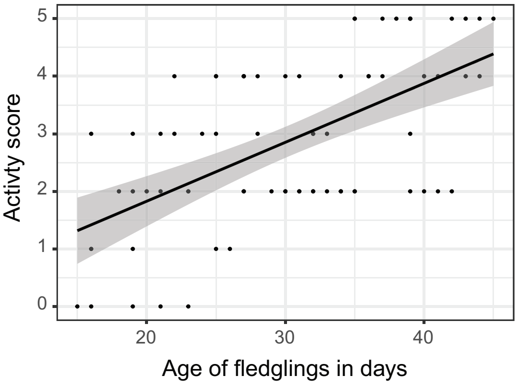

Fig. 5. Activity score (from 0 to 5, Table 1), calculated using flying and hunting behaviour of Red-backed Shrike fledglings with different age in days, for data from Gribskov, Melby Overdrev and agricultural habitats in Northern Zealand for the year 2021 (n = 74 pairs). Regression line was calculated using a Poisson Generalized Linear Model (black line) with standard error (grey area).

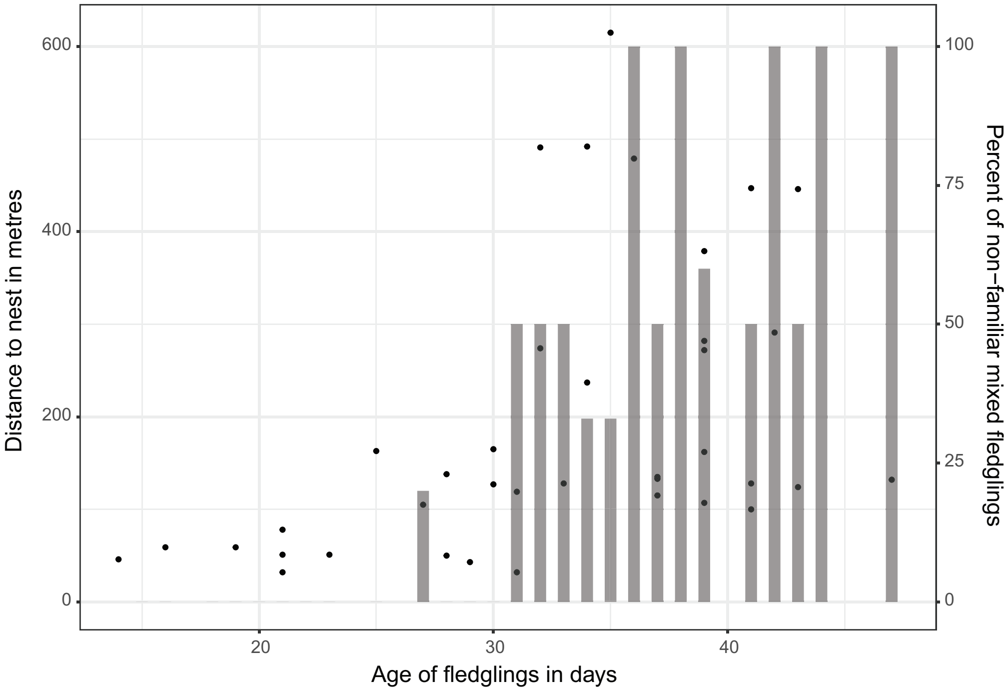

Fig. 6. Observed maximal distance to the nest in metres of Red-backed Shrikes fledglings (black points) and the percentage of pairs observed with non-familiar mixed fledglings (grey bars) across different age in days for data from Gribskov, Melby Overdrev and agricultural habitats in Northern Zealand for the year 2021 (n = 74 pairs).

4. Discussion

4.1. Effects of habitat types on breeding distribution and breeding performance

In this study, Red-backed Shrikes were found significantly more often in forests, semi-natural open habitats and synanthropic habitats but less often in agricultural habitats than expected from a random distribution. Significantly higher probability of occupying previous territories again and the earlier mean hatching date in forests further indicates a preference for nest-sites in this habitat, since territories of higher habitat quality are usually occupied first and over several years (Marcum & Yosef 1998, Söderström & Karlsson 2011). Söderström & Karlsson (2011) found this shift to higher occurrence in forests also for Red-backed Shrikes in Sweden and it can also be found in other birds which were previously mainly found in farmlands, like the yellowhammer (*Emberiza citrinella*) and the Eurasian wryneck (*Jynx torquilla*, Söderström & Karlsson 2011, Bakx *et al*. 2020). Although this study is limited by the low resolution of CLC data (Matyjasiak 1995), several studies also revealed that Red-backed Shrikes avoid arable land as well as prefer heterogenous and extensively managed habitats, like forests (Marcum & Yosef 1998, Vanhinsbergh & Evans 2002, Latus *et al*. 2004, Golawski & Golawska 2008, Morelli *et al*. 2012, Bakx *et al*. 2020). Furthermore, the importance of suitable habitat types is underlined by the link of local population declines to landscape changes (Kuper *et al.* 2000, Tryjanowski *et al*. 2006, Morelli *et al*. 2016, Tellería 2018).

Results in this study indicate that habitat types also influence the breeding performance of Red-backed Shrikes, besides their distribution. A significantly higher number of successful breeding pairs were found in forests compared to agricultural or semi-natural open habitats. Moreover, the breeding pairs in forests produced more fledglings. Most studies on post-fledging survival of passerines found effects of the habitat type (Cox *et al.* 2014) and other studies on Red-backed Shrikes also support that habitats with high heterogeneity have positive effects on both, the breeding success and productivity, while intensive agriculture has negative effects (Matyjasiak 1995, Golawski & Meissner 2008, Söderström & Karlsson 2011). However, the effect of breeding productivity was only significant for the larger dataset and not from the 1-year study solely, likely due to fluctuations of productivity between years and bias caused by a small sample size (Schmidt *et al.* 2008). It is noteworthy, that also our data on breeding success was limited by a small sample size (n = 72 pairs) due to the lack of certain failure records in larger data sets.

Distribution and breeding performance of Red-backed Shrikes might differ between habitat types because of differences in food abundance and availability, as well as the predation risk (Roos 2002, Pedersen *et al*. 2012). Heterogeneous and extensively managed semi-natural open habitats are correlated with high invertebrate richness and abundance (Latus *et al*. 2004, Bech *et al*. 2020). Windthrows or artificial clearings within forests create sun-exposed patches which can act as invertebrate biodiversity hot spots (Bouget & Duelli 2004), while farmlands show a vast decline in invertebrate biodiversity (Stoate *et al*. 2001). Moreover, Red-backed Shrikes are adapted to these heterogeneous forest-steppe habitats with perches and open patches, which are crucial for their hunting strategy (Baláž 2007, Svendsen *et al*. 2015, Morelli *et al*. 2016). Although our data on avian predators was too limited, other studies found that the higher abundance of Eurasian Magpie, Hooded Crow and Eurasian Jay in farmland territories increase the predation risk (Söderström 2001). Nest-sites in spatially aggregated shrub patches within open habitats are likely also more conspicuous for nest predators (Matyjasiak 1995, Roos 2002, Söderström & Karlsson 2011).

4.2. Mean breeding productivity and post-fledging survival at different sites and across Denmark

This study revealed a stable but striking low mean breeding productivity of 2.3 fledglings per successful breeding pair across Denmark. To compensate for mortality and maintain a stable population each pair should produce between 2.3 and 3.0 fledglings per year (Jakober & Stauber 1987, Ryttman 1996, Hemerik *et al*. 2015). It is noteworthy that these studies also include unsuccessful pairs with no fledglings, which usually leads to a severely lower number than by including solely successful pairs, as done in our study (Olsson 1995). Other stable populations across Europe show a remarkable higher breeding productivity of 3.6 to 4.4 fledglings per successful pair (Jakober & Stauber 1987, Kuźniak 1991, Olsson 1995, Horvath *et al.* 2000, Jørgensen *et al.* 2013, Hemerik *et al.* 2015, Table S13). Nevertheless, our results on Denmark-wide productivity should be treated as a minimum number, since Citizen Science data does not consist of a targeted effort, likely necessary for an accurate monitoring (Ekberg *et al.* 2011). Moreover, the high standard error in the data indicates variation between sites and fluctuation over the years, due to varying environmental factors (Schmidt *et al.* 2008).

Spatial variation in the breeding productivity of Red-backed Shrikes can be also explained by potential core areas, besides solely the habitat types. High breeding productivity of pairs in forest clearing of Gribskov, but also in the extensively managed dune-heathland and grassland areas Hulsig Hede (Jørgensen *et al.* 2013) and Mols Bjerge, indicates that potential core areas can be also found in semi-natural open habitats. In these sites, we found a higher mean breeding productivity compared to Denmark-wide data and Rørvig, despites the also high breeding pair abundance at Rørvig. The data from Hulsig Hede and Mols Bjerge was not suitable for statistical comparisons because it was recorded over different and shorter time periods. For Gribskov the difference was significant, which supports statistical evidence that this site is likely a core area regarding breeding productivity. Furthermore, the low return rates of individuals with geolocators and colour-rings in previous studies (Tøttrup *et al.* 2017, Pedersen *et al.* 2018a) could reveal a connectivity of Gribskov to a larger metapopulation. A low breeding site fidelity, caused by this connectivity, was also seen in other local populations with high reproductive success (Geertsma *et al.* 2000, Tryjanowski *et al.* 2007). The high importance of Gribskov as a breeding location could be explained because it is a relatively large forest on Danish scale and contains many grazed clearings with deadwood, which show an especially high habitat quality over many years (Ekberg *et al.* 2011, Overballe-Petersen *et al.* 2014, Bakx *et al.* 2020). Also, the predation risk is lower in patches within large forests than along the forest edge, because many nest predators are adapted to forage and breed in habitat edges (Matyjasiak 1995, Roos 2002). Potential core areas might improve the breeding productivity also due the high density and clustering of breeding pairs (Fornasari *et al.* 1994). For true colonially nesting passerines like Fieldfares (*Turdus pilaris*), it has been shown that larger colonies are more effective in defending their nests (Wiklund & Andersson 1994). Cooperative nest defence was not observed for Red-backed Shrikes in this study, nevertheless, we could expect a similar increase of warning and aggression intensity against potential predators by their higher breeding pair density (Tryjanowski & Golawski 2004). However, it is important to consider possible observer bias as a reason for the high breeding productivity in Gribskov. Ekberg *et al.* (2011) argued that targeted monitoring is important for obtaining accurate data on the number of fledglings and showed that more pairs were found with improved monitoring efficiency. While this may explain differences between targeted project sites and the Denmark-wide Citizen Science data, it cannot explain the differences between sites with targeted monitoring projects, like Gribskov and Rørvig.

In order to estimate the required productivity for maintaining a stable population, post-fledging survival rates are important to consider (Hušek *et al.* 2010). In this study, all pairs with ringed nestlings were successful in producing fledglings and had a high young survival of 0.73 (se = 0.07) over the study period, which can be used as an indication for their post-fledging survival. Other studies calculated lower post-fledging survival rates, between 0.48 and 0.62 (Baláž 2007, Hušek *et al.* 2010). Certainly, the results in this study are not representative for the entire Danish population, rather for a local population in Northern Zealand, mainly Gribskov. Therefore, further studies are needed on a larger scale.

