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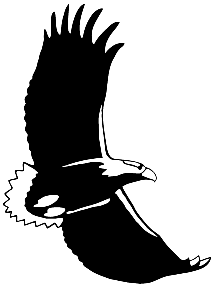

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Publisher Contact – Julkaisijan yhteystiedot – Utgivarens kontaktinformation
BirdLife Suomi ry / BirdLife Finland
Annankatu 29 A, FI-00100 Helsinki, Finland
Phone: +358 9 413 533 00
Telefax: +358 9 413 533 22
E-mail: office@birdlife.fi
Sähköposti – E-post: toimisto@birdlife.fi

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Facultative migration in two thrush species (Fieldfare and Redwing): Rowanberry abundance is more important than winter weather

Svein Dale*

S. Dale, Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, P.O.Box 5003, NO-1432 Ås, Norway
** Corresponding author's e-mail: svein.dale@nmbu.no*

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Facultative migration is thought to be influenced by food and weather, with birds remaining in northern areas if food is abundant and weather conditions are benign, but migrating south when food is scarce and weather is harsh. However, the relative importance of these two factors has rarely been tested with long-term data, and effects of weather are poorly documented. Here, I assess whether winter numbers of the Fieldfare (*Turdus pilaris*) and the Redwing (*T. iliacus*) in southern Norway during the period 1980–2020 varied in relation to the abundance of an important source of winter food (rowanberries, *Sorbus aucuparia*) and indices of winter harshness (North Atlantic Oscillation index, temperature, duration of snow cover). Two regions with contrasting winter harshness (western Norway with a maritime climate, eastern Norway with a continental climate) were compared. Winter numbers of Fieldfare in both regions, and Redwing in eastern Norway, were highest in years with high rowanberry abundance. Weather had mixed influence on thrush winter numbers, but interacted with rowanberry abundance in several cases so that small numbers of thrushes occurred with the combination of low rowanberry abundance and harsh weather. Such interactions occurred both in eastern and western Norway, and for both species, including for the Redwing in western Norway. In conclusion, facultative migration was strongly related to food availability with large numbers wintering in years with large rowanberry crops, and with additional effects of harsh weather working in concert with low rowanberry abundance to reduce wintering numbers to low levels in some years.

1. Introduction

Migratory patterns in birds show substantial variation, from obligate migrants with consistent timing of movements between fixed breeding and wintering areas, to facultative migrants in which timing of movements in particular during autumn is variable, dependent on food availability and weather conditions, so that wintering areas may differ between years (Newton 2008, 2012). Facultative migration typically occurs in species utilizing food sources that are spatially and temporally variable such as fluctuating rodent populations or seed crops from masting trees (Newton 2008). Extreme examples of facultative migration are the so-called irruptive species which in some years may occur in large numbers outside their regular ranges (Bock & Lepthien 1976, Koenig & Knops 2001, Newton 2006, 2008, 2012). Facultative migrants also often occur in northern regions so that southward migration may be triggered by severe winter weather (Haila *et al.* 1986, Newton 2008).

Rowanberries (*Sorbus aucuparia*) are an important food resource during autumn and winter for several European bird species, ranging from irruptive species (Bohemian Waxwing *Bombycilla garrulus*, Bullfinch *Pyrrhula pyrrhula*, Pine Grosbeak *Pinicola enucleator*) to facultative migrants (Fieldfare *Turdus pilaris*, Redwing *T. iliacus*). Rowan is a typical masting tree and produces large crops at 2–3 year intervals in northern Europe (Kobro *et al.* 2003, Gallego Zamorano *et al.* 2018, Dale 2023a). Previous studies have shown a wide range of responses to annual variation in rowanberry crop size. Bullfinches occur irruptively in autumn and winter in southern areas when there is crop failure further north (Fox *et al.* 2009), Pine Grosbeaks move south to exploit abundant crops every 2–3 years (Dale 2023a), whereas waxwings show a more complex pattern with southward migration mostly in years with good crops, but sometimes also in years with poor crops (Dale 2023b). In facultative migrants such as the Fieldfare, parts of the populations stay in northern areas when there is high rowanberry availability, but most individuals migrate south in other years (Tyrväinen 1975, Haila *et al.* 1986, Kanerva *et al.* 2020).

However, there is much less knowledge of how species consuming large amounts of rowanberries when they are available (“rowanberry specialists”) are affected by weather, and there are also few quantitative studies of how facultative migrants in general respond to weather (Newton 2008). Snow cover may be a smaller disadvantage for species foraging in trees than for species feeding on the ground (Newton 2008), whereas cold spells will increase energy demands and may trigger southward migration and limit wintering in northern areas independent of foraging site (Ulfstrand 1963, Zuckerberg *et al.* 2011). Kanerva *et al.* (2020) found that temperature had little influence on the timing of autumn migration in Finland for a variety of irruptive species and facultative migrants. The study of Kanerva *et al.* (2020) is also one of the few that have assessed the relative importance of crop size and weather, and found that crop size was most important for determining timing of autumn migration, including for all the rowanberry specialist species. Similarly, partial migration in many Finnish landbird species was influenced more by tree seed and berry crops than temperature (Meller *et al.* 2016). Interestingly, weather is in general not considered to be important for movements of irruptive species (Newton 2006). Thus, there is mixed evidence for relationships between harsh weather and large-scale winter distribution of facultative migrants.

Here, I analyse 41-year time series of winter numbers of two facultative migrant birds, the Fieldfare and the Redwing, in relation to rowanberry abundance and indices of winter harshness (North Atlantic Oscillation index [NAO], temperature, duration of snow cover) in two parts of southern Norway. My main aim is to assess the relative importance of food and weather in determining wintering in Northern Europe. In general one would expect both factors to influence winter numbers, but the results from Kanerva *et al.* (2020) suggest that food availability might be more important than weather. Furthermore, I test the importance of weather in more detail by comparing winter numbers in two areas of southern Norway: eastern Norway which has a continental climate with snow cover during most winters, and western Norway which has a milder maritime climate with little snow in the lowlands along the coast. The prediction is that the impact of weather would be more evident in eastern than in western Norway. This prediction also follows from the foraging behaviour of these thrushes, because although rowanberries are important during winter, both species may also supplement their diet by foraging on the ground, and then especially snow cover may have a negative impact (Tyrväinen 1970, 1975, Cramp 1988).

2. Material and methods

2.1. Study species and study area

Although Fieldfares and Redwings winter in Norway in variable numbers, large parts of the populations, especially of the Redwing, are migratory. Autumn migration of Redwings is mainly during September–October, and they return in April, whereas Fieldfares migrate south mainly during October–November and return during March–April (Haftorn 1971). For birds staying in Norway and other parts of Fennoscandia during winter fruits and berries are important food sources, in particular rowanberries (Tyrväinen 1970, 1975, Haftorn 1971, Cramp 1988). Tyrväinen (1970) reported that winter food of Fieldfares consisted almost exclusively of rowanberries (rowanberries main food in 288 out of 300 observations) in the winter of 1964/65, and the same was the case in the winter of 1969/70 (rowanberries main food in 144 out of 157 observations; Tyrväinen 1975). He reported that minor food sources were mainly apples and berries of juniper (*Juniperus communis*) and hawthorn (*Crataegus* spp.). Quantitative studies of winter food of Redwings is lacking from Fennoscandia. In years with high rowanberry abundance, both species may occur in small–large flocks, whereas in years with few rowanberries birds winter singly or in small flocks (Haftorn 1971, Svorkmo-Lundberg *et al.* 2006).

Rowans are distributed over most parts of Fennoscandia but are most common in mixed forests in southern areas (Räty *et al.* 2016). Rowans are common in all parts of Norway, including both eastern and western Norway (Artsdatabanken 2023). Masting is normally synchronous over large areas, including across Fennoscandia (Kobro *et al.* 2003, Gallego Zamorano *et al.* 2018, Dale 2023a), because flowering is determined by large-scale patterns of temperature (Gallego Zamorano *et al.* 2018).

Data on Fieldfares and Redwings were collected from eastern and western parts of Norway to match data on rowanberries. Eastern Norway consisted of the counties Innlandet, Viken, Oslo, and Vestfold and Telemark (*ca.* 59–62.5°N, *ca.* 8–12°E). Western Norway consisted of the counties Rogaland, Vestland, and Møre and Romsdal (*ca.* 58–63.5°N, *ca.* 5–7°E). Eastern parts of Norway have cold winters with snow cover except close to the Oslo Fjord, but coastal areas in the west have January temperatures just above zero with little snow cover (Statens kartverk 1996).

2.2. Winter numbers of thrushes

To obtain data on the number of Fieldfares and Redwings observed during each winter, I searched the website of the National Biodiversity Information Centre in Norway (www.artsobservasjoner.no) and extracted all winter records. The website is an online portal for reporting observations of species, and is open to the public. Most reports of birds are submitted by members of BirdLife Norway. The website can summarize both the number of ‘records’ and the number of individuals observed in specified time periods. A ‘record’ is one or more individuals observed in one place at one time (at www.artsobservasjoner.no termed 'funn'). The seasonal number of records was positively correlated with the number of individuals recorded (eastern and western Norway combined; Fieldfare: $r = 0.72$, $n = 41$ years, $p < 0.001$; Redwing: $r = 0.97$, $n = 41$ years, $p < 0.001$). The number of individuals was used instead of the number records because the latter may contain many records of a few individuals, whereas the former also includes information that some records were of large flocks with many individuals, thereby better reflecting variation in total numbers of wintering thrushes.

For each year, the number of individuals was based on observations from December in one year and from January to February in the following year. For example, the number for 2020 included the total number of individuals from all observations during the period December 2020–February 2021. Thus, years refer to the beginning of the winter. Data were collected for the period December 1980–February 2021 to match the period for which rowanberry data were available (see below). Winter numbers were extracted separately for eastern and western Norway for each species.

The number of thrush records increased over time (Fieldfare eastern Norway: $r = 0.76$, $n = 41$

years, $p<0.001$; Fieldfare western Norway: $r=0.67$, $n=41$ years, $p<0.001$; Redwing eastern Norway: $r=0.46$, $n=41$ years, $p=0.003$; Redwing western Norway: $r=0.69$, $n=41$ years, $p<0.001$). This was likely due to increased observation activity or reporting because the total number of records of all bird species also increased over time (eastern Norway: $r=0.86$, $n=41$ years, $p<0.001$; western Norway: $r=0.85$, $n=41$ years, $p<0.001$). Thus, to control for observation effort, I calculated annual indices of thrush winter numbers as the total number of thrush individuals recorded divided by the total number of records of all bird species. Annual number of bird records was assumed to reflect observation effort better than annual total number of bird individuals observed, because the latter may be more heavily influenced by fluctuating numbers of other species (*e.g.* irruptive species) or by fluctuating weather conditions which could influence number of birds wintering (Supplementary Material Fig. S1–2; note in general smaller annual fluctuations in number of bird records than in number of bird individuals). Data on the total number of bird records were extracted from the online bird portal for the same areas and same time periods that were used for data on thrushes (*i.e.* for December–February for the eastern and western regions separately). Thrush indices showed relatively weak temporal trends (Fieldfare east: $r=–0.30$, $p=0.06$, Fieldfare west: $r=–0.15$, $p=0.36$, Redwing east: $r=–0.20$, $p=0.20$, Redwing west: $r=0.31$, $p=0.047$; Fig. 1).

One could argue that the index described above could mask thrush fluctuations if annual total number of bird records fluctuated more or less in synchrony with thrush numbers. Thus, as an alternative way of calculating thrush numbers,

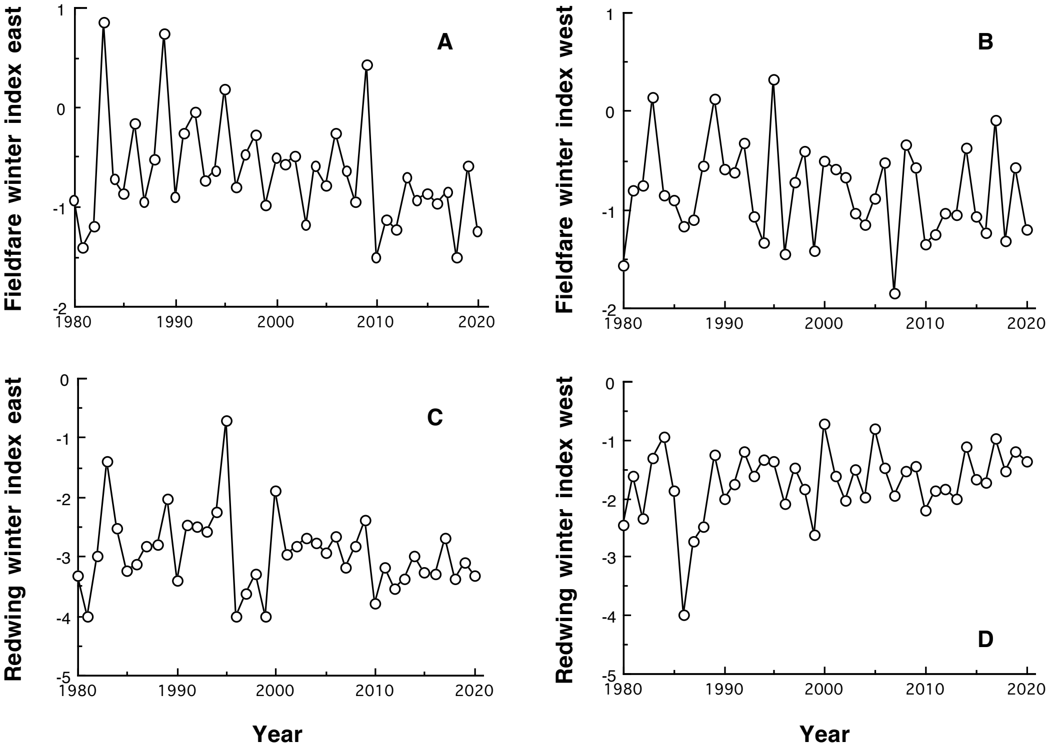

Fig. 1. Annual indices of winter numbers of Fieldfare (*Turdus pilaris*) and Redwing (*T. iliacus*) in eastern and western Norway during 1980–2020. Indices were log-transformed ratios of total number of thrush individuals recorded to total number of records of all bird species (an index of observation effort). For each year, the indices include records from December in one year and from January–February the following year. Thus, for instance, year 2020 includes records from the period December 2020–February 2021.

I also used detrending of the number of thrush individuals recorded. Detrended values were based on residuals from a regression of the number of individuals recorded ($\log_{10}(x)$ for Fieldfare, $\log_{10}(x+1)$ for Redwing) on year. However, note that detrended numbers were strongly correlated to the indices calculated above (Fieldfare east: $r = 0.90$, $p < 0.001$, Fieldfare west: $r = 0.92$, $p < 0.001$, Redwing east: $r = 0.93$, $p < 0.001$, Redwing west: $r = 0.85$, $p < 0.001$), most likely because total number of bird records did not show major fluctuations from year to year (Supplementary Material Fig. S1–2). Because the total number of records of all bird species submitted to the online bird portal has an increase from 2008 when the portal was launched (Supplementary Material Fig. S1–2), the detrended data are likely not as good as the index reported above, and results based on the index are given stronger weight in interpretations than results based on the detrended data.

Neither of the two thrush indices would capture a long-term trend of increasing number of thrushes due to climate warming because the citizen data do not easily reflect absolute numbers. There are no standardized winter counts of wintering birds in Norway. However, Swedish winter counts indicate that the Fieldfare has not had any long-term trend in numbers wintering during the period 1975–2020 (Green *et al.* 2021). Thus, the limited data available do not suggest that climate change has influenced winter numbers of thrushes.

2.3. Rowanberry indices

Rowanberry indices for southern Norway were taken from the "Varsling innen PlanteSkadegjørere" project (VIPS, see www.vips-landbruk.no/applefruitmoth) run by the Norwegian Institute of Bioeconomy Research (NIBIO) and Norsk Landbruksrådgivning (the Norwegian Agricultural Extension Office). VIPS monitors the risk of pest species attacks on a number of crop species. To forecast risk of attack by apple fruit moths (*Argyresthia conjugella*) on apple, the moth's alternative host rowan has been monitored at 59 sites in both eastern and western Norway from 1979 (see Kobro *et al.* (2003) for details). The number of flower clusters was counted on reference rowan trees in the vicinity of apple orchards in May each year. Because of a strong correlation in most years between this rowanberry index based on flower clusters and a Finnish rowanberry index based on actual counts of berries in early autumn (Gallego Zamorano *et al.* 2018), Dale (2023a) argued that flower clusters predict rowanberry abundance well.

Some monitoring sites had shorter time series or several years with missing data. First, only six sites were monitored in 1979 compared to ≥ 27 sites during 1980–2020. Following Dale (2023a), 1979 was excluded from analyses. Furthermore, 14 sites that had < 30 years of data (mean 18.9) during the period 1980–2020 were excluded. The remaining data used for analyses were from 45 sites [14 from eastern Norway (*ca.* 58–60° N, *ca.* 9–11° E), 31 from western Norway (*ca.* 59–62° N, *ca.* 6–7° E)] and had data for 32–41 years (mean 38.0). For both eastern and western Norway the yearly rowanberry index was calculated as the median number of flower clusters across sites. Annual rowanberry indices in eastern and western Norway were strongly and positively correlated (log-transformed data; $r = 0.88$, $n = 41$ years, $p < 0.001$).

The rowanberry index in both eastern and western Norway showed negative temporal trends during 1980–2020 (log-transformed indices; $r = -0.33$, $n = 41$ years, $p = 0.036$ and $r = -0.37$, $n = 41$ years, $p = 0.019$, respectively) which could be due to either natural factors or temporal changes in study sites, including habitat changes and changes in methodological procedures. Dale (2023a) performed analyses of Pine Grosbeak irruptions based on a detrended rowanberry index (*i.e.* using residuals from a regression of number of flower clusters [log-transformed] on year) using the same rowanberry dataset. However, the detrended and the non-detrended rowanberry indices were strongly correlated ($r = 0.93$, $n = 41$ years, $p < 0.001$), and analysis results were similar when using non-detrended indices (Dale 2023a). Thus, the choice of index is unlikely to influence results much, and the non-detrended rowanberry index was used here in line with no detrending of the main index of thrush numbers (based on number of thrush individuals relative to total number of bird records).

2.4. Weather variables

Weather variables included the NAO index, temperature and snow cover. The North Atlantic Oscillation index (NAO) was used as a general indicator of the weather conditions in southern Norway. Indices for November–January were retrieved from the website of the National Weather Service in the US (www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml). In Norway, a high NAO index is associated with mild and moist winds from the west, and a low NAO index colder winds from the east (Store norske leksikon 2018). In addition to using monthly values, the mean value for these three months was also used to assess whether the number of thrushes remaining in Norway during winter was affected by winter weather conditions. The reason for using a time period starting one month earlier than for the bird data, was that conditions during November may have a large influence on the birds' decision to stay or to migrate south. Similarly, conditions during December and January may also affect winter numbers, whereas conditions during February only affects a smaller number of birds, either because most birds have migrated south during December–January or because of mortality.

To assess how specific weather conditions in the eastern and western regions of southern Norway affected thrushes, I retrieved data on temperature and duration of snow cover for the eastern and western regions separately. For each region, data for the largest cities (Oslo and Bergen, respectively) were used both because they were situated roughly in the geographical centres of each region, and because fairly large proportions of the bird data come from within and around these cities due to their large human populations, and, hence, more birders. Data were extracted from the website of the Norwegian Meteorological Institute (www.yr.no) for the period November–January each year. Temperature over these three months (both monthly and mean across each three-month period) and total number of days with snow cover (at least 1 cm; both monthly and sum across each three-month period) were used for analyses. For Bergen, data on snow cover was missing for all months during the two first years, and for November in the third year so that there was data for 38–39 years. Both meteorological stations were in the lowlands (Blindern in Oslo: 94 m a.s.l., Florida in Bergen: 12 m a.s.l.) where the largest numbers of wintering thrushes occur. The term 'harsh winter conditions' is used for a low NAO index, low temperatures, and long duration of snow cover.

2.5. Statistical analyses

Pearson correlations were initially used to explore the relationships between annual indices of the number of thrushes during winter in the two regions, between indices of the two species, between thrush indices and rowanberry indices ($\log_{10}$-transformed), and between thrush indices and weather variables. The Fieldfare index was $\log_{10}$-transformed. The Redwing index had a few zero observations and the index values were small. Thus, the Redwing index was $\log_{10}(x+0.0001)$-transformed. There were no temporal autocorrelations in the thrush time series (one year lag; Fieldfare eastern Norway: $r=-0.11$, $p=0.45$, Fieldfare western Norway: $r=-0.25$, $p=0.09$, Redwing eastern Norway: $r=0.04$, $p=0.78$, Redwing western Norway: $r=0.14$, $p=0.36$). Thus, numbers wintering in one year were not related to numbers wintering the previous year, and yearly values were therefore considered as independent data points.

The main analyses of the relative importance of the influence of rowanberry abundance and weather variables on thrush winter numbers in the two regions of Norway were conducted with GLM with least squares estimation. Three sets of analyses were compared: (1) models with only rowanberry abundance (based on expectations from Kanerva *et al.* 2020, and results of the exploratory analyses), (2) models with rowanberry abundance and weather variables, and (3) models with rowanberry abundance, weather, and interactions between rowanberry abundance and weather. Due to significant correlations between many weather variables (especially positive relationships within and between NAO indices and temperature, but often negative relationships between NAO indices/temperature and duration of snow cover; Supplementary Material Table S1), each model included only one weather variable. Predictors were centred (mean = 0) and scaled (sum of squares = 1) to obtain standardized parameter estimates in order to assess the relative importance of the predictors (rowanberry abundance and weather). Models were compared with AIC_c, and were based on n = 41 years of data except analyses including duration of snow cover in western Norway where n = 38 years due to missing data (see above). Analyses were conducted separately for each species and region.

To test for effects of region on the relationships between thrush numbers and weather, data for eastern and western Norway were merged and region was included as a covariate. The prediction that weather should have a larger impact in eastern than in western Norway was tested by including the interaction between region and weather. For each of the two thrush species, analyses were conducted where the weather variables included were based on the best models in the previous analyses.

Because the total number of records of all bird species submitted to the online bird portal increased over time, data from more recent years may be more reliable. Thus, data from the period 2008–2020 (chosen because of larger amounts of data from 2008 after the online portal was launched in that year) were used to evaluate whether analyses based on this period gave similar results as analyses based on the whole 41-year data set. This shorter time period for analyses is likely also less influenced by climate change (see above regarding thrush indices). Results were qualitatively similar despite much smaller sample size (n = 13 years; Supplementary Material Tables S9–S10). Thus, the main text reports analyses based on the full data set.

Finally, the results from the main analyses were relatively similar when using detrended thrush numbers instead of the main index based on number of thrush individuals relative to total number of bird records (Supplementary Material Table S11). Note, however, that analyses based on the main index were considered to be most reliable. Thus, the main text reports analyses based on the main thrush index. All statistical analyses were conducted in JMP Pro version 16 (SAS 2021).

3. Results

3.1. Thrush winter numbers

The number of Fieldfare individuals recorded each winter during 1980–2020 in southern Norway constituted on average 2.0% of all bird individuals recorded (median = 1.1%, range = 0.3–13.2%, n = 41 years). In total, 507,232 Fieldfare individuals were recorded, of which 63.1% were from eastern Norway and 36.9% from western Norway. The number of Redwing individuals constituted on average 0.11% of all bird individuals recorded (median = 0.06%, range = 0.002–0.67%, n = 41 years). In total, 34,861 Redwing individuals were recorded, of which 6.1% were from eastern Norway and 93.9% from western Norway.

The annual thrush indices (log-transformed ratios of total number of thrush individuals recorded to total number of records of all bird species [an index of observation effort]) for eastern and western Norway showed pronounced variation from year to year (Fig. 1), and were positively and significantly related between the two regions in both species (Fieldfare: r = 0.62, n = 41 years, $p < 0.001$; Redwing: r = 0.40, n = 41 years, p = 0.010; Supplementary Material Fig. S3). The Fieldfare indices were also positively and significantly related to the Redwing indices (eastern Norway: r = 0.69, n = 41 years, $p < 0.001$; western Norway: r = 0.45, n = 41 years, p = 0.003; Supplementary Material Fig. S4).

3.2. Thrush numbers and rowanberry abundance

The Fieldfare indices were positively and significantly related to the rowanberry indices (eastern Norway: r = 0.61, n = 41 years, $p < 0.001$; western Norway: r = 0.49, n = 41 years, p = 0.001; Fig. 2a,b). The relationship for western Norway was also significant without an outlier (left hand data point in Fig. 2b; r = 0.52, n = 40 years, $p < 0.001$).