4.3. Survival rate and behavioural activity during the post-fledging period

Our data on the previously under-studied post-fledging period (Anders & Marshall 2005, Cox *et al.* 2014) revealed linked pattern in survival and behaviour of young Red-backed Shrikes. The characteristics of mark-resighting models without known fate do not allow to date mortality events with a high accuracy (Cooch 2008), but our results showed the highest mortality during the few days of transition from nestling to fledgling and first days in their natal territories. This pattern is also found in studies on the Great Grey Shrike (*Lanius excubitor*, Yosef 1993) and other passerines (Yackel *et al*. 2006), particularly in species with short nestling periods (Cooch 2008, Cox *et al*. 2014). The increasing apparent survival rate of young Red-backed Shrikes could be explained by the decrease in vulnerability to predation, bad weather and starvation due to their increasing behavioural activity and gradual independence from parental care. This study reveals a significant increase in the activity of the fledglings, especially in more independent behavioural traits, such as flying and hunting. Comparable behavioural studies have only been conducted on Woodchat Shrikes (*Lanius senator*), a closely related species with similar ecology but more southern distribution, and showed similar results (Marcum & Yosef 1998, Nikolov & Hristova 2007). Higher behavioural activity can mostly be explained by the progression in growth of their flight feathers, which is completed three to four weeks after hatching (Cramp & Perrins 1993, Nikolov & Hristova 2007). This study showed that Red-backed Shrikes can start self-feeding already one week after fledging, four days earlier than described by Cramp & Perrins (1993). Despites these early successful hunting attempts, they still depend on parental care until they fully learn the hunting techniques as well as develop their hooked bill and tomial tooth (Cramp & Perrins 1993, Nikolov & Hristova 2007). Extended post-fledging parental care is costly, but for passerines with short nestling periods, like the Red-backed Shrike (Cramp & Perrins 1993), it is substantially increasing young survival during the most vulnerable period (Grüebler & Naef-Daenzer 2010).

Two weeks after fledging, the Red-backed Shrikes started to spread out over 200 metres away from the nest and mix with fledglings from other families. At a similar age, Woodchat Shrikes also show increasing intra- and interspecific interactions, including with non-family members (Nikolov & Hristova 2007). Other studies on Red-backed Shrikes only showed an increasing overlap in the territories of adults (Fornasari *et al*. 1994, Marcum & Yosef 1998) and that fledglings start to disperse further away from the nest-site (Cramp & Perrins 1993, Olsson 1995). This dispersal could be a response to the predation pressure in their natal territories (Yosef 1993), first post-fledgling exploration movements (Baker 1993) or a response to the decrease in male territory defence which allows fledglings to mix between families and in some cases even leads to shared parental care (Fornasari *et al*. 1994).

5. Conclusion

This study revealed that especially forest clearings and to a certain degree also other heterogenous, extensively managed open habitats have positive effects on the breeding distribution, success and productivity of Red-backed Shrikes. Breeding productivity also differs between study areas, indicating the importance of potential core areas, like Gribskov, Hulsig Hede or Mols Bjerge in Denmark. Further studies should investigate these core areas and their importance as a potential population source. The low mean breeding productivity across Denmark emphasises the need for further studies including data on complete nest losses and the post-fledging survival on a larger scale (Cox *et al*. 2014). To fully understand what affects their breeding performance also other potential factors, like weather conditions and predation risk, needs to be considered over their entire annual life cycle (Tøttrup *et al*. 2012, Jørgensen *et al*. 2013, Bech *et al*. 2020). In this study, both the fledglings' behavioural activity and survival rate increased gradually during the post-fledging period. The higher activity of fledglings indicates their decreasing dependency on parental care, which explains the increasing survival rate. Also, changes in their spatial pattern and social interactions are closely linked to behavioural changes. It is important to further understand and describe complex behavioural changes during the post-fledging period to understand the post-fledging survival better, which is directly linked to the breeding productivity (Anders & Marshall 2005, Nikolov & Hristova 2007).

Pikkulepinkäisen (*Lanius collurio*) lisääntymisbiologia: levinneisyys, lisääntyminen ja lentopoikasvaiheen eloonjääminen Tanskassa

Maatalouden tehostaminen ja elinympäristöjen heikentyminen Euroopassa ovat 1900-luvulta lähtien vähentäneet avoimiin maisemiin sopeutuneiden lintujen, kuten pikkulepinkäisen (*Lanius collurio*), populaatioita. Niiden tehokas suojelu edellyttää kuitenkin tietoa lajin lisääntymisestä. Tässä tutkimuksessa keskityimme erityisesti siihen, mitkä tekijät vaikuttavat pikkulepinkäisen pesintään liittyviin muuttujiin, kuten levinneisyyteen, suorituskykyyn, sekä pesinnänjälkeiseen eloonjäämiseen ja käyttäytymiseen. Keskityimme erityisesti lentopoikasvaiheeseen, sillä vaikka se on tärkeä vaihe lisääntymisen kannalta, sitä ei ole tutkittua paljoa. Tutkimusaineistomme koostui eri elinympäristötyypeissä pesivistä pareista, ja sen havainnot perustuivat koko Tanskan kattavaan kansalaistieteelliseen aineistoon. Lisäksi aineistoa täydennettiin Pohjois-Sjellannin ja Pohjois-Jyllannin paikallisprojektien tiedoilla. Pikkulepinkäispareja löydettiin merkittävästi vähemmän maatalousympäristöistä ja toisaalta enemmän metsäisistä, osittain luonnontilaisista avoimista ja synantrooppisista (ns. ihmisen luomista) elinympäristöistä. Metsissä pesivien parien tuottavuus oli huomattavasti korkeampi kuin maatalouympäristöissä tai osittain luonnontilaisissa avoimissa elinympäristöissä pesivien parien tarkastelujaksolla 2000–2021. Joissakin tutkimuskohteissa poikasia syntyi huomattavasti keskimääräistä enemmän, mikä viittaa siihen, että alueet ovat pesinnän ydinalueita. Keskimääräinen poikastuottavuus on ollut vakaa Tanskassa kahden viime vuosikymmen ajan: 2.3 poikasta paria kohden. Rengastettujen poikasten eloonjäämistodennäköisyys parani lentopoikasvaiheen jälkeisenä aikana, johtuen todennäköisesti niiden aktiivisemman ja itsenäisemmän käyttäytymisen lisääntymisestä. Tässä tutkimuksessa havaittu suhteellisen alhainen poikastuottavuus vaatii kuitenkin lisätutkimusta ja tarkempaa aineistoa mahdollisista toissijaisista elinympäristöistä (esim. maatalousalueet), jotta saamme paremman kokonaiskuvan elinympäristöjen vaikutuksesta pikkulepinkäispopulaatioiden vaihteluihin.

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Online supplementary material

Supplementary material available in the online version of the article includes Tables S1–S13 and Figures S1–S2.

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Temporal occurrence and species composition of birds on artificial feeding sites maintained for game mammals in the Dinaric Mountains, Slovenia

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Artificial feeding is a widely used management tool, but it often attracts nontarget species, including birds, to permanent feeding sites. This study used camera traps to monitor the presence of birds at selected sites used for bear management in Dinaric forest. A large number of bird species (35) were recorded, representing roughly half of all species breeding in the surrounding area. These species were grouped based on monthly and hourly presence, and corresponded to food groups, with most belonging to granivores or scavengers. Some species, such as Pigeons (*Columba* sp.), Raven (*Corvus corax*) and Buzzard (*Buteo buteo*), adapted their presence to the availability of food at the feeding sites, while others were not affected by this. Both Chaffinches (*Fringilla coelebs*) and Jays (*Garrulus glandarius*) frequented the feeding sites, but their temporal presence was influenced by their biology rather than by food availability. The Sparrowhawk (*Accipiter nisus*) also adapted its presence to food availability, and its presence was closely associated with that of the Jay. This study confirms the temporal differences in the use of feeding sites by birds and mammals, which is likely due to their different biology and past management. This can be used to make wildlife management more efficient and reduce the undesirable effects of artificial feeding.

1. Introduction

Human activities result in the provision of large quantities of food for wildlife, either unintentionally (Perkins *et al.* 2007, Plaza & Lambertucci 2017) or intentionally for various purposes (Robb *et al.* 2008). Some wildlife populations, such as northern populations of the Great Tit (*Parus major*) or vultures, rely heavily on artificial feeding (Orell 2008; Cortés-Avizanda *et al.* 2016), while others are affected in all aspects of their ecology, including reproduction, behaviour, demography and distribution (Robb *et al.* 2008).

Artificial feeding of wildlife, including birds, occurs in many forms. For example, bird feeders are common in urban areas worldwide (Robb *et al.* 2008). In some parts of the world, carrion feeding stations are a common practice for vulture conservation (Cortés-Avizanda *et al.* 2016). In addition to intentional feeding (*e.g.*, bird feeders), birds are offered artificial food in large quantities at feeding stations maintained (usually by hunters) for mammals for the purposes of hunting, monitoring, conflict prevention and/or wildlife watching. This type of feeding is a common practice in much of the world, has a long tradition and can be fairly intensive. For instance, in Slovenia, about 12.5 tonnes of corn per 100 km^2 are fed to wildlife annually by hunters (Krofel & Jerina 2016). This artificial feeding is usually intended for only a few species. In Europe, such species include ungulates (*i.e.*, Milner *et al.* 2014), mesopredators and Brown Bears (*Ursus arctos*) (Graf *et al.* 2018). However, numerous non-target species also visit these feeding sites, including several bird species (Fležar *et al.* 2019).

Most research on the effects of artificial feeding on birds has focused on bird feeders in urban areas (Jones & James Reynolds 2008; Robb *et al.* 2008). Although bird feeders are designed to provide sustenance during harsh conditions and to foster a connection between people and nature (Robb *et al.* 2008), unanticipated ecological and behavioural consequences can arise. For example, birds can colonise areas with feeders beyond their natural range (Robb *et al.* 2008) or at densities not seen in nature (Wilson 1994). Artificial feeding can also allow some non-native species to survive (Clergeau & Vergnes 2011) or even dominate over native species (Galbraith *et al.* 2017) in new areas. Furthermore, artificial feeding may also alter breeding through increased breeding success (Harrison *et al.* 2010) or increased nest predation rates (Selva *et al.* 2014; Oja 2017).

Although artificial feeding sites intended for hunting have been studied primarily from the perspective of ungulate game species (Wirsing & Murray 2007; Sorensen *et al.* 2014; Pedersen *et al.* 2014; Milner *et al.* 2014) and Brown and Black Bears (*U. americanus*) (Bowman *et al.* 2015; Selva *et al.* 2017; Graf *et al.* 2018; Candler *et al.* 2019; Fležar *et al.* 2019), effects on birds have received little attention. Previous studies have primarily focused on nest predation (Cooper & Ginnett 2000; Selva *et al.* 2014; Oja 2017) and breeding success (Pedersen *et al.* 2007). Most studies have noted the presence of birds among non-target species without further investigation (Lambert & Demaris 2001; Selva *et al.* 2014; Bowman *et al.* 2015; Fležar *et al.* 2019), and surprisingly, even basic information on bird use of these feeding sites is lacking.

The main objective of the present study was to investigate the temporal occurrence of birds at artificial feeding sites maintained by hunters for game mammals. The temporal availability of the food offered at these sites differs from that of natural food. In some cases, such as in Slovenia, artificial food may be available almost continuously (Fležar *et al.* 2019), which could potentially impact the seasonal and circadian activity of birds. Despite its potential effects, the topic has received limited attention, with no existing data on the influence of artificial feeding sites for game animals on the temporal occurrence of birds. The study aimed to (i) analyse the species composition of birds visiting feeding sites; (ii) examine the seasonal and circadian use of feeding sites by selected bird species, with an emphasis on the timing of occurrence and the overlap of different species at artificial feeders; and (iii) compare this use of the sites with that of better-studied game mammals (Candler *et al.* 2019).

2. Material and methods

2.1. Study area

The study area includes a large part of the Dinaric Mountains in southern and central Slovenia (Fig. 1). The region is the core habitat area for several large ungulate species, including Red Deer (*Cervus elaphus*) and Wild Boar (*Sus scrofa*) as well as large carnivores such as Brown Bear, Wolf (*Canis lupus*) and Lynx (*Lynx lynx*). The study area spans an altitude range from 300 to 1,796 m a.s.l. and is primarily covered by mixed forests dominated by Silver Fir (*Abies alba*) and Common Beech (*Fagus sylvatica*). This area is the most forested in Slovenia (over 80% covered by forest), with settlements located in Karst fields and a few river valleys. The area has a high vertebrate diversity, especially that of mammals

(Fležar *et al.* 2019). However, permanent water sources are scarce, especially at higher elevations, and open habitats are limited to the edges of the mountain massifs. As a result, breading bird density and diversity is relatively low, consisting mainly of forest specialists (Mihelič *et al*. 2019).