The Redwing indices were positively and significantly related to the rowanberry indices for eastern Norway (r = 0.48, n = 41 years, p = 0.001; Fig. 2c), but not for western Norway (r = 0.10, n = 41 years, p = 0.53; Fig. 2d). The relationship for western Norway was also not significant

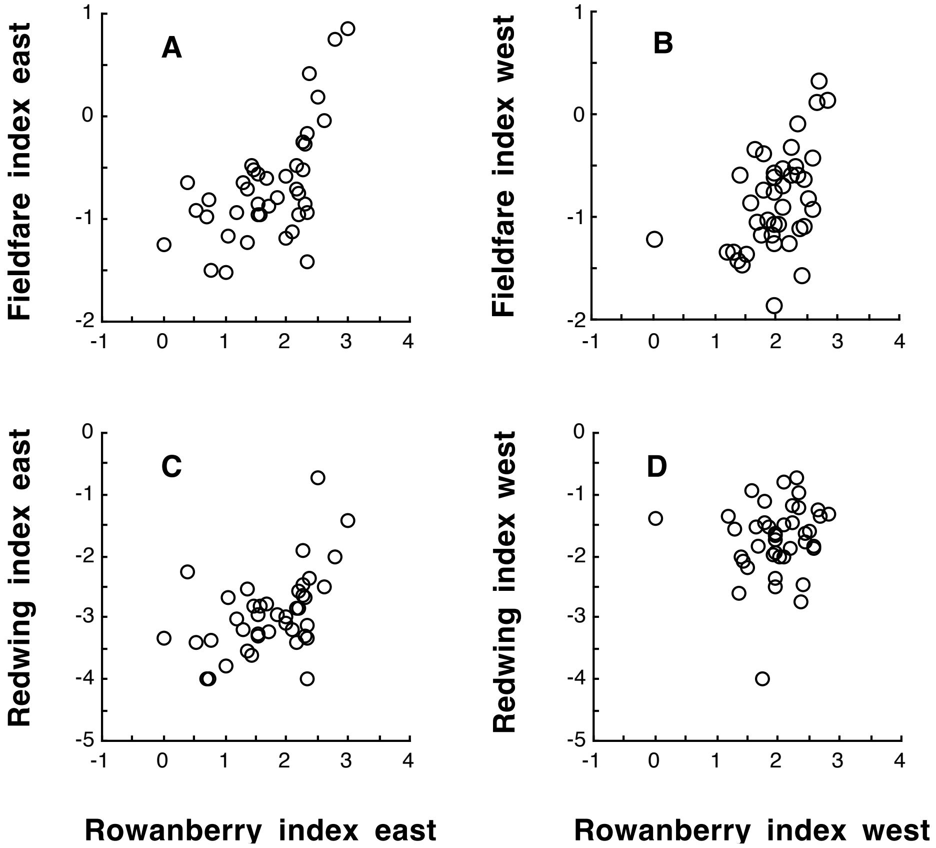

Fig. 2. Annual indices of winter numbers of Fieldfare (*Turdus pilaris*) and Redwing (*T. iliacus*) in eastern and western Norway during 1980–2020 in relation to rowanberry (*Sorbus aucuparia*) abundance in corresponding parts of Norway. Thrush indices were log-transformed ratios of total number of thrush individuals recorded to total number of records of all bird species (an index of observation effort).

without two outliers (left hand and bottom data points in Fig. 2d; r = 0.17, n = 39 years, p = 0.30).

3.3. Thrush numbers and weather

There were no significant relationships between any weather variables and Fieldfare and Redwing indices in simple correlation analyses, not even without correction for multiple testing (Supplementary Material Table S2). The strongest relationships (uncorrected $p \leq 0.10$) were for negative relationships between the NAO index in November and December and the Fieldfare index in western and eastern Norway, respectively (mild weather, fewer Fieldfares), and between duration of snow cover in December and the Fieldfare index in eastern Norway (longer duration of snow cover, fewer Fieldfares; Supplementary Material Table S2).

3.4. Multiple factor analyses: Fieldfare

3.4.1. Eastern Norway

All GLM analyses indicated that the Fieldfare index in eastern Norway was strongly and positively related to the rowanberry index (Supplementary Material Tables S4–5). Weather variables had mixed influence (Supplementary Material Tables S4–5). The best model

Table 1. Parameter estimates for best models explaining winter numbers of Fieldfare (*Turdus pilaris*) and Redwing (*T. iliacus*) in eastern and western Norway during 1980–2020 in relation to rowanberry abundance, weather variables and the interaction between rowanberries and weather.

Thrush indices were log-transformed ratios of total number of thrush individuals recorded to total number of records of all bird species (an index of observation effort). Parameter estimates are for centered and scaled predictors.

Model/variables	Estimate	SE	p
Fieldfare, eastern Norway			
Rowanberry abundance	1.88	0.39	<0.001
NAO index December	–0.85	0.38	0.026
Rowan * NAO	–1.15	0.39	0.003
Fieldfare, western Norway			
Rowanberry abundance	1.70	0.45	<0.001
NAO index November	–0.60	0.43	0.16
Rowan * NAO	–1.02	0.44	0.021
Redwing, eastern Norway			
Rowanberry abundance	1.77	0.51	<0.001
NAO index December	–0.62	0.51	0.23
Rowan * NAO	–1.89	0.51	<0.001
Redwing, western Norway			
Rowanberry abundance	0.85	0.59	0.15
Duration of snow cover December	–0.49	0.59	0.41
Rowan * Snow	1.37	0.61	0.026

(Supplementary Material Table S3) indicated that winter numbers of Fieldfare were also negatively related to the NAO index in December, and with a significant interaction between rowanberry abundance and the NAO index in December (Table 1). The interaction showed that in mild winters rowanberries had small influence on Fieldfare numbers whereas in harsh winters Fieldfare numbers were very small when there were few rowanberries, but large when there was a large rowanberry crop (Fig. 3a).

3.4.2. Western Norway

Rowanberry abundance had strong positive relationships with Fieldfare numbers also in western Norway (Supplementary Material Tables S4–5). Again, weather variables had mixed influence (Supplementary Material Tables S4–5). The best model (Supplementary Material Table S3) indicated that a significant interaction between rowanberry abundance and the NAO index in November also influenced Fieldfare numbers (Table 1). This interaction was very similar to the one for eastern Norway reported above, so that Fieldfare numbers were lowest with the combination of low NAO index (harsh weather) and few rowanberries, and highest with the combination of harsh weather and large rowanberry crop (Fig. 3b). Other models that were within $\Delta AIC_c < 2$ replaced the NAO index with December instead of November, or replaced the NAO index with temperature in November or snow in December, or did not include interactions, or only included rowan (Supplementary Material Table S3).

3.5. Multiple factor analyses: Redwing

3.5.1. Eastern Norway

All GLM analyses indicated that the Redwing index in eastern Norway was strongly and positively related to the rowanberry index (Supplementary Material Tables S6–7). Weather variables had mixed influence (Supplementary Material Tables S6–7). The best model (Supplementary Material Table S3) indicated that a significant interaction between rowanberry abundance and the NAO index in December also influenced Redwing numbers (Table 1).

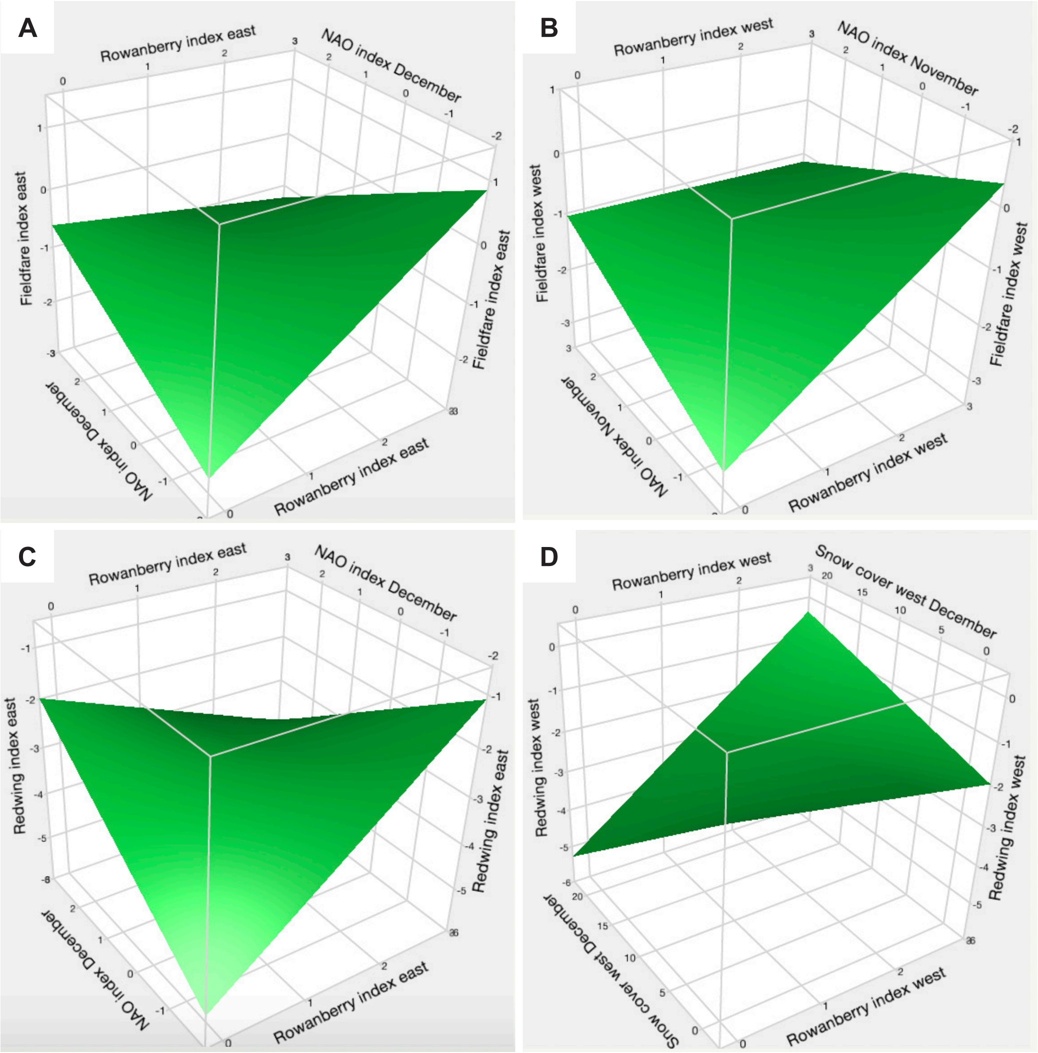

Fig. 3. Influence of the interactions between rowanberry (*Sorbus aucuparia*) abundance and weather variables on annual indices of winter numbers of Fieldfare (*Turdus pilaris*) and Redwing (*T. iliacus*) in eastern and western Norway during 1980–2020. A: Fieldfare eastern Norway; B: Fieldfare western Norway; C: Redwing eastern Norway; D: Redwing western Norway. Thrush indices were log-transformed ratios of total number of thrush individuals recorded to total number of records of all bird species (an index of observation effort).

This interaction was similar to those found for the Fieldfare: Redwing numbers were lowest with the combination of low NAO index (harsh weather) and few rowanberries, but low numbers were also found with the combination of high NAO index (benign weather) and large rowanberry crop (Fig. 3c).

3.5.2. Western Norway

In western Norway, Redwing numbers were not directly influenced by rowanberry abundance, and the NAO index and temperature had no influence (Supplementary Material Tables S6–7). However, the best model (Supplementary Material Table S3) included an effect of the interaction between snow cover in December and rowanberry abundance (Table 1). Thus, rowanberry abundance had a positive effect when snow cover in December lasted longer (Fig. 3d). However, this model was only marginally better than a model with only intercept (Supplementary Material Table S3).

3.6. Interactions between region and weather

There were no significant interactions between region and weather in analyses comparing eastern and western Norway (Supplementary Material Table S8).

4. Discussion

4.1. Influence of rowanberries on thrush numbers

I found that numbers of Fieldfares and Redwings during winter in southern Norway were strongly related to rowanberry abundance, except for Redwings in western Norway. However, in western Norway an interaction between rowanberry abundance and snow cover indicated that rowanberries had a positive influence on Redwing numbers when there was snow cover lasting for longer periods, whereas rowanberries did not influence Redwing numbers when there was little snow. These results are in line with those of Kanerva *et al.* (2020) who found that large crop size of several tree species delayed autumn migration of a number of facultative migrants and irruptive species. This included how Rowan affected, for instance, Fieldfare and Redwing, as well as how crop sizes of birches (*Betula spp.*) and Norway spruce (*Picea abies*) affected other bird species (Kanerva *et al.* 2020). Delayed autumn migration is likely to result in larger numbers of these species remaining for winter, so these are alternative ways of analysing facultative migration.

Rowanberry abundance usually varies in synchrony over large areas in Fennoscandia (Kobro *et al.* 2003, Gallego Zamorano *et al.* 2018, Dale 2023a). This may explain synchronous variation in winter numbers of both thrush species between eastern and western Norway, and between the species within each region. This suggests that facultative migration is influenced by yearly variation in food availability at large spatial scales. Thus, thrushes breeding across Fennoscandia may obtain information at an early time (already during summer) that availability of rowanberries will be high in a specific year, and thereby ‘know’ that staying in northern areas may be possible the coming winter.

4.2. Influence of weather on thrush numbers

Kanerva *et al.* (2020) did not find any influence of weather on timing of autumn migration, and weather is not thought to affect movements of irruptive species (Newton 2006). Similarly, there were few direct relationships between weather and winter numbers of Fieldfares and Redwings in the present study. However, more detailed analyses, in particular including the interactions between rowanberry abundance and weather variables, revealed that weather affected both species, and in both eastern and western Norway, in some years. The most common interaction effect was that thrush numbers were particularly low when there were combinations of harsh weather and low rowanberry abundance, but high when there was harsh weather and high rowanberry abundance. This suggests that high availability of rowanberries may buffer against the negative effects of harsh weather.

The mechanistic relationships between NAO indices and thrush numbers are difficult to assess because the NAO index reflects overall weather patterns. However, the analyses of specific weather variables suggested that weather effects may operate through the duration of snow cover as suggested by the interaction for Redwings in western Norway. For the Fieldfare, some models included significant effects of snow (Supplementary Material Table S5), although these models were not the best based on AIC_c. In years with long-lasting snow cover during early winter (*e.g.* November–December), access to food on the ground may be more or less blocked, and if rowanberry abundance is low the thrushes may have no other option than to leave the northern wintering areas and migrate further south. Snow cover has a large impact on many bird species foraging on the ground, such as on arable land (Golawski & Kasprzykowski 2010, Bosco *et al.* 2022).

The analyses suggested that thrush numbers were mostly influenced by weather indices from December. Thrush indices were based on total numbers for the period December–February, and weather in December may therefore have a stronger impact than in January simply because weather later in winter affects only parts of the data material included in the indices. However, it is likely that snowfalls and cold spells in January may also affect those individuals that are still present.