The practice of artificially feeding wildlife in the Dinaric Mountains is widespread and has a long tradition, with some feeding sites dating back to the late 19th century (Garshelis *et al.* 2017). The feeding sites are managed by local hunters and serve various purposes. As observed in other countries (Selva *et al*. 2014; Bowman *et al*. 2015; Oja 2017), the sites typically offer two main types of food: corn (or other grain) and carrion. While corn is widely available and often available year-round at many feeding sites, carrion is supplied more opportunistically and in smaller quantities (mostly offal from hunted game species and road carcasses of ungulates; see Mohorović *et al*. 2015 and Graf *et al*. 2018 for a detailed description).

2.2. Selected feeding sites

As part of the Life DinAlp Bear project, 23 representative feeding sites were selected primarily to study the effect of artificial feeding on brown bears (Krofel *et al*. 2015). Corn was available year-round at all feeding sites, with smaller amounts (or none at all) in winter, but methods of delivery differed between some sites. Corn was either distributed in the afternoon using automatic dispensers or delivered manually during the day. In both cases, a few kilograms of corn were distributed to feeding sites daily. During the 2016–2017 study period, carrion was provided to the monitored feeding sites (Graf *et al*. 2018). Carrion in the form of hunting remains and road carcasses of ungulates were provided throughout the year, with a peak during the hunting season (fall). The selected study sites were located in small clearings within the forest, and were on average 2 km from the forest edge and 2.6 km

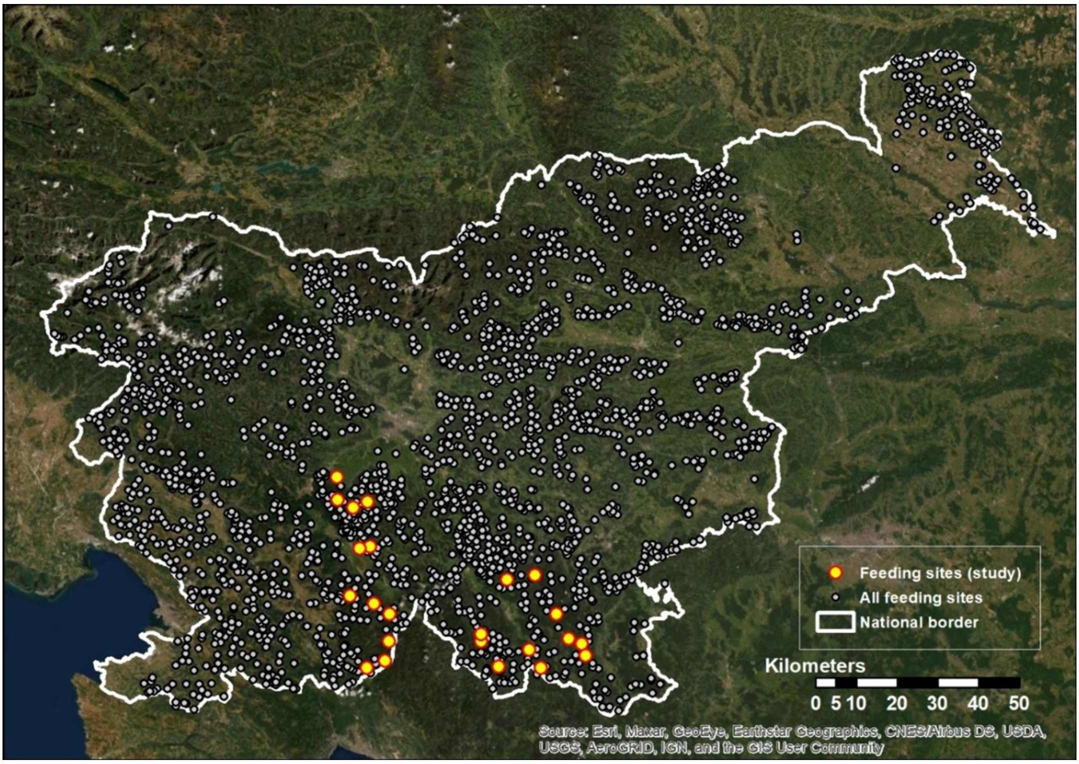

Fig. 1. Locations of artificial feeding sites for game mammals in Slovenia and those used in the study.

from the nearest settlement. The clearings varied in size, and vegetation was mowed and removed at least once a year, usually in summer, to ensure good visibility and prevent overgrowth.

2.3. Methods

The selected feeding sites were monitored 24 hours per day for 2 years with automatic photo/video cameras (UOVision IR PLUS BF HD UV 565). Camera traps were placed so that the feeder was in front of the camera and the view was not obstructed by woody vegetation. A 30-second video was recorded after each photo. The cameras were set so that the next possible photo could not be taken until a five-minute period had elapsed. If the camera took more than one photo within this five-minute interval, we analysed only the first photo and omitted the others (11.0% of photos). The cameras were checked approximately every two to three weeks. If a system malfunction occurred or the batteries were depleted between checks, the date and time were automatically reset to default settings. Unless they were corrected in the field, we considered these date settings to be incorrect. Periods with incorrect date settings were excluded from the temporal occurrence analysis (6.4% of photos). Temporal occurrence in this paper includes both seasonal occurrence expressed in monthly presence and circadian occurrence expressed in hourly presence. The study and feeding sites were set up for Brown Bears as the primary target species. At one feeding site, the feeder was only suitable for bears, and no food was available for other species. Therefore, we did not include the data collected at this feeding site in the study. Several feeding sites experienced problems with feeders, such as a malfunction of the automatic dispenser or damage to the feeder from Brown Bears or falling trees. Periods when cameras or feeders were not working resulted in gaps in our data set. When gaps extended over several months, the entire dataset for that year from that feeding site was excluded from temporal analyses. Only feeding sites with complete data sets (16 sites) were used for circadian and monthly presence analyses. Due to the inaccessibility and poor maintenance of feeding sites and cameras during the winter months (December–February), there were many gaps in the data. In addition, during this period, food is supplied at a lower frequency. For this reason, we did not include data gathered during the winter (4.5% of all photos). More detailed descriptions of camera settings, maintenance of feeding sites and cameras, data collection, photo review and species identification from photos can be found in Graf *et al*. (2018) and Fležar *et al*. (2019).

2.4. Bird species occurring at feeding sites

For the photo analysis, we focused on all identifiable bird species down to the size of tits (Paridae), including smallest species such as the Coal Tit (*Periparus ater*) and Marsh Tit (*Poecile palustris*). We did not separate individuals in the different photos, but considered each photo as a separate event, even if it may have captured the same individual. This approach was adopted based on previous studies that showed that temporal autocorrelation in camera trap data diminished after one minute (Kays & Parsons 2014, Kays *et al.* 2017, Kellner *et al.* 2022). Therefore, we grouped consecutive pictures taken five minutes (or greater) apart into sequences that were considered independent records. In this way we ensured that the capture events are more likely independent and the pseudo-replication impact is mitigated. We used the independent records of birds to model the temporal activity of birds and describe the relative degree of site use (*i.e.*, the amount of time birds spent at feeding sites). Given the similarities in feeding station characteristics, such as the use of camera traps over a long period of two years and the provision of the same food supplement (corn), we expected that, for a given species, the temporal activity pattern at feeding stations would be similar.

For species with greater than 10 records, we used hierarchical clustering analysis to group species with similar activity patterns (both seasonal and circadian, see below). To this end, we applied an unweighted pair-group clustering algorithm based on the arithmetic averages (UPGMA) to the dissimilarity matrix. This matrix was calculated based on the Kulczynski distance of the abundance data. The optimal number of clusters (*i.e.*, groups) was determined by applying the Kelley–Gardner–Sutcliffe penalty function (KGS) (Kelley *et al*. 1996). This analysis was performed using the “vegan” R package (Oksanen *et al*. 2017).

2.5. Seasonal and circadian occurrence of birds at feeding sites

For species with over 100 records, temporal activity for each species was estimated by pooling data across years and summing the number of independent records of a given species per hour and month. We then related the temporal data to relative solar time (Nouvellet *et al*. 2012) using the “SunTime” function in the “Overlap” R package (Meredith & Ridout 2020). We then compared temporal activity patterns between species statistically using the Watson-Wheeler test (Zar 1999) and graphically (Fig. 3). This test, a common approach to assess differences between two circular distributions (Frey *et al*. 2017; Massara *et al*. 2018), was performed using the “hms2rad” function implemented in the “astroFns” R package to convert species activity time from angular format (hh:mm:ss) to radians where 1 hour $= \pi / 12$ (Harris 2012). By doing this, we created a vector of activity time for each species and used the Watson-Wheeler test to compare the mean time of day in which species were active.

2.6. Comparison of temporal occurrence between birds and mammals

We measured the daily activity overlap between mammal and bird species using the sum of individuals in five-minute intervals using the framework developed by Ridout and Linkie (2009), which fits a kernel density to temporal data. We then estimated the degree of overlap between the two density curves by calculating the coefficient of overlap (Dhat1), which is most appropriate when the sample size is small (at least 10 records/species) (Linkie & Ridout 2011; Frey *et al*. 2017). The value of Dhat varies between “0” (*i.e.*, no overlap) and “1” (*i.e.*, complete overlap) (Linkie & Ridout 2011). This analysis was performed using the “Overlap” R package (Ridout & Linkie 2009).

3. Results

3.1. Bird species occurring at feeding sites

We detected a total of 35 bird species at all sites (Table 1, Appendix 1). Of these species, eight were recorded with only one photo and five species were present in five or fewer photos. Only 14.8% of all photos (36,686) had a bird, representing 1.63% of all possible five-minute time intervals when camera traps were in

Table 1. Number of photographs on selected artificial feeding sites in Slovenia for eight species of birds with more than 100 photographs.

Species	No. of photos	Percentage of all possible 5 min intervals*
Jay, *Garrulus glandarius*	19,356	0.86%
Raven, *Corvus corax*	9,882	0.44%
Common Wood Pigeon, *Columba palumbus*	9,748	0.43%
Common Chaffinch, *Fringilla coelebs*	2,416	0.11%
Common Buzzard, *Buteo buteo*	1,537	0.07%
Common Blackbird, *Turdus merula*	1,237	0.05%
Stock Dove, *Columba oenas*	577	0.03%
Great Tit, *Parus major*	332	0.01%

* - a proxy for proportion of time with the species present at feeding sites

operation (serving as a proxy for the percentage of time with bird presence). Most photos with birds included only one species (87.8%), with a maximum of four species in a single photo (only 20 photos). The Jay (*Garrulus glandarius*) was the most common species at feeding sites and the top three species (including Raven, *Corvus corax,* and Wood Pigeon, *Columba palumbus*) accounted for 85.8% of all photos with birds. Among all species, eight were present in more than 100 photos (Table 1).

3.2. Temporal occurrence of birds at feeding sites

When comparing temporal patterns of occurrence, most species were divided into three clusters. The largest cluster included eight species, including Sparrowhawk (*Accipiter nisus*), with Sparrowhawk and Jay being the closest, followed by White-tailed Eagle (*Haliaeetus albicilla*) and Raven and Wood Pigeon and Stock Dove (*Columba oenas*) (Fig. 2).

Seven out of the eight species with more than 100 photographs were present throughout the study period from March to November (Fig. 3). The only exception was Stock Dove, which was present in only nine photographs after July and completely absent in October and November. Although most species were present throughout the studied period, there were marked differences in the frequency of their presence. For example, Jay, Wood Pigeon, Raven and Stock Dove had unimodal monthly distributions; Chaffinch (*Fringilla coelebs*) and Great Tit had bimodal distributions; and Blackbird (*Turdus merula*) and Buzzard (*Buteo buteo*) had multimodal monthly distributions. Each species had its peak or peaks in different months (Fig. 3). Four species (Jay, Wood Pigeon, Chaffinch, Great Tit) peaked in late summer, two (Raven and Buzzard) peaked in fall and only one peaked in May (Stock Dove) and April (Chaffinch).

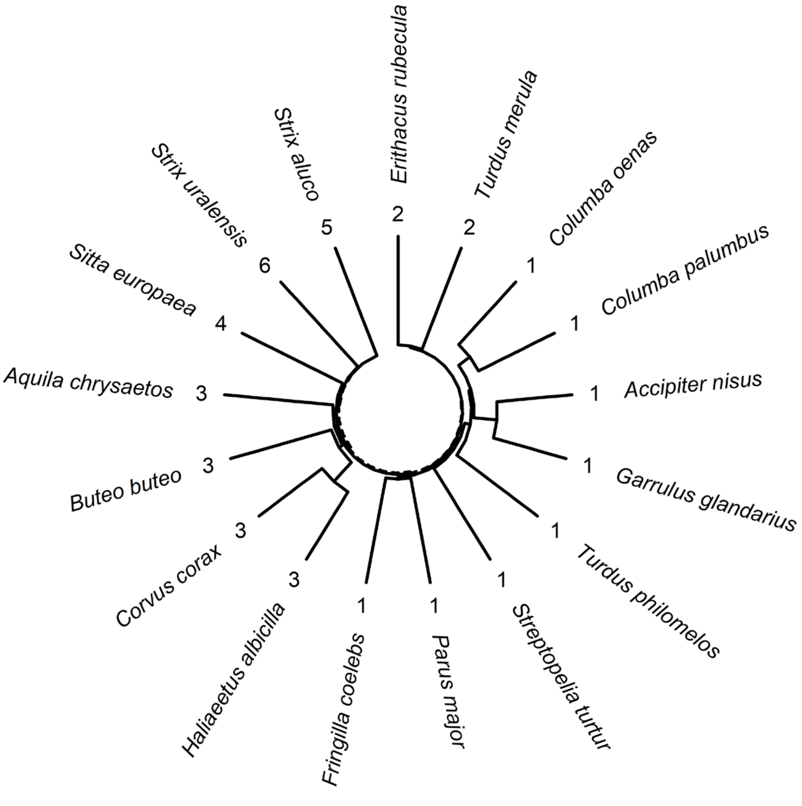

Fig. 2. Cluster dendrogram based on temporal distribution (circadian occurrence in hours per day, and seasonal presence in months per year) of bird species with more than 10 records. Species with a similar colour are similar in their temporal activity.

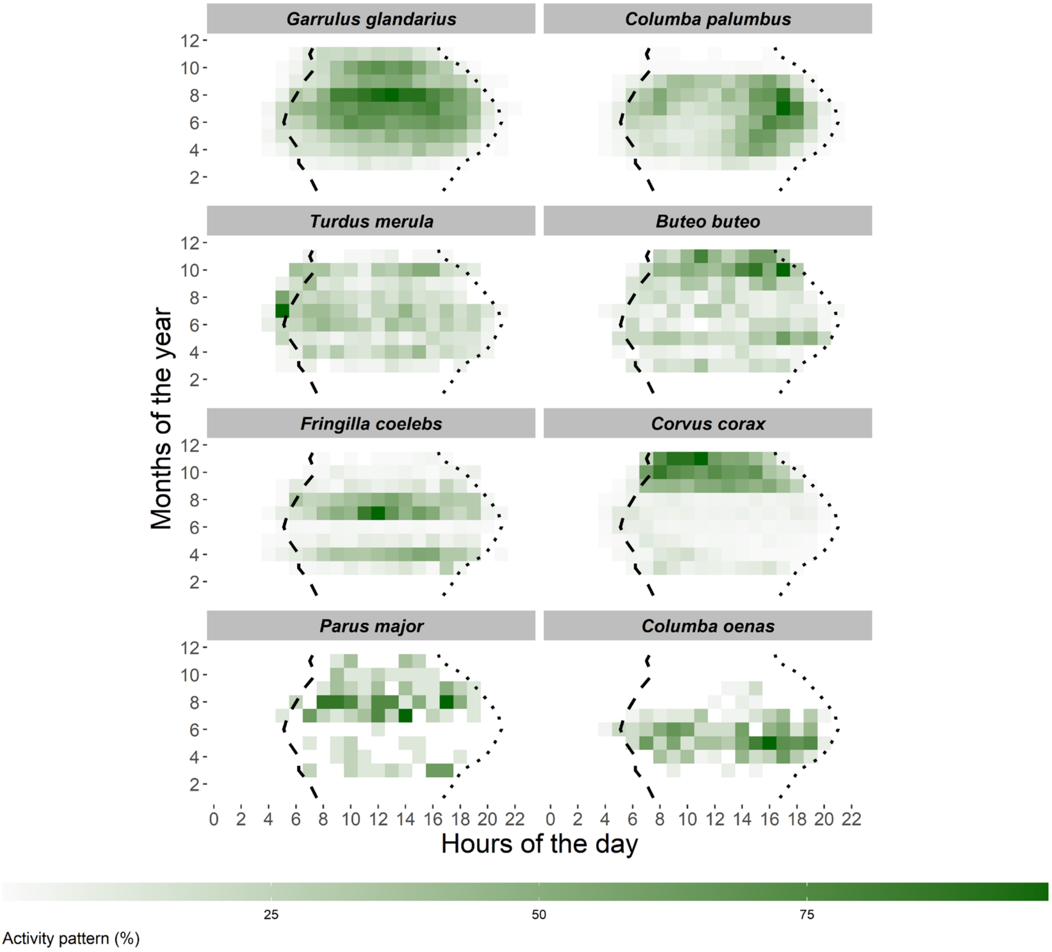

Fig. 3. Temporal distribution of selected species according to detected monthly and hourly occurrence at artificial feeding sites in Slovenia. The activity pattern is a scaled index between 0 and 100%. It was calculated by dividing the number of independent records in a given hour by the maximum number of independent records in an hour for a given species. Lines indicate an average monthly sunrise (dashed line) and sunset (dotted line).

Although all selected species were present throughout the day, the Watson–Wheeler test for differences in activity distributions showed significant differences ($p=0.001$ at $df=2$) in the temporal activity patterns for all species comparisons: Ravens and Blackbirds were more often present in the morning; Chaffinches and Jays in the middle of the day; and Wood Pigeons, Stock Doves and Buzzards in the afternoon (Fig. 3).

3.3. Temporal occurrence of birds and comparison with mammals

The highest percentage of birds was photographed in September (Fig. 4). The overall distribution of the monthly presence of birds and mammals was similar, but the correlation was not significant (Spearman's $r=0.53$, $df=8$; $p=0.1475$). Birds peaked in fall while mammals were more abundant in summer (Fig. 4). The only month in which there were more birds than mammals was October, and both groups had similar presence in September.

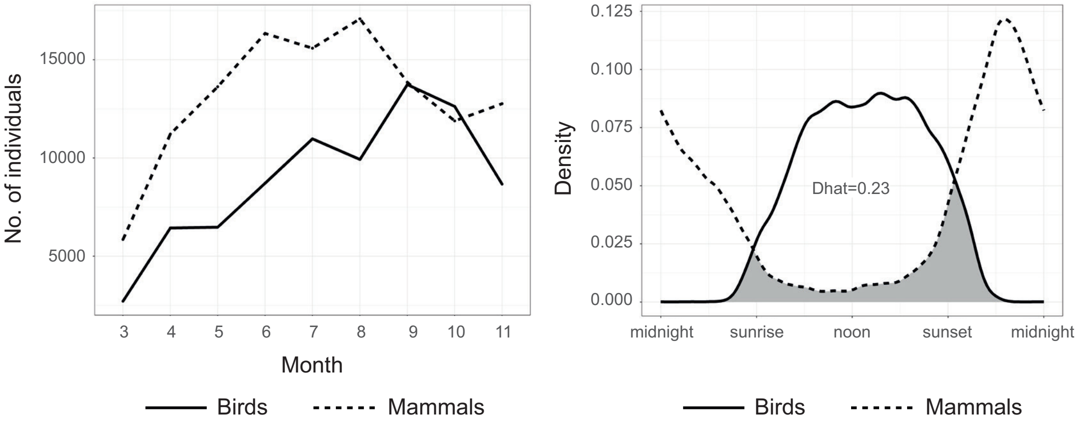

Fig. 4. Monthly and hourly (adjusted to sun time) distribution of mammals (dashed line) and birds (solid line) captured with camera traps in Slovenia between March and November.

Birds were photographed exclusively during the day (Fig. 4), with the exception of a few photos of owls taken at night. Most birds were photographed in the afternoon, with a peak between 2 and 3 pm (9.3% of photos). The occurrence of birds at feeding sites had an "inverted" hourly distribution compared to mammals (Spearman's r=–0.75, df=22; p<0.001). They were almost completely absent at night when most mammals were present, but abundant during the day when mammals were rare. The shift occurred just before sunrise in the morning and just after sunset in the evening (Fig. 4).

4. Discussion

4.1. Bird species occurring at feeding sites

The present study reports the highest number of bird species (35) reported to date at a wild game feeding site. To date, most studies have reported fewer than 10 taxa (Lambert & Demaris 2001; Bowman *et al.* 2015; Selva *et al.* 2017; Candler *et al.* 2019; Fležar *et al.* 2019), but this may be due in part to the grouping of species into passerine birds (Lambert & Demaris 2001), unknown birds (Bowman *et al.* 2015) or small and medium-sized birds (Fležar *et al.* 2019). Other possible reasons for the greater species diversity of birds in our study compared to other studies include shorter monitoring periods in other studies (Lambert & Demaris 2001; Bowman *et al.* 2015; Fležar *et al.* 2019), specific baits (Candler *et al.* 2019) and a focus on a specific group, such as potential nest predators (Selva *et al.* 2014). We detected about half of all breeding species in surrounding Karst upland forests (Mihelič *et al.* 2019; Fležar *et al.* 2019). It is possible that some species were overlooked in the study because they are too small to trigger cameras (Randler & Kalb 2018), but this seems unlikely for two reasons: 1) Most smaller species that breed in the surrounding forests and were not detected at feeding sites are either insectivorous or foraging specialists (Mihelič *et al.* 2019) and would only be accidental at feeding sites; 2) Only a few species found in surrounding forests are smaller than Coal, Blue and Marsh Tits (*e.g.*, Goldcrest, *Regulus regulus*) and most avoid open areas such as clearings. On the other hand, a few abundant species breeding in the vicinity were expected but not recorded in the study, such as several finch species (*e.g.*, Goldfinch, *C. carduelis,* or Hawfinch, *C. coccothraustes*) and two remaining tit species (Crested Tit, *Lophophanus cristatus,* and Willow Tit, *Poecile montanus*). Also, more species could have been observed during the migration and winter periods, such as the abundant Marsh Harrier (*Circus aeruginosus*), which often feeds on carrion and hunts rodents (Orta *et al.* 2020), or Starling (*Sturnus vulgaris*), which feeds on corn and visits feeders (Cabe 2020).

Although we divided birds into groups based on their temporal occurrence at the feeding sites, the groups actually represent the types of food the birds ate. Most detected species were either granivores (7 species) or scavengers (4 species) and were grouped as such. There were a few exceptions, the most important of which was the Sparrowhawk, which was grouped with granivorous species, indicating a predatory response to the temporal presence of its prey (Botts *et al.* 2020). Out of five species not included in the two biggest clusters, two formed a separate group. These two were probably not attracted to either type of food offered (corn and carrion) or to potential prey attracted to the food (mice, birds). Both feed on seeds and grains and likely eat some of the available corn, but the majority of their diet consists of invertebrates (Collar 2020; Collar & Christie 2020). Both species likely only take advantage of forest clearings that result from maintained feeding sites and do not adjust their presence to the availability of offered food.