Although thrush numbers were influenced by harsh weather in negative ways according to several analyses (see above), there were also some analyses suggesting a different pattern. First, the NAO index often had negative effects (Fieldfares, Tables S4–S5), and, hence, lower thrush numbers were sometimes associated with mild winters with many rowanberries (Fig. 3a,c). Wintering thrushes in Norway may also originate from northeastern populations such as Sweden, Finland and perhaps also Russia (Haftorn 1971, Franks *et al.* 2022). Because Rowan masting is synchronous over large areas in Fennoscandia (Kobro *et al.* 2003, Gallego Zamorano *et al.* 2018, Dale 2023a), a high NAO index, in particular combined with a high rowanberry index, could mean that fewer thrushes arrive to winter in Norway because they can remain in Sweden or Finland for a longer time through the winter (Tyrväinen 1970, 1975).

Second, the largest number of thrushes sometimes occurred with the combination of harsh weather and high rowanberry abundance (Fig. 3). In addition to a likely relationship with the spatial distribution of thrushes across Fennoscandia discussed above, this may to some degree also be a methodological effect because snow and cold weather may drive thrushes into urban areas (Tyrväinen 1975) where they are more easily recorded by birders. However, the strong effect of rowanberry abundance on thrush numbers suggests that the combination of harsh weather and high rowanberry abundance was associated with larger numbers of wintering thrushes than the combination of benign weather and low rowanberry abundance.

There was in general little support for the prediction that weather should have an influence mainly in eastern Norway where the climate is more continental. There were weather effects on both species in both regions. Overall, however, it appears that thrush winter numbers is governed to a large degree by food availability, with numbers modulated by weather to a lesser degree, mainly when food availability is low. The conclusion of a larger importance of food than weather was based on 1) the univariate analyses which showed significant effects of rowanberry abundance (except for Redwing in western Norway), but not of weather variables, 2) the multivariate analyses which generally showed significant main effects of rowanberry abundance and non-significant main effects of weather, and interactions between rowanberry abundance and weather having variable effects, 3) that centred and scaled parameter estimates in multivariate analyses indicated larger effect sizes of rowanberry abundance than of weather variables or most interactions, and 4) no interaction between region (eastern and western Norway) and weather on thrush numbers.

My study confirms previous findings that food availability is more important than weather (Kanerva *et al.* 2020), but in contrast to the latter study, I found that weather had some impact. My study and Kanerva *et al.* (2020) are among the few studies that have evaluated the relative importance of food and weather for facultative migration, although other studies have investigated food or weather separately (Newton 2008).

4.3. Why was food more important than weather?

Although both the Fieldfare and the Redwing forage extensively on the ground, especially in the summer season, fruits and berries in trees and bushes, in particular rowanberries, are important food sources during autumn and winter (Tyrväinen 1970, 1975, Haftorn 1971, Haila *et al.* 1986, Cramp 1988, Kanerva *et al.* 2020). Rowanberries are accessible also after snowfalls when food on the ground has become covered. Thus, compared to bird species that forage mostly on the ground, snow cover may have little influence on wintering Fieldfares and Redwings provided that rowanberries are available. In line with this, harsh weather affected these two species negatively mainly when rowanberry abundance was low. Furthermore, unlike some food types thrushes utilize when foraging on the ground, such as earthworms, rowanberry availability is not affected by frost. The thrushes consume rowanberries even when the berries are frozen. As an example, the 1995/96 winter had one of the highest Fieldfare indices in eastern Norway, and the highest for the Redwing (Fig. 1a,c), yet the mean temperature in Oslo in December that year was –6.4 °C (only three other years had lower temperature in December) and only a few days had maximum temperatures above 0 °C. Finally, feathers have high insulating capacity (Herreid & Kessel 1967) so that temperature in itself may not be a problem as long as the birds have reliable access to enough food.

For bird species relying on rowanberries during winter, the decision to stay in northern areas may be based on a simple and easily assessed cue: rowanberry abundance can be monitored directly on trees through the autumn months. However, because rowanberries are consumed by a number of different bird species (see Introduction) from early autumn, availability declines progressively. Rowanberry supplies may in some years, at least locally, be depleted as early as in November–December (Suhonen & Jokimäki 2015, Suhonen *et al.* 2017), whereas in other years the supplies may last to January–February (Tyrväinen 1970, 1975). This suggests that wintering should be flexibly adjusted not only to initial size of the rowanberry crop, but also to how much of the crop remains at any time. Thus, migratory movements, at least of the Fieldfare, are known to occur also during winter months when rowanberries have disappeared (Tyrväinen 1975). Yet, it seems likely that food availability for rowanberry specialists is more predictable than the weather conditions in specific winters, and facultative migration related to food availability may be the rule for rowanberry specialists and for other species utilizing seed and fruit crops in trees. For species foraging mainly on the ground, I speculate that weather may be more important. Such species may face sudden periods of food shortage, for instance, due to snowfalls, that may trigger migration to warmer regions (Newton 2008, Golawski & Kasprzykowski 2010, Resano-Mayor *et al.* 2020). Thus, the relative importance of food and weather depends not only on the amount of food available or on weather by themselves, but also on how food availability interacts with weather in determining how much food is accessible for facultative migrants.

Kahden rastaslajin, räkättirastaan ja punakylkirastaan, fakultatiivinen muutto: pihlajanmarjojen runsaus on tärkeämpää kuin talvisää

Fakultatiivista muuttoa ohjaavat yleensä ruoan ja sään vaikutukset. Linnut pysyvät pohjoisilla alueilla, jos ruokaa on runsaasti ja sääolot ovat suotuisat, mutta muuttavat etelään silloin kun ruokaa on niukasti ja sää on ankara. Näiden kahden ympäristötekijän suhteellista merkitystä on harvoin testattu pitkillä aikasarjoilla, ja myös sään vaikutuksia on dokumentoitu vähän. Tässä tutkimuksessa arvioin, vaikuttaako talviruoan runsaus (pihlajanmarja, *Sorbus aucuparia*) ja/tai talven ankaruus (NAO-indeksi, lämpötila, lumipeitteen kesto) räkättirastaiden (*Turdus pilaris*) ja punakylkirastaiden (*T. iliacus*) määriin talvella. Tutkimusaineisto on kerätty Etelä-Norjassa vuosina 1980–2020 ja vertailun kohteena on kaksi aluetta, joissa talven ankaruus eroaa toisistaan: läntisellä tutkimusaluella on lauhkeampi meri-ilmasto ja itäisemmällä tutkimusalueella on vaihtelevampi mannerilmasto.

Talvehtivien räkättirastaiden määrä molemmilla alueilla ja punakylkirastaiden määrä itäisessä Norjassa olivat korkeimpia vuosina, jolloin pihlajanmarjoja oli paljon. Sää vaikutti vaihtelevasti rastaiden määriin, mutta havaitsin sään ja pihlajanmarjojen välillä vuorovaikutusta: rastaita oli vähän silloin, kun sääolosuhteet olivat ankarat ja pihlajanmarjoja vähän. Vastaava ilmiö esiintyi molemmilla tutkimusalueilla ja molemmilla rastaslajeilla.

Yhteenvetona voidaan todeta, että fakultatiivinen muutto liittyi vahvasti ruoan saatavuuteen. Enemmän rastaita talvehtii hyvinä pihlajanmarjasatovuosina. Ankarilla talvilla oli eniten negatiivisia vaikutuksia talvehtivien rastaiden määriin silloin, kun myös pihlajanmarjasadot olivat huonoja.

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Online supplementary material

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A new contact zone in the Chiffchaff distribution range: Caucasian and European subspecies meet in the south of Russia

Irina Marova, Vladimir Ivanitskii*, Irina Ilina, Anastasya Pecheneva, Pavel Kvartalnov, Yury Belocon & Maryana Belokon

I. Marova, V. Ivanitskii, A. Pecheneva, P. Kvartalnov, Lomonosov Moscow State University, GSP-1, Leninskie Gory, Moscow, 119991, Russia
I. Ilina, Shemyakin-Ovchinnikov Institute of Bioorganic Chemistry, Russian Academy of Sciences, Miklukho-Maklaya st., 16/10, Moscow, 117997, Russia
V. Belocon, M. Belokon, Vavilov Institute of General Genetics, Gubkina st. 3, 119333, Moscow, Russia & Russian Academy of Science, Leninsky Prospekt, 14, Moscow, 119991, Russia
**Corresponding author's e-mail: vladivanit@yandex.ru*

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The study of contact zones between closely related taxa of animals sheds light on many important issues of evolution biology and taxonomy. Several such zones were described earlier within the huge distribution range of the chiffchaff species complex (*Phylloscopus collybita*). We have documented for the first time the existence of a new contact zone between Caucasian (*Ph. c. caucasicus*) and European (*Ph. c. abietinus*) subspecies of the Chiffchaff in Ciscaucasia (southern Russia). We predicted the occurrence of hybridization between these subspecies belonging to the same group of "greenish" chiffchaff. In eastern Ciscaucasia, a population was found in which the *abietinus* and *caucasicus* haplotypes co-occur in a significant number. A mixed pair of Chiffchaff (male *caucasicus* and female *abietinus*) was also found here. The colour of the plumage of Chiffchaffs in Ciscaucasia varies more widely compared to allopatric populations. In many specimens bearing the *abietinus* haplotype in Ciscaucasia, the wing formula is identical to that typical for *caucasicus* and differs from that typical for *abietinus* in allopatric populations. The tret calls typical of *caucasicus* are included in the song of Chiffchaffs, which carry the *abietinus* haplotype and do not have notes characteristic of *caucasicus* in their song. Chiffchaffs from Ciscaucasia occupy an intermediate position between *abietinus* and *caucasicus* in the duration of individual song phrases and syllable time-frequency characteristics. During the captures, the males of *caucasicus* readily reacted to the broadcast of the *abietinus* song, and vice versa. Thus, all the results suggest hybridization between *abietinus* and *caucasicus* in Ciscaucasia.

1. Introduction

Zones of secondary contact and hybridization are called “windows into the evolutionary process” (Harrison 1990). Their study provides unique opportunities for investigating the processes of differentiation of populations and speciation in nature. Therefore, it is not surprising that such zones remain in the focus of researchers' attention across many decades (Mayr 1966, Dixon 1989, Aliabadian *et al.* 2005, Swenson & Howard 2005, Rheind & Edwards 2011, Carpenter *et al.* 2022). The current stage of ornithological research in this area is marked by the synthesis of morphological, genetic and bioacoustic approaches. Songbirds are particularly attractive for such studies. Many of them have complex vocalizations, which could be involved in the analysis along with other signs

Many hybrid zones arise due to anthropogenic changes in natural landscapes, leading to the introduction of one species into the range of another. For example, artificial afforestation and watering in the once-treeless steppe areas create excellent opportunities for the arboreal bird species to settle here. A well-known example is the Great Plains of North America, where many previously completely isolated western and eastern bird taxa began to disperse towards each other and form zones of contact and hybridization (Remington 1968, Rising 1983, Rhymer & Simberloff 1996). A similar situation exists in Ciscaucasia, the southern part of European Russia, the area between the foothills of the Greater Caucasus in the South, the Manych Depression in the North, and the coasts of the Azov and Caspian Sea in the West and East. The length of this area, from south to north, is about 200 km. Vast territories of the formerly treeless steppe of Ciscaucasia have seen massive forest cultivation and the development of forest belts for more than 100 years. Currently, this region holds many old, artificially planted forests. In addition, almost all of its territory is covered with a dense network of forest belts of different ages, widths, and vegetation compositions established in 1940–1950. Such large-scale transformation of Ciscaucasian landscapes induced a massive redistribution of various bird taxa. Caucasian species and subspecies moved from the South to the North, and European boreal species settled towards them from the North to the South. As a result, modern Ciscaucasia has become an arena of mass mixing of northern and southern closely related forms, many of which enter into hybridization here (Belik 2009).

In particular, the history of the Chiffchaff, represented here by the Caucasian (*Phylloscopus collybita caucasicus*) and the Eastern European subspecies (*Ph. c. abietinus*), is interesting. According to count results conducted in the early 1970s, the Chiffchaff number in Ciscaucasia was indicated as extremely low (Belik 2009). It nested in large numbers only in the floodplain of the Kuban River, which at that time was essentially the northern boundary of the distribution of the Caucasian subspecies (Belik *et al.* 1981, Loskot 1991). To the north of the Kuban River, the Caucasian Chiffchaff nested only in the forests of the Stavropol upland, without penetrating the Ciscaucasian plain (Likhovid & Tertyshnikov 1994). The Eastern European Chiffchaff, on its move in a southerly direction, arrived at the lower reaches of the Don only by the mid-1950s. Until that time, Chiffchaff had not been found here. Thus, in the early 1970s of the past century, vast areas of the Ciscaucasian steppes between the Kuban and Don rivers were not inhabited by Chiffchaff. In particular, it did not nest in artificial forest belts, which by this time were widely represented in this region (Belik 2009).

Half a century later, the situation has changed dramatically. We found the Chiffchaff to be numerous breeding species throughout Western Ciscaucasia, from the Kuban Valley up to the central districts of the Rostov region. In Eastern Ciscaucasia, the Chiffchaff was found nesting from the northern parts of the Stavropol region in the south up to Salsk in the north. At present, the Chiffchaff nests everywhere in great numbers, not only in artificially planted forests, but also in all forest belts, being one of the most numerous birds here (up to 12 singing males per 1 km). Such a large-scale expansion raises many intriguing questions. Among them is the question of which subspecies were involved in the settlement and whether there is a zone of contact and hybridization between them.

In this article, we describe a new zone of contact and probable hybridization of two Chiffchaff subspecies in the south of Russia in addition to the previously described ones in the

Pyrenees (Salomon & Hemin 1992, Helbig *et al.* 2001), in Scandinavia (Hansson *et al.* 2000), and in the Southern Urals (Marova *et al.* 2017). We analyze the morphological, bioacoustic, and genetic differentiation of Chiffchaff in western and eastern Ciscaucasia: from Krasnodar and North Ossetia to the north up to the central regions of the Rostov region and from the northern part of the Stavropol region to the North up to Salsk (Fig. 1). For comparison, we use our bioacoustic data from the Kursk and morphological data from the Moscow and Kursk populations of *abietinus*.

2. Materials and methods

2.1. Studied taxa

Both *abietinus* and *caucasicus* belong to the group of "greenish" Chiffchaffs. Both subspecies are coloured very similarly and have almost the same body size, so their distinction by external appearance is problematic. However, these subspecies differ well in wing formula, mitochondrial DNA, and song (Helbig *et al.* 1996, Marova *et al.* 2021). In particular, the tret calls in the songs of *abietinus* and *caucasicus* differ well and are the same throughout the vast distribution range of each of these subspecies (Ivanitskii *et al.* 2021).

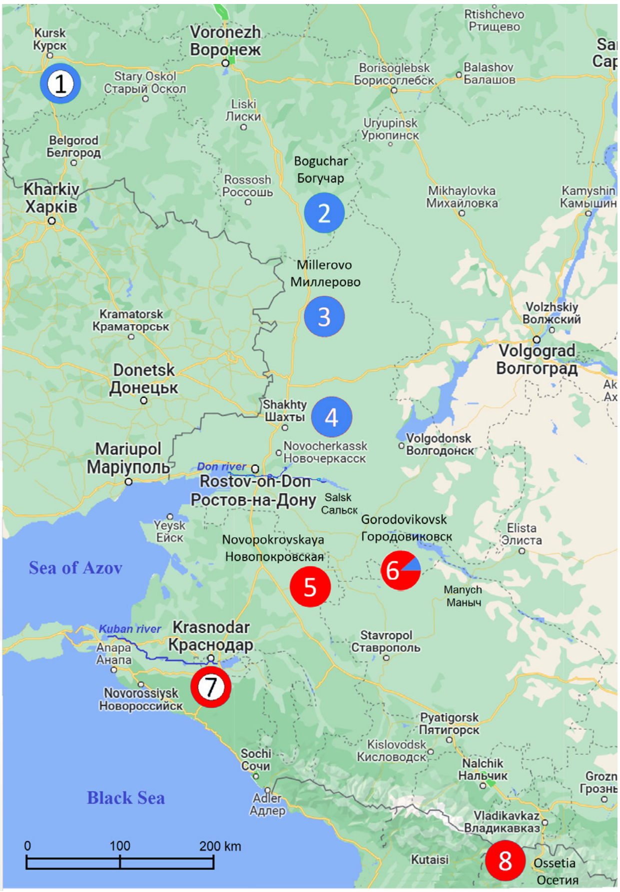

Fig. 1. Chiffchaff populations studied (the number of males tape-recorded in the population is indicated in square brackets): 1 – Kursk region [19]; 2 – Boguchar (Don river valley) [13]; 3 – Millerovo [8]; 4 – Shakhty [12]; 5 – Novopokrovskaya [20]; 6 – Gorodovikovsk (western Kalmykia) [20]; 7 – Krasnodar [20]; 8 – North Ossetia [20]. Blue circles represent pure *abietinus*; red circles represent pure *caucasicus*; white circles with blue and red represent allopatric populations not typed for mtDNA.

2.2. Capturing method and genetic analysis

Field studies were conducted in May-June 2017, 2019 and 2021. Singing males were tape-recorded and then captured in an Ecotone mist net (6 x 2.5 m, mesh 16 mm) after being lured by song playback. Once photographed, measured and blood sampled (from *vena brachialis*), the birds were ringed and immediately released. We analysed 66 blood samples (dried on a paper filter) collected in five locations: Gorodovikovsk (Kalmykia), n = 34; Millerovo, n = 8; Shakhty, n = 4; Novopokrovskaya, n = 6; Krasnodar, n = 14 (Fig. 1). DNA was isolated from blood samples using the Diatom^{TM} DNA Prep 100 kit (Isogen Lab.ltd., Russia). We examined the mtDNA cytochrome *b* gene (902 bp). The cytochrome *b* fragments were amplified with the primers L-14995 and H-16065 (Helbig *et al.* 1996). PCR was performed under the following conditions: initial denaturation of DNA (94°C for 2.5 min), 35 cycles of amplification (30 s at 93°C, 30 s at

54°C, and 180 s at 72°C), and final elongation (72°C for 3 min) with a GenPak® PCR Core kit (Isogen Lab.ltd., Russia). PCR products were purified with a Diatom™ DNA Clean-up purification kit (Isogen Lab. Ltd., Russia). Sequences of cytochrome *b* were initially aligned and then optimized manually using the BioEdit Sequence Alignment Editor 5.0.9 (Hall 1999).

The phylogenetic relationships between the haplotypes were reconstructed by Median Joining Network using PopART v. 1.7 (Leigh & Bryant 2015). To determine the subspecies of samples, we conducted the phylogenetic analysis for cytochrome *b* sequences using the Bayesian analysis with MrBayes v. 3.2.7 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). In addition, we analysed the cytochrome *b* sequences of six different subspecies of Chiffchaff and a sequence of willow warbler (*Phylloscopus trochilus*) as an external group from the GenBank. The accession numbers of all analyzed sequences are shown in Supplementary Table 1. The phylogenetic tree was built after Markov chain Monte Carlo run for 300,000 generations with a burn-in of 10,000 generations.

2.3. Morphology

A total of 56 Chiffchaffs (55 males and 1 female) from populations localized in a possible contact zone were captured, measured (wing and tail length), and photographed. In addition, 57 specimens from allopatric populations in North Ossetia (*caucasicus*), Kursk and Moscow regions (*abietinus*) were captured and processed. For each specimen, a verbal description of the colour of its plumage was prepared, and the wing formula (the position of the tips of the primary flight feathers relative to each other) was determined. All the measurements and wing formula descriptions were made according to Svensson (1992).

2.4. Song recording and analysis

For sound recording, we used solid-state recorders (Marantz PMD-660) with Sennheiser K6-ME66 cardioid condenser microphones (sampling rate 44.1 kHz, 16-bit resolution). Each individual male was recorded only once from a distance of 10–15 m. Since the birds were not marked, we made special efforts to avoid recording the same males. In particular, in dense settlements, we usually started recording the next male only when we heard the previous one. One recording lasted 5–10 minutes. In total, we analysed the recordings of 132 males from eight populations. The geographical position of the latter corresponds to the transition from pure *abietinus* (in the north) to pure *caucasicus* (in the south) (Fig. 1). We used recordings from two pure populations of *abietinus*, two pure populations of *caucasicus* and four populations located in the area of contact between these subspecies in Ciscaucasia and the Rostov region. Data on the number of males recorded in each population are presented in the caption of Figure 1.

We used common terminology to describe song units (Prúchová *et al.* 2017). An “element”

Table 1. Haplotypes and wing formulas of Chiffchaff in Ciscaucasia and in allopatric populations.

Wing formula	Populations in Ciscaucasia			Allopatric populations			
	Total Chiffchaffs	Genetically identified as *P. c. abietinus*	Genetically identified as *P. c. caucasicus*	Total Chiffchaffs	*P. c. abietinus*		*P. c. caucasicus*
					Moscow	Kursk	North Ossetia
7<2<6	5	3	2	25	13	12	0
8<2<7	24	9	15	6	0	6	16
9<2<8	23	4	19	0	0	0	10
10<2<9	4	0	4	0	0	0	0
Total	56	16	40	57	13	18	26

is a single continuous trace on the spectrogram. A “syllable” consists of one or more elements that are always combined in the same way. Usually, gaps between elements are very short, so they appear as a single sound to the human ear. The largest gap between elements within a syllable was about 0.05 ms. Elements, or syllables, thus represent the smallest building blocks of songs. Chiffchaff's song consists of well-differentiated syllables separated by clear pauses. The syllables are grouped into phrases separated by much longer gaps. The repertoire of syllables was determined for each male recorded. Then, for each population sample, we determined the number of males whose repertoire contained a particular syllable (as a percentage of the total number of males in this sample).

To analyse the frequency and temporal characteristics of the song, three samples were created: pure *abietinus* (Kursk and Boguchar), pure *caucasicus* (Krasnodar and North Ossetia), and Chiffchaffs from a contact zone in Ciscaucasia (Novopokrovskaya and Gorodovikovsk). Each sample included recordings of 20 males: 10 males from each of the two populations. We randomly selected three 3-second samples from the continuous singing of each male for detailed analysis. Each segment included 9–10 syllables. Thus, 180 segments from 60 males were included in the analysis. For each segment, we determined: 1) maximum frequency (top limit of a frequency range); 2) minimum frequency (bottom limit of a frequency range); 3) mean length of the song syllables; 4) mean length of the pauses between song syllables. In addition, for each male included in the analysis, we measured the duration of 10 individual song phrases randomly selected from his recording. We calculated medians for all parameters for each male for subsequent statistical analysis.

The spectrograms were created in Syrinx 2.5s (software developed by John M. Burt; University of Washington, Department of Psychology, Seattle, WA 98195, USA) with settings FFT = 512 and Blackman window. For automatic sound measurement, we used AviSoft-SASLab Pro with spectrograms created with settings FFT = 512 and Blackman window. The spectrogram’s time resolution was 2.9 ms, and its frequency resolution was 170 Hz. To fix the upper and lower limits of the frequency range, we used a default threshold of –20 dB (referenced to the peak amplitude). Consequently, the maximum and minimum frequencies could be identified as the highest and, respectively, the lowest frequencies, at which the amplitude was –20dB or more. We applied a “hold time” parameter of 50 ms in order to fix the beginning and end of the elements.

2.5. Statistics

We used the software packages STATISTICA V. 8.0 (StatSoft, Inc.USA) and PAST V. 2.13 (Hammer *et al.* 2001) for statistical data processing. The results obtained from the individual repertoires study were subjected to cluster analysis. We used a matrix containing 8 rows (populations) and 74 columns (elements). Each cell of the matrix contained the number of males performing this element in this population (as a percentage of the total number of recorded males). We used the Bray–Curtis similarity index, the unweighted paired group average as an agglomeration method, and 999 replicates for a bootstrapping calculation. The Kruskal–Wallis nonparametric test was used to assess the statistical significance of the differences between the three song samples by two frequencies (maximum and minimum frequency) and three temporal characteristics (the length of the song syllables, the length of pauses between them and the phrase length). The PCA analysis was carried out on these data. For this, we used a matrix containing five columns (song characteristics) and 60 rows (males). Prior to analysis, the data was standardized. Then, the significance of the differences between the values of the first main component was evaluated using the Kruskal–Wallis nonparametric test.

3. Results

3.1. Genetics

According to phylogenetic analysis, 16 of the birds we studied were associated in the same clade with 7 specimens of *abietinus* from the GenBank, and 50 other birds were combined in the other well-separated clade with two specimens of *caucasicus* from the GenBank (Fig. 2). We identified 66 sequences of cytochrome *b* of 902 bp in length. In this sample, 25 haplotypes were found. The Median-Joining network of haplotypes showed a clear separation between two subspecies groups, differing in at least five nucleotide substitutions (Fig. 3). The *caucasicus* haplotypes prevail in most of the studied areas in both western (Novopokrovskaya) and eastern (Gorodovikovsk) Ciscaucasia (Fig. 1, circles 5 and 6). Only the *abietinus* haplotype was found to the north of Rostov-on-Don.

Both haplotypes were found in Western Kalmykia's population and the adjacent parts of the Stavropol Region (Fig. 1, circle 6). Four of the 34 (11.8%) specimens carried the *abietinus* haplotype, and the rest carried the *caucasicus* one. Here, we succeeded in capturing both members of one breeding pair from which the male was determined as *caucasicus* and the female as *abietinus* according to their haplotypes.

3.2. Morphology

We found no significant differences in tail and wing length between *abietinus* and *caucasicus* males (Marova *et al.* 2021). However, the wing formula is a trait that reliably separates individuals taken from the Moscow and North Ossetia allopatric populations. The wing of *abietinus* is sharper; the tip of the second primary is between the 6 and 7 primaries. The wing of the *caucasicus* is more rounded; the tip of the second primary is between 7 and 8, 8 and 9, or even 9 and 10. The situation looks much less clear in the Kursk region, especially in Ciscaucasia. In six of the 18 Chiffchaffs caught there, the wing formula was closer to *caucasicus* than to the typical *abietinus*. In Ciscaucasia, most of the Chiffchaffs bearing the haplotype *abietinus*, had a rounded wing, and only three individuals had a wing shape typical of allopatric populations. Two Chiffchaffs carrying the *caucasicus* haplotype did not differ in wing formula from typical *abietinus* (Table 1).