4.2. Seasonal and circadian occurrence

The availability of certain types of food at feeding sites changes over time, and the temporal activity of birds reflects these changes for some, but not all, species. Automatic feeders generally dispensed corn in the late afternoon or evening, while sites supplied by hand were visited by managers during the day. Wood Pigeons and Stock Doves, which are primarily grain feeders and frequently feed on corn (Billerman *et al.* 2020), peaked in the afternoon when corn was most available. Ravens and Buzzards also likely responded to carrion availability, peaking during the period of highest human hunting activity from September to November, confirming the importance of human-provided carrion for Ravens (Legagneux *et al.* 2014). On the other hand, the availability of artificial food does not appear to strongly influence the temporal presence of Chaffinches and Jays, although both frequently feed on grains (Clement 2020; Madge *et al.* 2020). Chaffinches, for example, peaked in the middle of the day and in April and late summer, most likely due to migration and dispersal (Clement 2020). In addition, seeds are only an important food for Chaffinches outside of the breeding season (Clement 2020), which at least partly explains their lower presence in May and June, when they feed mainly on invertebrates. It is less clear why they peak in the middle of the day, since most of their food is available in the afternoon. One possible explanation is competitive niche displacement (Carother & Jaksić 1984) in combination with predator pressure. Chaffinches occurred when few other species were present, so they avoided possible predators and larger and more competitive granivores that feed on the ground (*e.g.*, pigeons). Although Jays are also granivores, they peaked at midday rather than in the afternoon like pigeons. One explanation for the observed difference could be a feeding adaptation. The Jay's ability to feed along branches allows it to feed on corn high up on artificial feeders that is inaccessible to most mammals. Although the quantities are small, corn is thus available to jays for most of the day. In fact, they were often observed feeding on corn directly from feeders. In addition, Jays occur in smaller groups (Madge *et al.* 2020; present study), each of which requires a smaller amount of food than a group of pigeons.

Artificial food also indirectly influences bird activity and food choice through the presence of other species. At the studied feeding sites, this is true for predators such as Sparrowhawks and owls. Constantly available corn attracts small rodents and several small to medium-sized bird species (Fležar *et al.* 2019). While owls attracted to rodents did not change their temporal presence (both rodents and owls are active at night), the Sparrowhawk synchronised its presence at feeding sites with its prey of small and medium-sized birds (Meyburg *et al.* 2020). It probably also hunts smaller species in the granivore group, especially smaller males, but its main prey at feeding sites appears to be Jays, with which it was most closely associated in the cluster analyses. Of the 31 analysed records of Sparrowhawks in our data, four photos/film clips show successful capture and another seven show a close pursuit. The Jay was the most common bird species at feeding sites, but is also at the upper size limit of Sparrowhawk prey (Meyburg *et al.* 2020), suggesting a shift in prey size preference due to prey availability and accessibility. Aside from the high presence of Jays at feeding sites, the habitat and position of prey may also be favourable for the Sparrowhawk. It prefers to hunt in clearings (Meyburg *et al.* 2020), which are not unlike typical managed feeding sites. In addition, most of the food is scattered on the ground in the middle of the clearing, allowing the Sparrowhawk to surprise its prey from above. Overall, feeding sites appear to be a highly concentrated food source for raptors as well.

Although there are a number of similarities between the selected feeding sites, there are some differences that are worth exploring. The biggest difference between feeding sites is in the method of distributing corn. Corn is distributed manually at a few feeding sites. This means that there may be slight variations in the time of distribution, and that there is also the increased presence of people on the site. Also, the presence of some species can influence the temporal distribution of other species (Carother & Jaksić 1984), as was also discussed with respect to Chaffinches. Thus, different feeding sites offer the opportunity to study a possible niche shift.

4.3. Comparison of temporal presence between mammals and birds

The apparent difference in the circadian occurrence of birds and mammals at feeding sites is due to differences in biology and probably also to differences in management between the two groups. Most birds feed during the day, which is clearly reflected in their circadian distribution at feeding sites, where all birds except owls were observed during the day. In contrast, most mammals were detected at night, a pattern also observed at Black Bear bait sites (Candler *et al.* 2019). Most mammals detected at feeding sites are game species, and while some are naturally nocturnal, many became nocturnal due to long-term human disturbance and hunting (Russo *et al.* 1997; Marchand *et al.* 2014; Hertel *et al.* 2016). In the Slovenian Dinarics, most game species are hunted at feeding sites, making these sites areas of higher "predation risk" in the "landscape of fear" (Laundré *et al.* 2010) and possibly even exacerbating nocturnal behaviour at feeding sites. The difference in the circadian occurrence of mammals and birds provides an opportunity to reduce the amount of food at feeding sites, reduce costs and reduce impacts to birds (non-target species) while maintaining all of the desired effects of artificial feeding on game mammals (target species). Although birds were detected on approximately 30% fewer photographs than mammals at feeding sites and their biomass is an order of magnitude lower, birds still occur often and likely consume a significant portion of the available food. Most feeding sites are designed for mammals, not birds. Therefore, if the majority of the food is to reach the desired species, it should be available just after sunset when bird presence is decreasing and mammals can be present in notable numbers.

Although there are some similarities between birds and mammals in terms of monthly occurrence, there are also some important differences. One of the possible reasons for the earlier decline in mammals in autumn could be the hunting season, which begins in September for many game species in Slovenia (Adamič & Jerina 2010). Almost all mammal species detected at feeding sites are game species. The decline of game species at feeding sites during the hunting season has also been documented in other studies (*e.g.*, Candler *et al.* 2019). On the other hand, of the birds recorded, only the Jay and the Hooded Crow (*Corvus cornix*) (only one record in the study) are hunted in Slovenia, and although the Jay was the most frequently recorded species, hunting interest in this species is low (up to 4000 individuals culled in the country, compared to more than 40,000 Roe Deer, *C. caprelous*). The avoidance of feeders by game species because of hunting is likely since preliminary results in mammal temporal distribution suggest that at least some species (*e.g.*, Wild Boar) are less often observed during the day in the hunting season than outside of it. In addition, in years with a good beech mast, a huge quantity of preferred natural food is available for many game species. Beech masting affects the presence of birds at feeders (Chamberlain *et al.* 2007), but the effect at feeding sites appears to be less pronounced for birds than for game mammals. The peak of bird occurrence in early October also coincides with the peak migration period for many species at feeding sites, *e.g.*, Wood Pigeon, Blackbird, Chaffinch and Buzzard (Billerman *et al.* 2020).

4.4. Conclusions

The study offers valuable insights into the temporal occurrence of birds in natural systems and the impact of artificial food on this phenomenon. For some bird species, artificial food constitutes a significant food source, causing them to adjust their temporal occurrence to the availability of this food, either directly or through an increase in the presence of the prey. For other species the influence is less direct, since they can be attracted to the food offered but their presence is also shaped by the presence of other species. The role of different types of feeding methods is worth studying, particularly for the species demonstrating greater temporal adaptation to artificial feeding. However, for some bird species, feeding sites simply provide a suitable habitat. The study raises several questions. A more in-depth investigation of bird-mammal interactions and avoidance behaviours is necessary, particularly during sunrise and sunset when the overlap is greatest. Additionally, exploring the relationship between the temporal availability of food and bird-mammal relations by manipulating the time of food availability would also be a noteworthy area of study.

Lintujen lajikoostumus ja ajallinen esiintyminen riistanisäkkäille tarkoitetuilla ruokintapaikoilla Dinaarisilla vuorilla Sloveniassa

Lisäruokinta on laajalti käytetty riistanhoitomenetelmä. Se kuitenkin houkuttelee ruokintapaikoille usein muitakin kuin kohdelajeja, esimerkiksi lintuja. Tässä tutkimuksessa seurasimme karhuille suunnattuja ruokintapaikkoja ja niillä vierailevia lintuja Dinaaristen Alppien metsissä. Tarkkailuun käytettiin kameroita. Ruokintapaikoilla havaittiin 35 eri lintulajia, mikä edustaa noin puolta lähialueen pesimälajeista. Ryhmittelimme lajit niiden ajallisen esiintymisen perusteella, mutta ryhmät vastasivat myös lajien ruokavaliota suurimman osa kuuluessa siemen- tai raadonsyöjiin. Joidenkin lajien, kuten kyyhken (*Columba* spp.), korppien (*Corvux corax*) ja hiirihaukkojen (*Buteo buteo*) läsnäolo riippui ravinnon saatavuudesta ruokintapaikoilla. Toisiin lajeihin tämä ei vaikuttanut. Sekä peipot (*Fringilla coelebs*) että närhet (*Garrulus glandarius*) kävivät usein ruokintapaikoilla, mutta niiden ajalliseen läsnäoloon vaikuttivat lajien biologia, ei ravinnon saatavuus. Myös varpushaukat (*Accipiter nisus*) sopeuttivat läsnäoloaan ravinnon saatavuuteen, minkä lisäksi niiden läsnäolo liittyi närhien esiintymiseen. Tutkimuksemme osoittaa, että ruokintapaikkojen käyttö on linnuilla ja nisäkkäillä erilaista, mikä todennäköisesti johtuu niiden erilaisesta biologiasta. Tutkimuksen tietoa voidaan hyödyntää esimerkiksi riistanhoidossa, ja lisäksi se auttaa vähentämään lisäruokinnan ei-toivottuja vaikutuksia.

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Appendix

Appendix 1. Recorded species and the number of photographs per species and the number of photographs with only one individual of a species taken on artificial feeding sites in the Dinaric Mountains of Slovenia in 2016 and 2017.

Species	No. of photos	No. of photos with just one individual
Garrulus glandarius	19356	12783
Corvus corax	9882	3446
Columba palumbus	9748	4415
Fringilla coelebs	2416	1197
Buteo buteo	1537	1423
Turdus merula	1237	1050
Columba oenas	577	333
Parus major	332	254
Erithacus rubecula	58	52
Sitta europaea	31	29
Accipiter nisus	31	31
Motacilla alba	28	23
Aquila chrysaetos	28	28
Strix aluco	25	25
Turdus philomelos	22	22
Strix uralensis	22	22
Accipiter gentilis	21	21
Streptopelia turtur	15	12
Haliaeetus albicilla	13	13
Turdus viscivorus	13	13
Poecile palustris	11	8
Cyanistes caeruleus	9	6
Dendrocopos major	5	5
Pernis apivorus	4	4
Phoenicurus ochruros	4	4
Milvus milvus	2	2
Dendrocoptes medius	2	2
Hirundo rustica	1	0
Falco subbuteo	1	1
Falco peregrinus	1	1
Caprimulgus europaeus	1	1
Dryocopus martius	1	1
Periparus ater	1	1
Corcus cornix	1	1
Chloris chloris	1	1

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Home-range, movements and use of powerline poles of Eagle-Owls (*Bubo bubo*) at an island population in northern Norway

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A dense island population of Eagle-Owls (*Bubo bubo)* close to the Arctic circle had suffered considerable mortality due to powerlines (electrocution and collision) throughout many decades. A study using GPS transmitter technology was carried out between 2009 and 2014. We studied home-range sizes, dispersal distances, mortality, and proposed mitigation techniques to prevent accidents. We found as expected that juvenile Eagle-Owls had larger home-ranges and moved farther than adults, but both age-groups moved much less than shown elsewhere in Europe. The probable reason for this was thought to be that this population was isolated by the surrounding sea, which might act as a barrier. The GPS data indicated that the poles of the grid were used as perching posts more than expected from a random distribution. This was explained by the lack of high trees and other elevated landscape features on these low islands. As a mitigation effort, we contributed to designing a perching-device for fitting on the poles that would prevent electrocution of the owls. This is now used by several grid-owners in coastal areas with high electrocution risk and is followed up by the National action plan for Eagle-Owl in Norway.

1. Introduction

The Eurasian Eagle-Owl (*Bubo bubo)* is the largest owl species in the world. It is a nocturnal raptor, is highly adaptive and can be found in many different environments, ranging from deserts to forests and arctic tundra (Penteriani & Delgado 2019). In Norway it is mainly distributed from southern Norway up to the Arctic circle in the north. The study took place at the archipelago of Solværøyane in Lurøy municipality, Nordland county, 12°35’ E, 66°22’ N (Fig. 1). The main food of the Eagle-Owl in our study area in Nordland is Water vole (*Arvicola amphibius)*, which has a yearly fluctuation in numbers (Frafjord 2022). In years of low vole numbers, the owls have access to a variety of other food species, as the Eagle-Owl is a versatile hunter and preys on a wide range of vertebrate species, such as small rodents, rats, hares, frogs, seabirds and even fish. Its diet depends on the availability of prey and might differ between locations (Willgohs 1974, Obuch & Bangjord 2016). The archipelago lies close to the Arctic circle, and therefore there is broad daylight during most of the hours during the summer months. The Eagle-Owls here must therefore hunt in light conditions during most of the summer.