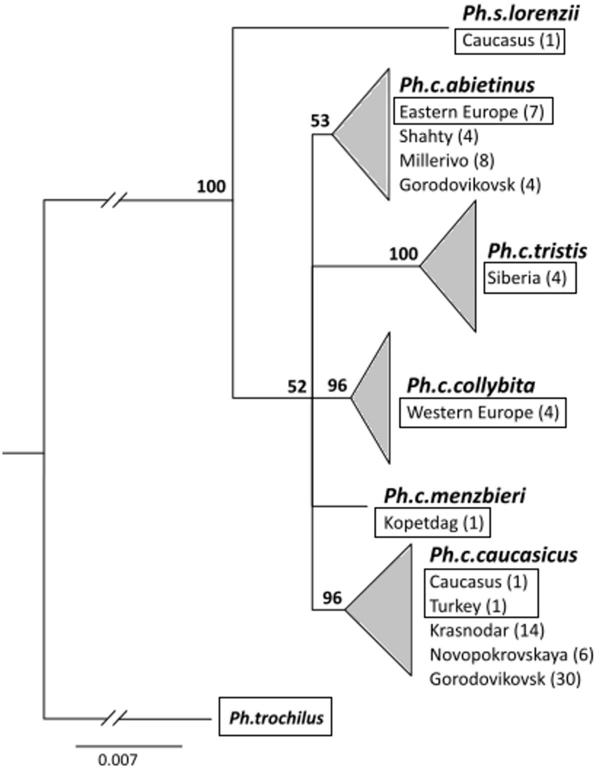

Fig. 2. The phylogenetic tree of the Chiffchaff subspecies cytochrome *b* haplotypes has been confirmed using Bayesian analysis (the figures at the bottom of the cluster show its support). The figures in parentheses right of the geographical names indicate the number of individuals studied. Rectangles indicate specimens from the GenBank.

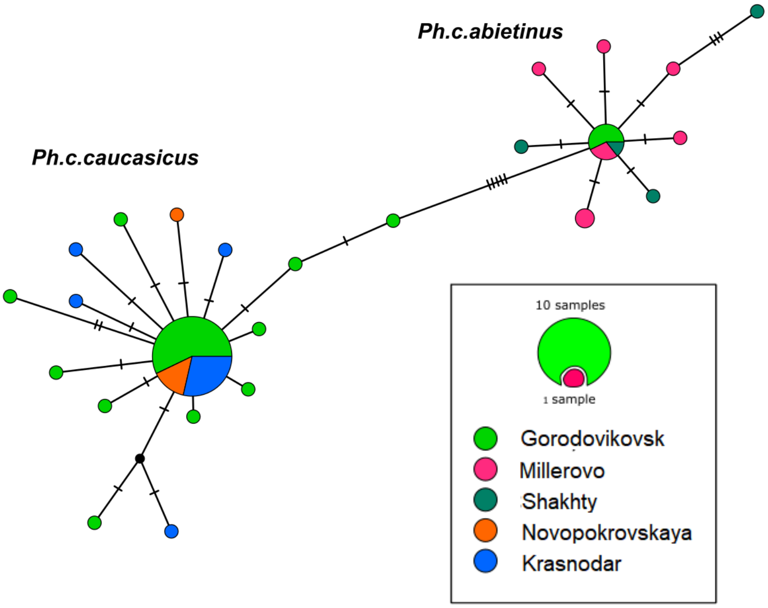

Fig. 3. Minimum-spanning network between the observed 25 mitochondrial haplotypes, representing five populations and two subspecies of Chiffchaff. Hash marks between the haplotypes indicate the number of nucleotide differences separating each haplotype. The size of the circle representing the individual haplotypes corresponds to the abundance of that haplotype. The black dot indicates an unobserved intermediate haplotype.

3.3. Song analysis

We identified 74 syllable types in our recordings. Syllables with a V-shaped frequency modulation (Fig. 4B) are characteristic of the *caucasicus* song (40% of males perform) and are completely absent in the *abietinus* song. We did not find any specific syllables in *abietinus*: *caucasicus* males presented all the syllables performed by males of the latter. The differentiation of syllables between the studied populations was rather weak (Fig. 4A). One cluster combines three populations: a typical *caucasicus* from Krasnodar and two populations from the transition zone between *caucasicus* and *abietinus*: from Western Kalmykia (Gorodovikovsk) and Novopokrovskaya. The population of the Shakhty located 200 km north of Novopokrovskaya adjoins the same cluster, but with much less bootstrap support. The second cluster combines two populations of pure *abietinus* (Boguchar and Kursk) and a population of Millerovo localised 130 km north of the Shakhty. Finally, the North Ossetia population occupies a separate position in relation to all others.

The data on the tret calls in the song shows a slightly different picture. Paradoxically, the tret calls typical of *caucasicus* are found in the song of Chiffchaffs, carrying the *abietinus* haplotype and having no notes characteristic of *caucasicus* in their song (Shakhty and Millerovo) (Fig. 4C).

The subspecies studied differ significantly in all measured frequency and time parameters of their song. The analysis of the main components identified six factors, of which two had eigenvalues greater than 1. The first factor (the first main component) selects 43.5% of the variation, the second factor selects 18.1%. In all characteristics, including the first main component values, the song of the Chiffchaffs from Ciscaucasia falls in between the songs of *abietinus* and *caucasicus* (Fig. 5).

4. Discussion

Modern Ciscaucasia, whose natural environment has been radically transformed by human activity, has become a real contact zone hotspot. At least 10 pairs of subspecies and closely related species, spreading towards each other from the north and the south, formed contact zones in Ciscaucasia (*Dendrocopos major candidus* / *D. m. tenuirostris, Garrulus glandarius glandarius* / *G. g. krynicki, Lanius collurio collurio* / *L. c. kobylini, Aegithalos caudatus caudatus* / *Ae. c. major, Sylvia atricapilla atricapilla* / *S. a. dammholzi, Luscinia luscinia*

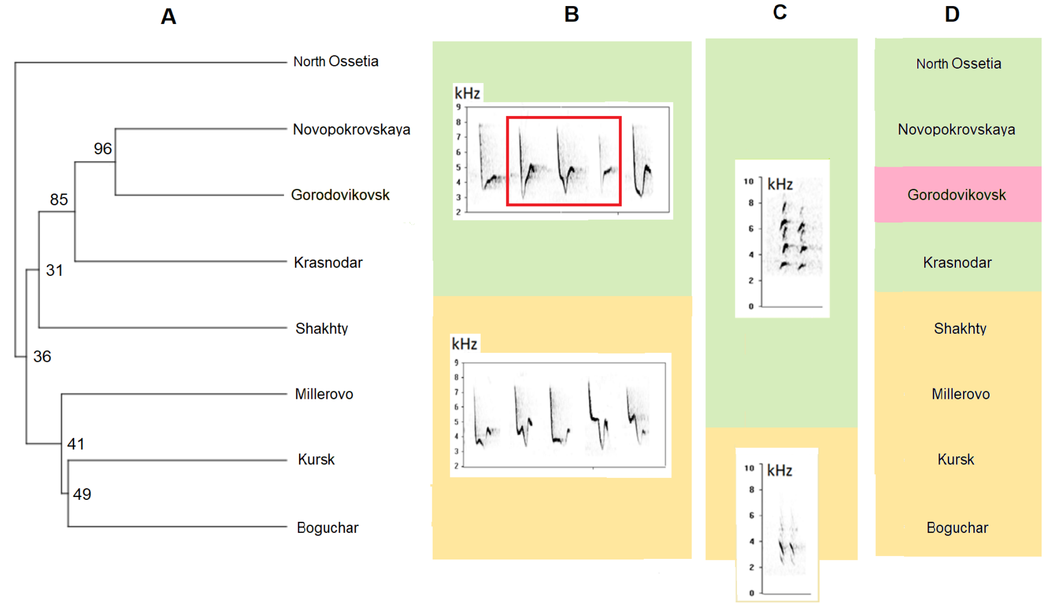

Fig. 4. Distribution of the acoustic and genetic traits among the populations studied. Column A – the song similarity (the numbers show bootstrap support for the cluster); column B – the most characteristic song syllables (the *V*-shaped syllables most typical of the *caucasicus* song are highlighted in a red frame); column C – tret calls; column D – haplotypes. Green colour is *caucasicus*; yellow colour is *abietinus*; pink colour is mixed population.

/ *L. megarhynchos, Fringilla coelebs coelebs* / *F. c. caucasica, Chloris chloris chloris* / *Ch. ch. bilkevitchi, Carpodacus erythrinus erythrinus* / *C. e. kubanensis, Coccothraustes coccothraustes coccothraustes* / *C. c. nigricans*) (Belik 2009).

We have documented for the first time the existence of a new contact zone between two subspecies of the Chiffchaff. The main results obtained are as follows:

1) In many specimens bearing the *abietinus* haplotype in Ciscaucasia, the wing formula is identical to that typical of *caucasicus* and differs from that typical of *abietinus* in allopatric populations;

2) The tret calls typical of *caucasicus* are included in the song of Chiffchaffs, which carry the *abietinus* haplotype and do not have notes characteristic of *caucasicus* in their song.

3) Chiffchaffs from Ciscaucasia occupy an intermediate position between *abietinus* and *caucasicus* in the duration of individual song phrases and syllable time-frequency characteristics.

4) In the eastern Ciscaucasia, a population was found in which the *abietinus* and *caucasicus* haplotypes co-occur in a significant number. A mixed pair of Chiffchaff (male *caucasicus* and female *abietinus*) was also found here. Mixed populations have not been found in Western Ciscaucasia. It should be noted, however, that a rather small number of haplotypes were analyzed in this area, while the unexplored gap between Novopokrovskaya and Shakhty populations (Fig. 1, circles 4 and 5) is about 200 km. It is quite likely, for example, that both forms co-occur in the large urban parks of Rostov-on-Don, located just in the middle between Novopokrovskaya and Shakhty.

An additional result is the increased variability in the plumage coloration of Chiffchaffs in Ciscaucasia compared to allopatric populations. Both taxa studied have similar plumage coloration. However, there are certain differences as well. In *caucasicus*, dull greyish and brownish colours are more pronounced, whereas *abietinus* is more brightly coloured, with a greater proportion of greenish and yellowish lores. In almost all the populations studied in Ciscaucasia, specimens were caught with a bright colouration typical of *abietinus*, together with specimens with a duller colouration characteristic of *caucasicus*, as well as specimens with a variety of intermediate colouration. The mismatch between the plumage colour and the haplotype was also noted. Eleven specimens bearing the *caucasicus* haplotype were coloured more like *abietinus* and three specimens bearing the *abietinus* haplotype were coloured more like *caucasicus*.

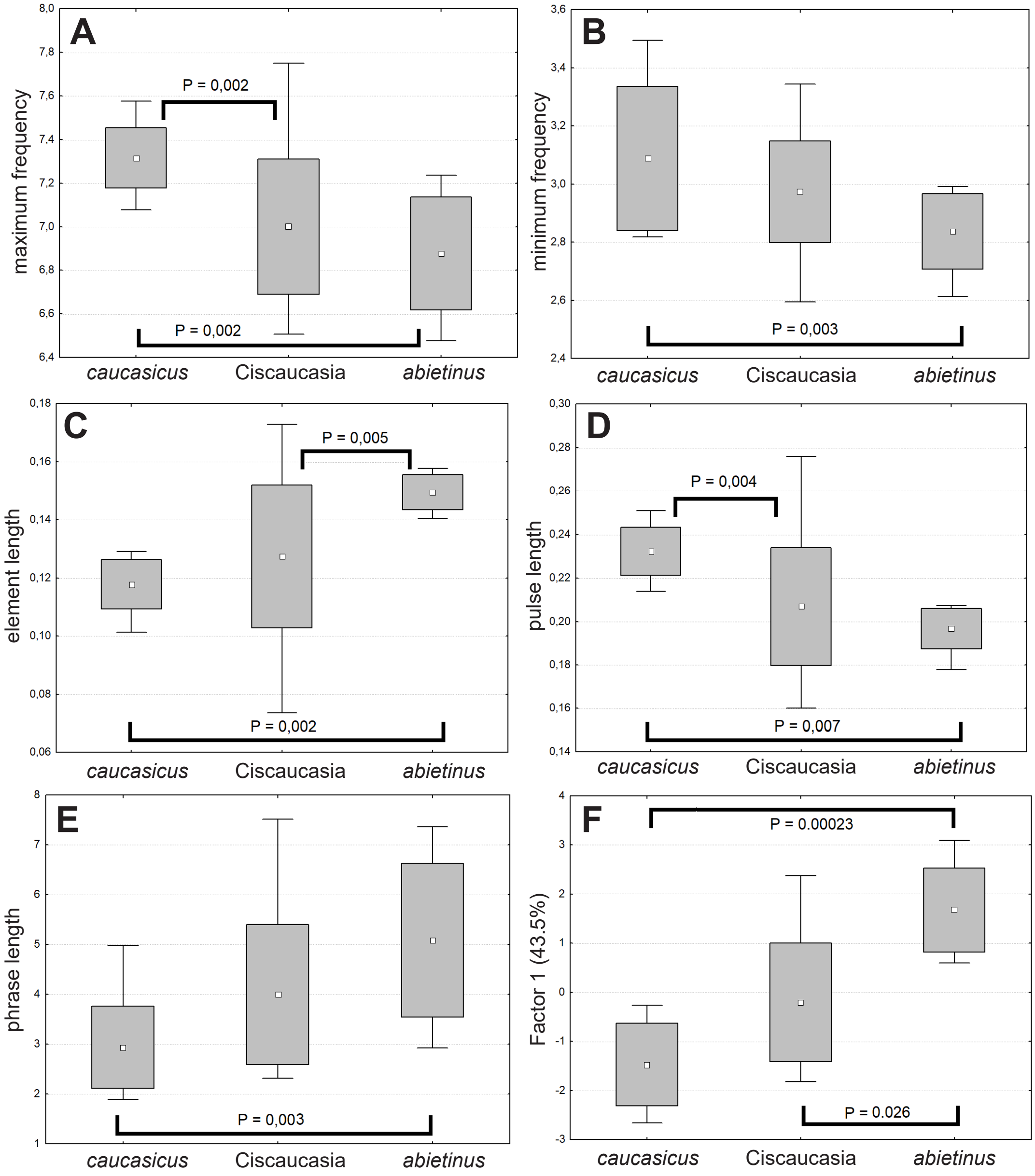

Fig. 5. Variations of song parameters in pure populations of *caucasicus* (Krasnodar and North Ossetia), in pure populations *abietinus* (Boguchar and Kursk), and in Ciscaucasia. A – maximal frequency (kHz), B – minimal frequency (kHz), C – syllable length (s), D – duration of inter-syllable pause (s), E – song phrase length (s), F – first principal component values. Significant differences in individual characteristics are illustrated (Kruskal–Wallis test; 2-tailed multiple comparison). Means, standard deviations, and limits are shown.