The Eagle-Owl population in Norway has declined since the 1900-century (Hagen 1952, Haftorn 1971). The species was protected in 1971 and is classified as an endangered species on the Norwegian Red List for Species (Stokke *et al.* 2021). The number of breeding pairs is now estimated at 451–681 (Øien *et al.* 2014). The Eagle-Owl has historically been severely persecuted in Norway. After it gained its protected status the decline has continued (Fremming 1986, Shimmings & Øien 2015), due to electrocutions, habitat changes, decline of prey stocks, environmental pollutants and disturbance (Frøslie *et al.* 1986, Heggøy & Shimmings 2020). Electrocution has been a major factor for the decline (Bevanger & Overskaug 1998), and is recognized as a major problem for the Eagle-Owl elsewhere in its range (Bevanger 1994, Bevanger 1998, Sergio *et al.* 2004, Fransson *et al.* 2019)

In the current study, we tracked Eagle-Owls using satellite telemetry, focusing on movements and mortality. Over the past 30 years, members

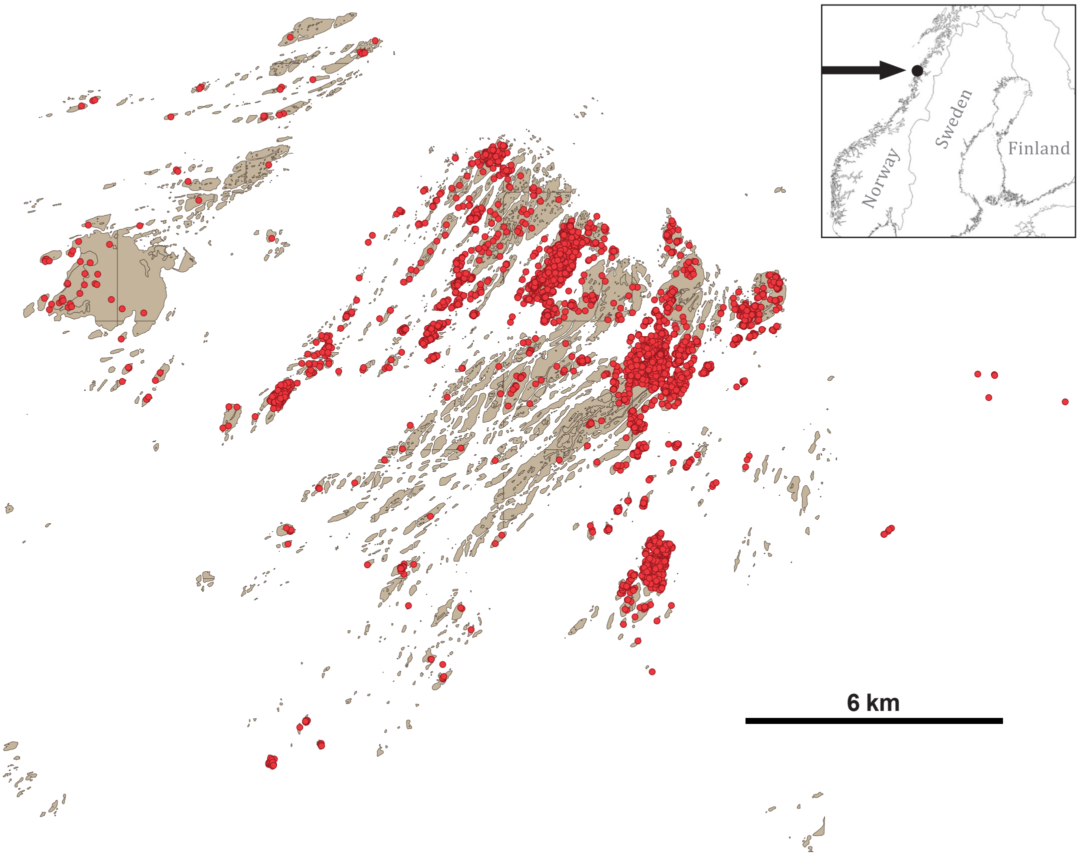

Fig. 1. All GPS positions of all individual Eagle-Owls tagged with GPS transmitters. Location map refers to the southern part of Fennoscandia with the study area of Solværøyane (12°35’ E, 66°22’ N) indicated with an arrow and a black dot.

of the Rana Zoological Society have found 30–40 dead Eagle-Owls in connection with power lines in the study area, of which about 90% of the individuals were probably killed by electrocution, the rest by collisions (Espen Rolv Dahl pers. comm. in Gjershaug *et al.* 2015). Being the densest population of Eagle-Owl in Norway, and because of the high mortality of owls found killed by the distribution grid here, Solværøyane was chosen as a good place to study movements of the owls in relation to the local power-grid. One of the main goals was to investigate the extent to which the Eagle-Owl used power poles as perches during hunting, to study dispersal and home ranges, and to locate dead tagged individuals and note the causes of deaths. To obtain this, we used accurate GPS satellite telemetry tags on the birds. The Norwegian authorities issued a national action plan for Eagle-Owl in 2009 (Direktoratet for naturforvaltning 2009). At the same time, the Norwegian Research Council was funding a research program OPTIPOL, which in part aimed at studying risks of, and potential mitigation methods for Eagle-Owl electrocutions. Our project was a part of this.

2. Material and methods

The study area is a group of low islands called Solværøyane and has a sparse human population. The area consists of a group of 1,841 islands and skerries. The total area is 30.1 km^2. Sheep are grazing the islands, and the vegetation consists mainly of heather, grass and low-growing birches. The shortest distance to the mainland is 14 km. The islands have a population of at most 26 breeding pairs of Eagle-Owls. The islands have 9 km of powerlines, with altogether 138 poles. The project started in 2008, and the tagging went on from 2009 to 2014. To study the movements of the owls, GPS back-pack tags of different designs were employed on both nestlings and adults. The study was carried out under a permission from the Norwegian animal welfare committee (Permits no. 2014/101595 and 2012/54696). The nestlings were tagged when they had just left the nest and were fully feathered, while the adults were caught in claptraps and bownets. In total, 18 nestlings and 5 adults were employed with satellite tags of a back-pack design with harnesses (Buehler *et al.* 1995). As the site is close to the Arctic circle, the light conditions were only adequate to power solar-powered transmitters during the summer season. Therefore, a combination of battery-powered tags (15 of Microwave Telemetry LC 40, (40 g) one on an adult and 14 on juveniles) and solar-powered tags (8 of Microwave Telemetry Argos/GPS 45 g, 4 on adults, 4 on juveniles) were used (Microwave Telemetry, Inc.) (Table 1). The LC 40 gave one position per day (at midnight), while the Argos/GPS 45 was programmed to give a position at 01, 05, 09, 13, 17 and 21 H. The first two adults were fitted with transmitters with harnesses made of Teflon ribbon (PTFE | Bally Ribbon Mills). We soon found out that the adults were able to remove the harnesses, presumably by snipping them off with the beak, so they were lost after a few days and giving very limited data for use. The ribbons were tubular, so we later reinforced them with inserted braided nylon thread, and subsequently reused the dropped transmitter tags. Maps and home-ranges were produced using QGIS (v.3.10 Coruna) and presented as minimum convex polygons (MCP) 100%, using all GPS data from the study period. Statistics and graphs were made using SPSS (v.27, IBM Corporation 2020). We created a smoothed buffer of 200 m distance from the row of poles. From the base-map we did the same, omitting the areas in the sea. The reason why we chose the 200 m buffer distance, was that within this distance the pylons were available as a choice for perching. There are no high trees at Solværøyene, only low bushes, mostly heather and bogs, and no high lookout-points. Then we created a buffer of 20 m radius around each power-pole as a "target area". The GPS transmitters have an expected accuracy of *ca.* +/–18 m (MTI: Choosing a Transmitter, microwavetelemetry.com), and we obtained accurate positions of the pylons by using our own GPS devices. We assumed that positions less than 20 m from the poles probably were of birds using a pole as a perch. Positions further away than 200 m from the gridlines were excluded from the calculations of perching preference, as they were too far away from the poles as perching alternatives. As the islands have very few and low trees, the poles serve as attractive places to perch and look for voles and other prey.

3. Results

Excluding the italicized individuals in Table 1, three adults gave 110–2,413 positions, while 12 juveniles gave 99–1,212 positions, excluding the day of tagging. Fig. 1 shows all the positions for all birds. The number of days from tagging to last signal of juveniles varied between 5 and 428, and of adults from 3 to 1,874. Juveniles with less than 100 days of data were, however, excluded from further calculations. The most short-lived transmitters could partly be explained by early death of juveniles, and of transmitter loss, especially in the adults. Consequently, during the further

Table 1. Home ranges, maximal dispersal distances and position data of the different Eagle-Owls tagged with GPS transmitters (day 0 excluded). For juveniles, individuals giving less than 100 days of data, found or likely dead are excluded from the overall calculations (in italics and marked with an asterisk). N was too small to calculate statistics for adults. Fate: T = transmitter loss, D = dead or likely dead.

Individual	Transmitter type	Sex	MCP 100, km^2	No. of days	No. of pos.	Pos./ day	Max dist. from nest (km)	Fate
Adults								
57268	Argos GPS 45 g	F	14.10	1874	2413	1.3	3.49	
*95335**	*Argos GPS 45 g*	F	0.24	5	97	19.4	0.59	T
95336*	Argos GPS 45 g	F	0.45	*4*	*53*	*17.7*	*0.76*	*T*
107843	LC4 40g	M	2.62	242	478	2.0	1.91	
195335	Argos GPS 45 g	M	0.67	734	110	0.1	1.01	D
Juveniles								
57269	Argos GPS 45 g	M	10.67	382	607	0.8	7.69	D
57270	LC4 40g	F	0.58	188	322	1.7	0.87	
95331	LC4 40g	M	27.47	138	132	1.0	8.13	
*95332**	*LC4 40g*	M	0.20	54	60	0.9	0.38	D
95333*	LC4 40g	*M*	*1.05*	*77*	*75*	*1.0*	*2.94*	
95334	LC4 40g	M	93.78	117	109	0.9	16.70	
*95337**	*Argos GPS 45 g*	*M*	*0.03*	*36*	*33*	*6.6*	*0.27*	*D*
107841	LC4 40g	M	24.09	123	212	1.7	13.13	
107842	LC4 40g	M	40.50	165	323	2.0	10.69	
107844	LC4 40g	M	0.83	112	211	1.9	1.83	
115976	LC4 40g	M	57.19	145	279	1.9	9.68	
115977	LC4 40g	M	31.37	133	259	1.9	7.29	
*115978**	*LC4 40g*	*M*	*0.01*	*21*	*48*	*1.2*	*0.21*	*D*
115979	LC4 40g	M	110.31	125	230	1.8	9.95	
195332	LC4 40g	M	19.87	100	99	1.0	7.68	
195336	Argos GPS 45 g	F	70.04	428	1212	2.8	10.69	
*195337**	*Argos GPS 45 g*	M	0.46	69	380	5.5	1.05	D
215978*	LC4 40g	*M*	*1.27*	*71*	*132*	*1.9*	*1.37*	
Average	Juveniles		37.44	166	307	1.5	8.03	
Minimum	Juveniles		0.58	100	99	0.8	0.87	
Maximum	Juveniles		110.3	428	1212	2.8	16.70	

calculation of home-ranges, the italicized juvenile and adult individuals in Table 1 were omitted. We assumed an individual had died when the last GPS coordinates of the transmitters came from the same place for a period of a few days (n=2).

3.1. Movements

Juveniles. As Fig. 2 shows, little dispersal happened between July 29 (week 30) and September 17 (week 37). From then, there was a gradual increase in movement distances up to October 27 (week 44), from when there was a pronounced increase in movements. Surprisingly, there seems to be a temporary return to the natal area at around November 21 (week 47). This seems to last for only about two weeks, as new movements take place at around December 6 (week 49). Even though the variation is high, these juveniles rarely went further away from their natal site than 5 km (Fig. 2), the maximum distance was 16.7 km.

Much mortality seemed to occur during late autumn or winter, as only three of the juvenile birds gave signals into their second year. The mean date of the last signal during the first year was 12 November, (median 19 Nov, sd=41 d), excluding those with less than 100 days. Three juveniles, born in the moderately high vole year of 2011 (Frafjord 2022), made it into the next calendar year (Ind nr 57269, 57270 and 195336). The last one was born in 2014, a low vole year (Frafjord 2022), and just barely made it into January next year. As most of the transmitters were powered by solar panels, death events were difficult to detect, as the dark winters at this latitude did not provide enough solar power for the transmitters to function properly. A single data point of a juvenile in year three was omitted from Fig. 2. It was from a bird found dead, the exact date of which was impossible to establish.

Adults. As two of the five adults shed their transmitters after a few days, we have usable movement data from only three adults. They did not move far, probably because they were territory-holders, and therefore did not take the risk to leave their territory open for competitors (Fig. 3). One exception was seen in female no. 57268, who took long excursions from her nesting place in the first, second and third autumn, but she was back in March (we lack winter data). The data indicate that she might have bred at a site *ca*. 1 km away from the

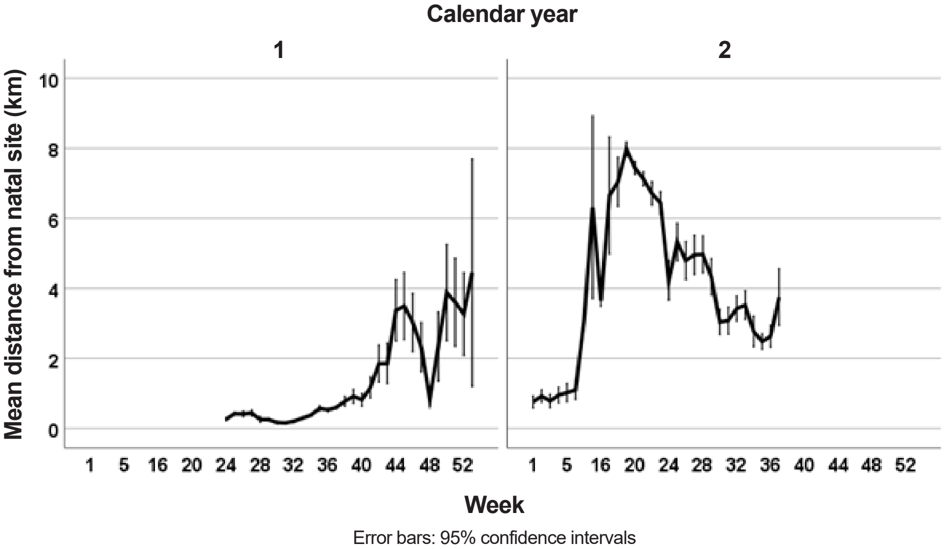

Fig. 2. Movements of juveniles shown as average horizontal distance from nest per bird per week, 95% confidence limits, during their first and second calendar year (n=18 from start, n=12 after Julian day 270).

original site in year three. She was unique in our dataset, as we were able to follow her through six calendar years. She is the only adult represented in the years four, five and six in Fig. 3.

3.2. Home-range

Juveniles. We got little data from many of the juveniles. We don't know the exact reason for this, but early death was probably a main cause. Therefore, we omitted all the juveniles who gave less than 100 days of data before calculating MCPs (minimum convex polygons) for their segment of the population. That left us with 12 birds (Fig. 4). MCP 100 of these juveniles varied from 0.58 to 110.3 km^2, the mean was 27.2 km^2. There may also have been some mortality among the 12 tagged birds that we included in the calculation that we have not been able to record. This could apply to birds no. 107844 and 57270. We did expect the juveniles to roam more than the breeding adults, and this was true in general. Juvenile no. 115979 used an area of 110 km^2, which covers almost the entire archipelago of Solværøyane, almost three times the average for the juveniles. All the tagged juveniles stayed in Solværøyane, none ever visited the mainland or nearby archipelagos.

Adults. The minimum convex polygons of the three remaining adults after exclusion of the two that gave signal for five days and less, varied from 0.67 to 14.1 km^2 (Fig. 5). The average MCP 100 of the three remaining adults were 5.8 km^2. Male no. 195335 was tagged on June 16 in 2009, with signals coming from his tag until July 21 the same year. Then the tag was silent until June 17 in 2010 and sent signals until July 21 in 2010. On July 6 2,011 signals were again received from this tag, and it kept transmitting until permanent silence on July 20 in 2011, more than two years after tagging. Such intermittences during the dark period of the year was also seen in female no. 57268, tagged in 2012 who transmitted signals again in May 2013, March 2014, May 2015, May 2016 and April 2017, each time after winter silence.

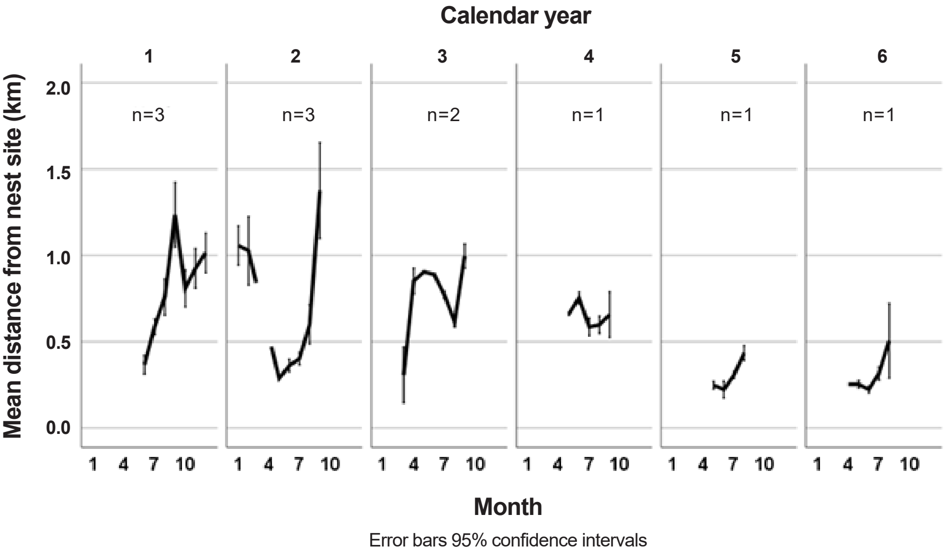

Fig. 3. Mean straight distance (km) between locations and tagging site (nest) by calendar year and month for adult eagle-owls (n = number of individuals). For years 4,5 and 6, only data is from female no. 57268.

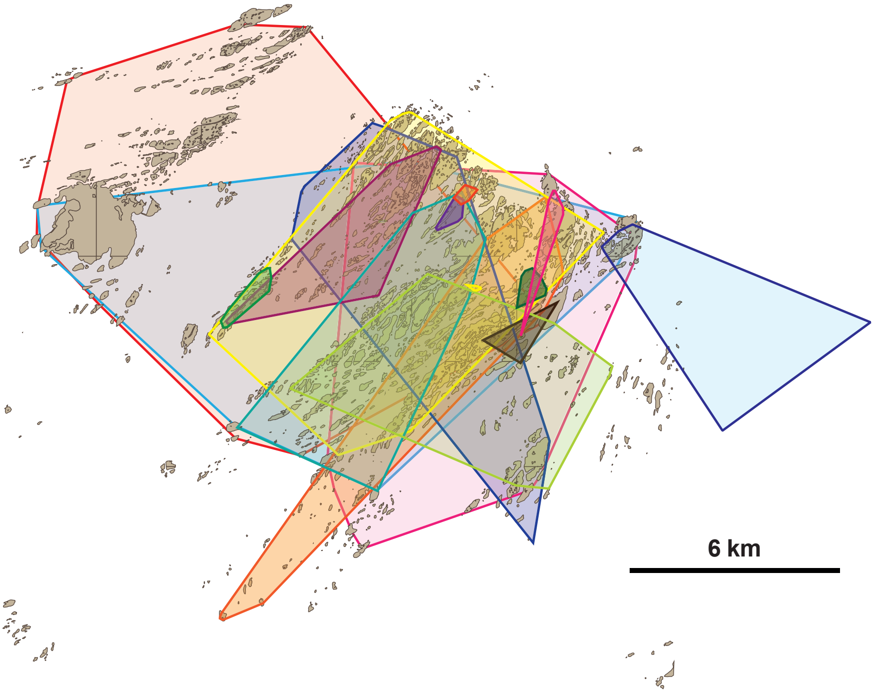

Fig. 4. Home-ranges of all juvenile Eagle-Owls, MCP 100 (n=18). For location reference see Fig. 1.

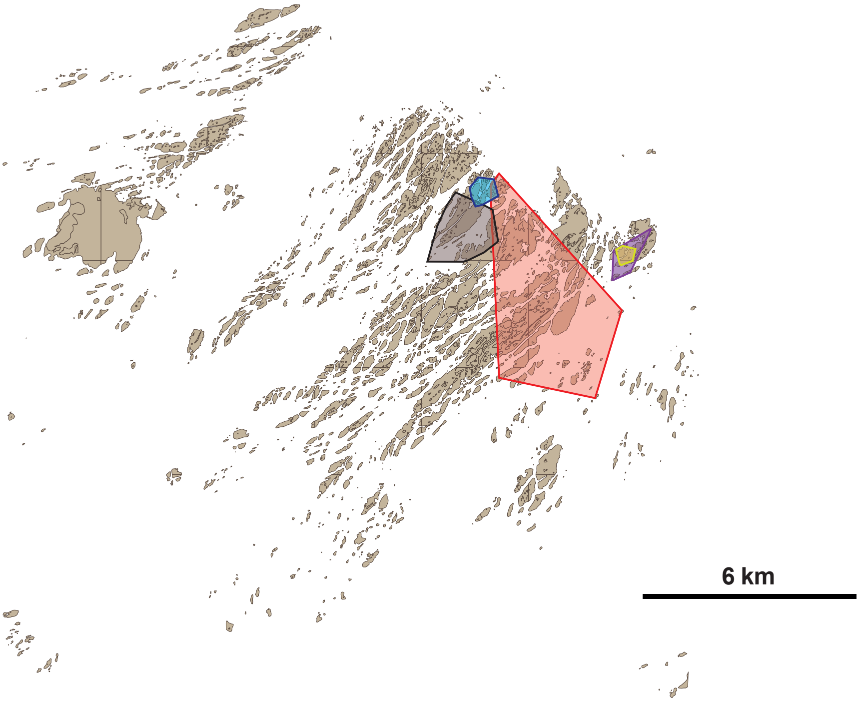

Fig. 5. Home-ranges of all adult Eagle-Owls, MCP 100 (n=5). For location reference see Fig. 1.

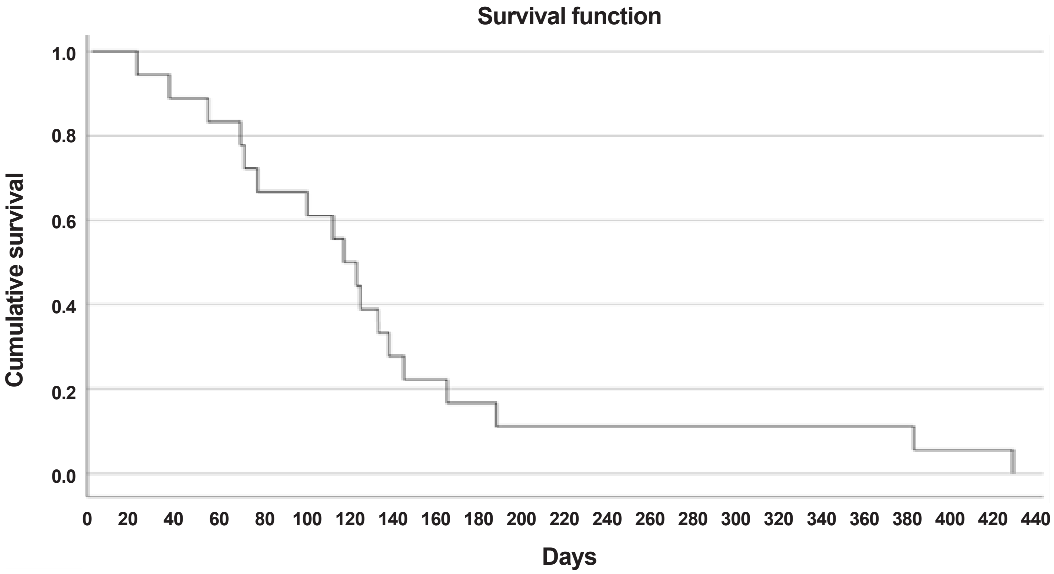

Fig. 6. Estimated survival of juveniles tagged with GPS transmitters (n=18) using the Kaplan-Meier method, in days after deployment. X-axis is days after deployment. Y-axis is fraction surviving (1 = all survived, 0 = all apparently dead).