Although we did not conduct playback experiments, it is interesting to note that, during the captures, the males of *caucasicus* readily reacted to the broadcast of the *abietinus* song and vice versa, which we also observed earlier (Marova *et al.* 2021).

Thus, the results suggest hybridization between *abietinus* and *caucasicus* in Ciscaucasia. A significant argument in favour of this assumption is the mismatch between haplotypes and phenotypic traits (Helbig *et al.* 2001, Fedorov *et al.* 2009, Marova *et al.* 2017). For example, the Chiffchaffs from Shakhty and Millerovo carry the haplotypes of *abietinus,* and their songs do not contain syllables characteristic of *caucasicus*. However, their songs contain tret calls typical of *caucasicus*, not *abietinus*. As noted earlier, the tret calls in the songs of Chiffchaff of all subspecies, including *caucasicus*, are performed unchanged in the most remote populations of the subspecies (Ivanitskii *et al.* 2021). This suggests the probably innate nature of tret calls, with the haplotype mismatch of which may be among the evidence of hybridization.

The mismatch between the haplotype and the wing formula seems to be particularly intriguing. Only three of the 16 specimens genetically identified as *abietinus* had a wing formula identical to that in allopatric populations. The wing of the remaining 13 specimens was rounded like that of *caucasicus*. Most of these 13 specimens were caught in populations of Western Ciscaucasia (Shakhty and Millerovo) where the *caucasicus* haplotype has not been found. So the differences in morphology between *abietinus* populations in the northern (allopatric) and southern (sympatric) parts of the distribution range could arise due to differences in the length of migration routes. The distance between the populations of Ciscaucasia and the allopatric populations of the Moscow region, where the measurements were made, is about 1,000 km. This is confirmed by our data on the Kursk population, which, according to both wing formula and geographical location (480 km from Moscow), occupies an intermediate position between Moscow and Ciscaucasia. It is quite possible that the inter-population differences in the wing formula are a consequence of clonal variability. It is well known that the wing sharpness of migrating birds increases in proportion to the increase in the length of their migration routes (Bowlin & Wikelski 2008, Corman *et al.* 2014).

Among all three contact zones of the Chiffchaff subspecies described earlier, the situation in Sweden (Hansson *et al.* 2000) has the greatest similarity with the situation in Ciscaucasia. In both cases, the very first stages of contact zone formation proceed right before our eyes. Despite the fact that the *collybita* and *abietinus* ranges in Sweden are separated by 500 km of a territory unpopulated by Chiffchaffs, 7 out of 60 individuals carried an mt-haplotype, which did not match with the population from where they were sampled. In Ciscaucasia, the gap between the ranges of phenotypically pure *abietinus* and *caucasicus* is absent (at least in the eastern area), and 4 out of 40 individuals carried a haplotype alien to the population in which they were caught. An important difference between the two situations is the degree of habitat similarity between the subspecies. In southern Sweden *collybita* inhabit rich, deciduous forests, while in the northern region *abietinus* is found in old coniferous forests. The authors believe that such differences will prevent hybridization after the formation of a geographical contact zone. In contrast, there is no difference in habitat between *abietinus* and *caucasicus*. In the south of Russia, both *abietinus* and *caucasicus* inhabit broad-leaved forests, which undoubtedly should contribute to hybridization between them.

Thus, according to our data, haplotypes of *caucasicus* currently prevail throughout the studied area of Ciscaucasia. The *abietinus* haplotype dominates only within the range of this subspecies north of Rostov-on-Don. Although the absence of *abietinus* haplotypes south of Rostov-on-Don may be due to a poorly studied gap between the extreme southern (Novopokrovskaya) and extreme northern (Shakhty) parts of the contact zone (Fig. 1), we assume that *caucasicus* moves north faster than *abietinus* moves south. Over the past half-century, the Caucasian subspecies has covered a distance of about 150 km, settling northward. We suggest that the increased mobility of *caucasicus,* at least in part, may be related to its hybrid origin (*menzbieri* x *brevirostris*), which was hypothesized earlier (Marova *et al.* 2021). There are cases when hybrids are better adapted and have greater reproductive success than parental forms (Barton & Hewitt 1985, Moore & Koenig 1986, Arnold *et al.* 2001).

Uusi kontaktivyöhyke tiltalttien levinneisyysalueella: Kaukasian ja Euroopan alalajit kohtaavat Etelä-Venäjällä

Lähisukuisten eläinlajien kontaktivyöhykkeiden tutkimus auttaa vastaamaan moniin tärkeisiin evoluutiobiologian ja taksonomian kysymyksiin. Tiltaltilla (*Phylloscopus collybita*) on erityisen laaja levinneisyysalue ja sen alalajien kontaktivyöhykkeitä on kuvattu paljon. Tässä tutkimuksessa dokumentoimme kahden tiltaltin alalajin, Kaukasian (*Ph. c. caucasicus*) ja Euroopan (*Ph. c. abietinus*) tiltaltin, uuden kontaktivyöhykkeen Etelä-Venäjän Ciskaukasiassa.

Ennustimme, että näiden kahden samaan “vihreiden tiltalttien” ryhmään kuuluvan alalajin välillä tapahtuu hybridisaatiota. Löysimme itäisestä Ciskaukasiasta populaation, jossa *abietinus*- ja *caucasius*-haplotyypit esiintyvät merkittävissä määrin yhdessä. Havaitsimme siellä myös hybridisoivan parin (*caucasicus*-koiras ja *abietinus*-naaras). Tiltalttien höyhenpeitteen väri vaihteli Ciskaukasiassa enemmän verrattuna allopatrisiin populaatioihin. Monilla *abietinus*-haplotyyppiä kantavilla yksilöillä Ciskaukasiassa siiven muoto (*wing formula*) oli identtinen *caucasius*-haplotyypin tyypillisen siipimuodon kanssa ja poikkesi abietinuksen tyypillisestä muodosta allopatrisissa populaatioissa. Ciskaukasian tiltalteille ominaisia toistokutsuja (*tret calls*) esiintyi *abietinus*-haplotyyppiä kantavilla yksilöillä, mutta *caucasicukselle* tunnusomaiset sävelet puuttuivat. Monet laulun ominaisuudet edustivat *abietinuksen* ja *caucasicuksen* välimuotoa. Kiinniottojen aikana *caucasicus*-koiraat reagoivat nopeasti *abietinuksen* lauluun ja päinvastoin.

Kaikki yllä kuvatut tulokset viittaavat hybridisaatioon *abietinuksen* ja *caucasicuksen* välillä tutkimusalueella Ciskaukasiassa.

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Conflict of Interest. Authors report no conflicts of interest.

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Online supplementary material

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Proximity of shrub nests to ground nests increases the chance of ground nest predation

Jenő J. Purger*, Kornélia Kurucz, Dragica Purger & Péter Batáry

J.J. Purger, K. Kurucz, Department of Ecology, Institute of Biology, Faculty of Sciences, University of Pécs, H-7624 Pécs, Hungary
D. Purger, Department of Pharmacognosy, Faculty of Pharmacy, University of Pécs, H-7624 Pécs, Hungary
P. Batáry, 'Lendület' Landscape and Conservation Ecology, Institute of Ecology and Botany, HUN-REN Centre for Ecological Research, H-2163 Vácrátót, Hungary
**Corresponding author's e-mail: purger@gamma.ttk.pte.hu*

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In nature, ground-nesting birds rarely nest under an active shrub nest of another species. In the case of the proximity of the two nest types, we assumed that if a nest predator finds one nest, it will most likely rob the other nest as well. To test this, we exposed artificial nests with one quail and one plasticine egg on shrubs and underneath on the ground, in oleaster shrub rows and forest edges. We found a higher predation on ground nests than on shrub nests in both habitats. More importantly, predation events in shrub nests resulted in a higher predation of more concealed ground nests too. Our results suggest that proximity of two nest types can be detrimental to predation pressure, especially in forest edges.

1. Introduction

Nest predation is the primary cause of bird mortality (Ricklefs 1969), thus selection of suitable nesting habitats for birds may be more critical than food resources (Martin 1988). The survival of nests on the ground or in shrubs can be significantly influenced by the type of vegetation and also by the edge effect (*e.g.* Bayne *et al.* 1997, Batáry *et al.* 2014). Fontaine *et al.* (2007) suggested that the risk of predation varies with nest types and predator abundance independently of parental care. Survival chances of different nest types (*e.g.* open cup shrub or ground nest) are affected by features of the nesting habitat and the predator community occurring surrounding the nest (*e.g.* Hoi & Winkler 1994, Söderström *et al.* 1998). The higher density of nests either in shrubs or on the ground increased overall predation on both types (Schmidt & Whelan 1999). Moreover, an increase in the density of one nest type increased the predation rate on the other nest type (Hoi & Winkler 1994). Nevertheless, most bird species are characterized by territorial behaviour (Nice 1941). For this reason, different solitary species rarely build their nests close to each other, but if they do, such associative nesting serves to reduce predation pressure for at least one species

(Quinn & Ueta 2008). Such associative nesting in nature is not frequent, but it is confirmed between the Woodchat Shrike (*Lanius senator*) and the Western Orphean Warbler (*Sylvia hortensis*), as well as the Red-backed Shrike (*Lanius collurio*) and the Barred Warbler (*Sylvia nisoria*). It suggests a mutualistic relationship in the fight against nest predators (Isenmann & Fradet 1995, Polak 2014). However, little is known about the effect of different co-occurring bird species with different nest types on their nesting success (Elmberg & Pöysä 2011). The survival chance of shrub and ground nests close to each other can be investigated by using artificial nests and eggs (Moore & Robinson 2004). This method is applicable to estimate the daily survival rate of nests in different habitats as well as to the identification of predators (Major & Kendal 1996, Bateman *et al.* 2017). A great advantage of this method is that during the experiment with artificial nests and eggs the real nests or the breeding birds are not disturbed (Major & Kendal 1996, Kurucz *et al.* 2015), and this contributed greatly to the spread of this method (Bateman *et al.* 2017).

The aim of our study was to estimate the survival rate of shrub and ground nests in two different habitats (forest edge and oleaster rows) and to provide answers to the questions: 1) what proportion of predation events are due to bird or mammal predator?; 2) what is the difference in the daily survival rate of the two nest types?; and 3) is the predation risk related to the type of nest location – ground or shrub?

2. Materials and methods

2.1. Study area

The study area was situated on the southern slope of the Mecsek Mountains, close to the north-eastern outskirts of the city of Pécs, in South Hungary. Intensive opencast coal mining in Mecsek Mountains lasted from 1968 to 1996, after that the northern part of the area extending over 15 ha was recultivated (latitude: 46.115710° N, longitude: 18.230088° E, a.s.l. 366 m). The covering soil layer has been planted with saplings of various tree species since 1996. In the time of our study (2003), the ground was overgrown by herbaceous vegetation of the initial stage of primary succession. Oleaster (*Elaeagnus angustifolia*) shrubs were successfully planted on the hillsides in rows (1.5–2.5 m high and 2 m wide) 15–25 m apart, and the spontaneously colonizing black locust (*Robinia pseudoacacia*) reached a height of 2–3 m. The recultivated area was bordered from the east, north and west by turkey oak forests (Purger *et al.* 2004a,b, Kurucz *et al.* 2015). We performed the artificial nest experiment in oleaster rows and along edges of these native forests with diverse canopy and shrub layers, while the herbaceous layer was very weak, and the ground was mainly covered by litter. Ornithofauna of the Mecsek Mountains is relatively rich (Bankovics 2006), though during our previous study in the shrubs on the forest edge were found only nests of Eurasian Blackbird (*Turdus merula*) and Turtle Dove (*Streptopelia turtur*), but in the oleaster rows several nests of the Red-backed Shrike were located (Purger *et al.* 2014a). There were only three ground nesting species, Common Pheasant (*Phasianus colchicus*), European Nightjar (*Caprimulgus europaeus*), and Yellowhammer (*Emberiza citrinella*) found in clearings, forest edge and inside forest (Purger *et al.* 2014b).