3.3. Mortality

In only four out of 18 juveniles we were able to observe or define death of birds with a reasonable degree of certainty. A Kaplan-Meier analysis of survival showed that at 100 days, 61% of the juveniles were expected to survive, but only 11% after 200 days (Fig. 6). Birds with missing signals without confirmed death are treated as censored in the analysis. The implied survival rates must be therefore taken with great care, as for most of the juveniles we were not able to confirm death, or to distinguish transmitter failure from death.

3.4. Use of power-poles for perching

In the QGIS analysis, we used only the birds that had an overlapping home-range with the 200 m buffer, and which had 50 or more positions within the buffer. Six juveniles and two adults fulfilled that criterium. Out of 4,792 datapoints of juveniles 635 were from within this buffer, but only 32 out of these were overlapping with the 20 m buffer around poles (5.0% of positions, 4.2% average between birds). Only two adults fulfilled our selection criteria, females 95335 and 57268. (Table 2). The adult female 57268 had far more positions than any other bird. From a total of 2,420 positions, 1,115 were within the 200 m buffer around poles. Out of these, 245 overlapped with the 20 m radius (22.0%). We assumed she was perching in these cases. Perching is the normal hunting preparation method of the Eagle-Owl (Penteriani & Delgado 2019). Using QGIS, we created 1,115 random points within the 200 m buffer. Only 80 of these overlapped with the 20 m radius buffers around the pylons. There was a highly significant difference between the random points and the actual points of female 57268 ($p<0.001$, Chi-square test) (Fig. 7). If we include female 95335 in the calculation, the average of adults becomes 13.9% of overlapping positions with poles.

One of the practical outcomes of the project was an effort to minimize the number of electrocutions caused by the Eagle-Owls perching on “killer-poles”. A deterrent device was constructed as a suggestion by the team, consisting of an arm fitted onto the crossbar that had an elevated extension to the side, and spikes extending upwards on the full length of the crossbar (Fig. 8). This was to encourage the birds to perch on the elevated extension, thereby

Table 2. The frequency of GPS positions of Eagle-Owls and power-poles within a 20 m radius around a power-pole and within a 200 m buffer around poles. Only birds with more than 50 positions within the buffer zone were included. Averages are the average between individual birds.

Bird no.	No. of GPS positions	No. of GPS positions inside 200 m buffer	No. of overlapping positions with 20 m radius	Fraction of overlapping positions with 20 m radius	Age
57268	2420	1115	245	22.0%	Adult
95335	121	103	6	5.8 %	Adult
Sum Adults	2541	1218	251	Average 13.9 %	Adult
57270	325	126	16	12.7 %	Juvenile
95333	77	56	1	1,8	Juvenile
95334	111	50	1	2.0 %	Juvenile
107841	215	158	11	7.0 %	Juvenile
195332	101	81	0	0 %	Juvenile
195336	1220	164	3	1.8 %	Juvenile
Sum juveniles	2049	635	32	Average 4.2 %	Juvenile
All Eagle Owls	4590	1853	283	Average 6.6 %	All

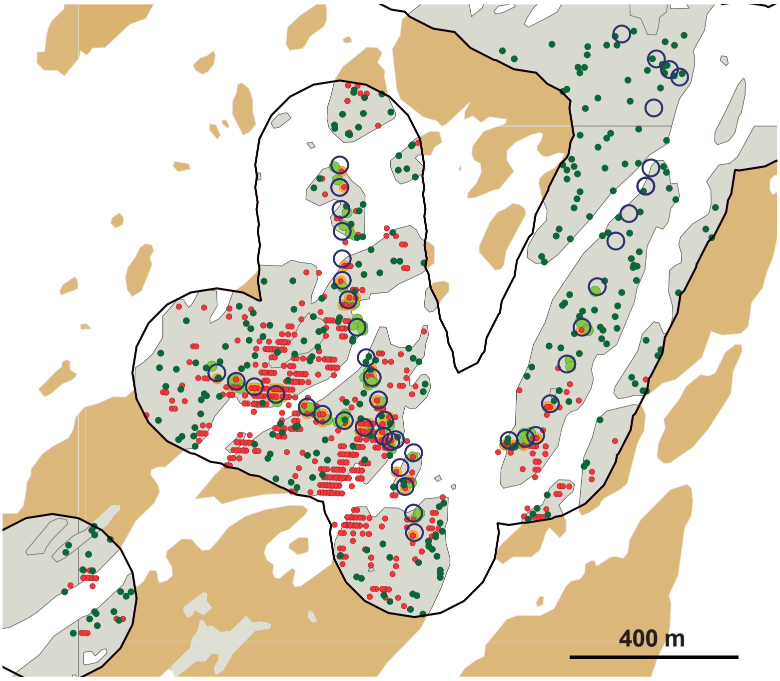

Fig. 7. Section of the map showing overlap between GPS positions of female 57268 (small red circles) and a buffer with radius 200 m around poles (solid line surrounding the area of observations). In cases where female GPS positions overlap with the 20 m radius buffers around poles (large unfilled circles) the GPS positions of female 57268 are highlighted as larger orange circles. Small dark green circles are randomly generated points, and in cases where these random points overlap the 20 m buffers (large open circles) they are highlighted as larger light green circles). All points are restricted within the section of overlap between the home-range of female 57268, the 200 m buffer around pylons and the dry land mass (shown in grey).

escaping from the risk of touching the hot leads. The local power-company has carried out several mitigating measures on the grid at Solværøyene in the period 2012–2014, by fitting a number of poles with deterrent devices as part of the follow-up of the national ‘Action plan for the Eagle-Owl’. This deterrent device has later been mass-produced by El-Tjeneste AS (Hubrostøtte Hsaus - El-tjeneste as | Steinkjer) and fitted on power-poles in Eagle-Owl terrain in several areas throughout the coast of Norway.

4. Discussion

The juveniles’ movement distances (natal dispersal) were much greater than those of the adults. This was as expected, as the adults were breeders, holding a territory. Juveniles are not expected to set up an own territory as a basis for future breeding close to their parents’, partly because the cost of potential inbreeding (Rosenfield & Henny 1992, Szulkin & Sheldon 2008), and partly because lack of vacant space to set up an own territory. The dispersal distance of juveniles normally was between 4 and 8 km from the natal site in our study area, much less compared to what other authors have shown (Olsson 1979, Scherzinger 1987, Saurola 2002, Melling *et al.* 2008, Aebischer *et al.* 2010, Penteriani *et al.* 2012). These authors report juvenile mean dispersal distances between 13 and 72 km. The short distances travelled by the juveniles at Solværøyane is probably best explained by the physical outline of the location. It is a group of islands, separated from the mainland by the open sea, which probably discourages the birds from crossing over. All the tagged juveniles stayed in the Solværøyane archipelago, none ever visited the mainland or nearby archipelagos. It could be done in short intervals through “island hopping”, but it was never proven. Also, the normally good supply of suitable prey on these islands, the Water vole, which is not present at most of the neighboring islands, is also a factor discouraging long dispersal distances. The obvious high mortality of juveniles during their first winter could be explained by the relatively low density of Water voles during most of the time of our study (Frafjord 2022). The mortality rates indicated by our data are considerably higher than those reported in Penteriani & Delgado (2019).

The apparent return to the natal site in late autumn after the first natal dispersal of juveniles is puzzling (Fig. 2), but the same has also been observed in Sweden (Olsson 1979). One possibility is that the juveniles check out whether the breeding site of their parents could offer a vacancy and an opportunity to set up their own

Fig. 8. Eagle-Owl perching on a power-pole with deterrent devices fitted. Photo: Karl-Otto Jacobsen.

territory. Another explanation could be that they are hoping to be fed by their parents at or near the place they were raised, or they return to a familiar place when food becomes scarce.

The size of the home-ranges expressed as MCP 100 were small. This may be explained in the same way as for dispersal; this is a very dense island population, and the propensity to leave the island was small. A study of dispersal in the southern part of Norway showed MCPs of 8.9 to 163.5 km^2 of adult Eagle-Owls during the time when they had chicks in their nests, with a mean of 72.3 km^2 (Heggøy *et al.* 2021). Our oldest female, no. 57268, showed a MCP 100 of only 14.1 km^2, combined over all six years, but we don't have any winter data for this bird. Periods of intermittent signal transmission could be caused by back feathers covering the solar panel wholly or partly, resulting in sufficient charge only during mid-summer.

The results indicate a use of power-poles (within the 20 m buffer) as perch in approximately 20% of the time spent within a range of 200 m from a pole (based on female 57268, as the quality of data for her was better than for any other bird).

The same for juveniles was on average 4.2% but as there were only six juveniles that had home-ranges that were included in the calculations, the results must be interpreted with caution. Even though the frequency of apparent use of the power-poles may seem low in juveniles, only one single contact with the leads could be fatal. Many of the GPS points were from the summer, probably before the juveniles started to hunt for themselves and were still fed by their parents.

We have documented that the Eagle-Owls used the deterrent devices after mounting (Fig. 9), which suggests that this may have an important effect of reducing the mortality caused by the electricity grid, especially at locations where high perches are naturally absent. The use of power-poles as perching-places is prone to increase the probability of Eagle-Owls to become electrocuted. High mortality of Eagle-Owls due to electrocution is shown elsewhere, such as in Italy (Rubolini *et al.* 2001), Finland (Valkama & Saurola 2005), Germany (Brauneis & Hormann 2005), France (Nadal & Balluet 2010), Sweden (Olsson 1979), Spain (Molina-Lopez *et al.* 2011), and Norway (Bevanger & Overskaug 1998). In Norway, pole-mounted transformers was identified as the most serious cause of bird electrocutions (Bevanger 1994). Therefore, mitigation measures are highly needed to prevent electrocutions of the Eagle-Owl. The device described here and shown in Fig. 8, seems to be highly promising, and is now fitted at many stretches of the grid in the vicinity of Eagle-Owl breeding-sites. Hopefully, this will lead to reduced mortality of this endangered species at those sites.

Huuhkajien (*Bubo bubo*) elinpiiri, liikkuminen ja voimalinjapylväiden käyttö Pohjois-Norjan saaristossa

Huuhkajien (*Bubo bubo*) tiheä Norjan saaristossa elävä populaatio lähellä napapiiriä on kärsinyt huomattavasta kuolleisuudesta useiden vuosikymmenten ajan voimalinjoista johtuvien sähköiskujen ja törmäyksien vuoksi. Tässä tutkimuksessa tutkimme huuhkajien elinpiirin kokoa, leviämisetäisyyksiä ja kuolleisuutta vuosina 2009–2014 GPS-lähetinteknologian avulla. Yhtenä tutkimuksen tavoitteena oli löytää sopivia toimintatapoja onnettomuuksien ehkäisemiseksi. Havaitsimme odotetusti, että nuorilla pöllöillä oli laajempi elinpiiri ja että ne liikkuivat kauemmas kuin aikuiset. Kuitenkin molemmat ikäryhmät liikkuivat vähemmän kuin muualla Euroopassa, mikä johtunee siitä, että huuhkajapopulaatio on ympäröivän meren eristämä. Keräämämme aineiston GPS-tiedot osoittavat, että voimalinjojen pylväitä käytettiin tähystys- ja lepopaikkoina enemmän kuin satunnaisjakauman perusteella odotettiin, mikä selittyy korkeiden puiden ja muiden paikkojen puutteella alavilla saarilla. Vahinkojen ehkäisemiseksi ehdotamme pylväisiin suunniteltavien alustojen asentamista sähköiskujen saamisen estämiseksi. Alustoja käyttävät jo useat voimalinjarakenteiden omistajat rannikkoalueilla, joilla on havaittu korkea sähköiskuvaara, ja ne on huomioitu myös Norjan kansallisessa huuhkajien toimintasuunnitelmassa.

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