2.2. Fieldwork

We prepared a total of 50 artificial shrub nests and 50 ground nests and exposed them on oleaster shrubs in the recultivated area on June 14, 2003. On the same day, we also exposed 50 artificial shrub nests and 50 ground nests in the forest edge. For shrub nests, we used wire mesh, attached them to branches at a height of about 1.5 m and lined them with dry grass (Purger *et al.* 2004a). Directly below the shrub nests, we established ground nests by making a shallow hole lining with dry grass. We placed one quail and one plasticine egg of similar size in each nest. Pairs of nests were located at least 20 m apart from each other (Bayne *et al.* 1997, Bayne & Hobson 1999). We controlled the nests on the first (15 June), second (16 June), fourth (18 June) and seventh (21 June) day after placement, between 13.00–19.00 hours each time. A nest was considered depredated if natural quail or plasticine eggs were damaged in some way or missing from the nest (Bayne

& Hobson 1999, Purger *et al.* 2004b). Based on the beak and tooth impressions on the plasticine eggs, it can be determined with certainty that the predator was a small or large bird or mammal (Ludwig *et al.* 2012, Bravo *et al.* 2020). Large mammal predators were identified by the help of our collection of mammal skulls. The most useful measures in the tooth imprints are the size and curvature of the incisors and the distance between the canines. Using imprints left in plasticine eggs a birds and small-bodied mammals (mice, voles, shrews) cannot be determined at the species level. This investigation was based on indirect sampling, therefore this article does not contain any studies with animals performed by any of the authors.

2.3. Statistical analysis

All statistical analyses were performed in R statistical environment using 4.0.3 program version (R Core Team 2020). First, we analysed the effects of nest type and habitat type and their interaction on the daily probability of nest survival using a generalized linear mixed-effects model (GLMM) with binomial error distribution, logit link function, and involving nest days as the denominator. This method is known as Mayfield logistic regression (Hazler 2004), and for this, we used the 'glmer' function and the maximum likelihood method from the 'lme4' package (Bates *et al.* 2015). Nest days were rounded up to the nearest day before analyses (Hazler 2004). In the model, we used the following random structure for accounting for spatial autocorrelation originating from our study design: nests were grouped in pairs, which were nested in transects, and transects were nested in East or West side of the recultivated area (in R language: Side/Transect/Pair). Furthermore, we made a pairwise post hoc (least square difference) comparison with the emmeans package in order to compare all possible combinations of nest and habitat types (Lenth 2021). Second, we also performed a GLMM model with ground nest survival (again predation event as numerator and nest day as denominator) and nest days of shrub nests as explanatory variable for directly testing the dependence of ground nest predation on shrub nest predation. In this case, the random structure was as follows: Habitat type/Side/Transect.

3. Results

During the week-long study, all nests were depredated except for the shrub nests in oleaster rows (34% of which remained intact). The plasticine eggs in the nests in the oleaster rows and in the forest edge were damaged in 75% and 94%, respectively. Most of the imprints preserved on plasticine eggs were left by small mammals and small-bodied birds (Fig. 1). Based on the tooth prints, the nest predators of the ground nests were red foxes (*Vulpes vulpes*) (in 2 cases), martens (in 6 cases), while the shrub nests were depredated by martens (in 5 cases), which are also able to remove quail eggs. Bill imprints of larger-bodied birds were found only on two plasticine eggs in shrub nests at the edge of the forest. From a total number (n = 169) of depredated plasticine eggs, 31% (n = 53) were missing. From the total number (n = 182) of depredated quail eggs, 88% (n = 161) were removed from nests, and remains of only

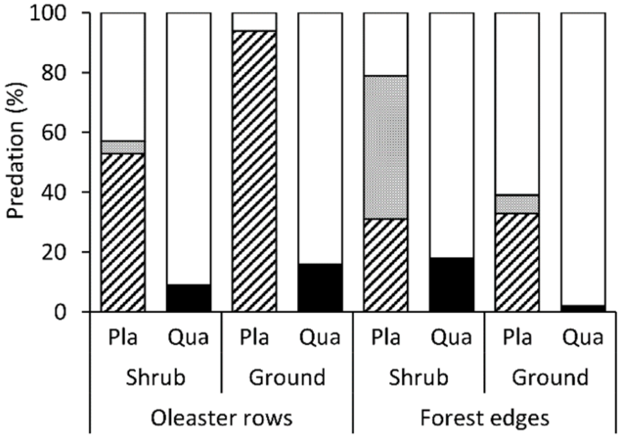

Fig. 1. Predation of plasticine (Pla) and quail eggs (Qua) in the shrub and ground nests at the two habitats: eggs taken away (white bars), eggs marked by birds (grey bars), eggs marked by mammals (hatched bars), broken and consumed quail eggs (black bars).

1.5% (n = 21) were found in the nests (Fig. 1).

Daily survival rates of nests varied significantly by habitat and nest type (Table 1, Fig. 2). The interaction of nest type and habitat type was non-significant and was discarded from the final model (Table 1). The daily survival rate of nests in oleaster tree rows was higher than at the forest edges with higher predation on ground nests in both habitats. Our direct model testing nest predation dependence showed that if shrub nests are depredated, it increases the chance that ground nests was also destroyed (estimate ± SEM = –0.16 ± 0.06, z = –2.85, P = 0.004).

Table 1. The effect of habitat type (Or – Oleaster rows) and nest types (Gn – Ground nests) on the daily probability of nest survival.

	Estimate	SEM	I value	*P*
(Intercept)	1.28	0.14	8.89	<0.001
Habitat type (Or)	0.84	0.17	5.03	<0.001
Nest type (Gn)	–0.54	0.17	–3.24	<0.001

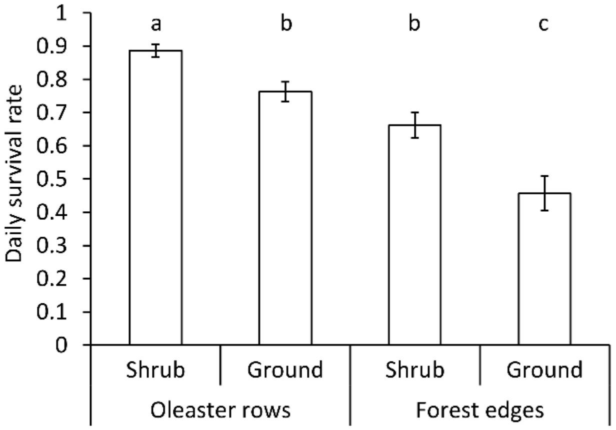

Fig. 2. Daily survival rates (± SEM) of shrub and ground nests in oleaster rows and forest edges.

4. Discussion

In our experiment based on the imprints preserved on plasticine eggs, most predators were mammals, however, a significant proportion of plasticine eggs and most quail eggs disappeared from shrub and ground nests at both habitats suggesting that birds played a more important role in predation. Larger-bodied mammals with good olfactory cues and nocturnal activity, such as red fox, European badger (*Meles meles*), and wild boar (*Sus scrofa*), which also occur in the study area, can only damage ground nests. However, martens and rodents can also damage nests on shrubs or trees. Some of the mammalian predators and birds can damage both types of nests. Small mammals and small-bodied birds can rarely break shells of quail eggs or take away from the nests, but their traces are preserved in plasticine eggs (Bayne *et al.* 1997). For predators with good eyesight, such as the corvids, both the shrub and the ground nests are available (Olsen & Schmidt 2004, Madden *et al.* 2015). Beak imprints of large-bodied birds were most likely left by Eurasian Jay (*Garrulus glandarius*) similarly as in our previous study which is performed in the same area (Purger *et al.* 2004a).

Both quail and plasticine eggs are mostly taken away from the nests by crows (Söderström *et al.* 1998), mostly broken up on hard substrates and consumed there. For this reason, usually these eggs are not found near the nests (Kurucz *et al.* 2015). Plasticine eggs are likely to be recognized by birds after a negative experience and left in the nest. The smell of plasticine can be attractive to mammals with good olfactory cues, and their visits leave more traces at the nests which can increase the predation rate (Bateman *et al.* 2017). For this reason, the predation rates of artificial nests are somewhat higher than those of real nests (Major & Kendal 1996). Using dummy birds in similar experiments increased the survival chance of artificial nests (Trnka *et al.* 2008), demonstrating the important role of the parent birds in hiding and protecting nests. Nonetheless, artificial nests and dummy eggs can be useful tools for comparative studies (*e.g.* Pärt & Wretenberg 2002, Batáry & Báldi 2005, Kurucz *et al.* 2012), however, it must be noted that artificial nests are suitable for measuring predation rates only but will not adequately measure breeding success.

In our experiment, the survival chances of both nest types were higher in the rows of oleaster trees in the recultivated area than at the forest edges, which is consistent with the finding that nest predation is often elevated at forest edges even compared to hedgerows (Batáry & Báldi 2004, Ludwig *et al.* 2012). Similar results were obtained a year earlier in the study area, even if there were exclusively plasticine eggs or only quail eggs in the shrub nests (Purger *et al.* 2004a). The results of previous study showed that predation pressure on the ground nests in the open recultivated area between forest edge and oleaster rows was also lower than on ground nests at the forest edges (Purger *et al.* 2004b). Our previous results suggested that for Black-headed Shrike and Yellowhammer, the oleaster rows in the recultivated area were more attractive to nesting in than the forest edge (Purger *et al.* 2004a). Both of these bird species prefer newly established shrubberies (such as in our study area) and, therefore, considered to be indicators of successional stages of abandoned agricultural areas with different woody vegetation cover (Mikulić *et al.* 2014).

In our study, the daily survival rates of shrub nests in both habitats were significantly higher than those of ground nests. Previous experiments with artificial nests have shown that ground nests are more often damaged by predators than shrub nests, but this may be mainly true for the species that breed in shrub and grassland habitats (Martin 1993). In contrast, ground-nesting species in forests are subject to lower predation pressure than shrub-nesting species. This can be explained by the fact that larger clutch size and longer nesting period of ground-nesting species in forests are indirect evidence that ground-nesting species have suffered lower nest predation over evolutionary time (Martin 1993). Consequently the habitat type and its condition (*e.g.* vegetation composition or level of disturbance) also influence which nest type has a higher survival chance (*e.g.* Batáry & Báldi 2004, Batáry *et al.* 2014, Wozna *et al.* 2017). The results of experiments with artificial shrub and ground nests in the temperate zone suggest that in open habitats close to the forest edge shrub nests suffered higher rates of depredation, predominantly robbed by avian predators (Söderström *et al.* 1998, Batáry & Báldi 2004). In shrub nests eggs can be discovered primarily by birds thanks to their good vision or possibly by tree-climbing mammals. When this happens, the predator can easily notice the eggs in the ground nests under the shrub nest so that they can also be depredated. Most mammals are more active at night and do not climb trees, so only ground nests can be depredated by them, while the shrub nests above them remain hidden in most cases.

5. Conclusion

In our study, we demonstrated that the features of the habitat (shrub rows, forest edge) and the type of nests (shrub, ground) had a significant effect on the daily survival rates of nests. Despite the increased presence of small mammals in both habitats, larger-bodied birds played a greater role in nest predation. The proximity of the shrub and ground nests adversely affected their survival chances.

Pensaspesien läheisyys maapesiin lisää maapesien saalistuksen todennäköisyyttä

Maassa pesivät linnut harvoin pesivät toisen pensaassa pesivän lintulajin alapuolella. Oletuksemme on, että jos pesäsaalistaja löytää yhden pesistä, se todennäköisesti löytää ja ryöstää myös toisen lähellä olevan pesän. Testataksemme tätä oletusta sijoitimme pensaisiin ja niiden alapuolelle maahan keinotekoisia pesiä, joissa oli yksi viiriäisen muna ja yksi muovailuvahamuna. Tutkimus toteutettiin kahdessa eri elinympäristössä, hopeapensasistutuksilla ja metsän reunoilla. Havaitsimme, että maassa oleviin pesiin kohdistui enemmän saalistusta kuin pensaspesiin molemmissa elinympäristöissä. Jos saalistus kohdistui pensaspesiin, se johti myös lisääntyneeseen saalistukseen vaikeammin havaittavissa maapesissä. Tuloksemme viittaavat siihen, että kahden pesätyypin läheisyys voi lisätä saalistuspaineen haitallisuutta, erityisesti metsän reunoilla.

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Apparent survival and dispersal in a White-throated Dipper (*Cinclus cinclus*) population from northern Iberia

Aitor Galarza, Luis Betanzos-Lejarraga & Juan Arizaga*

A. Galarza, L. Betanzos-Lejarraga, J. Arizaga, Departamento de Ornitología, Sociedad de Ciencias Aranzadi, 20014 Donostia, Spain
**Corresponding author's e-mail: jarizaga@aranzadi.eus*

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River systems are some of the habitats most drastically affected by climate change. Consequently, many riparian species are amongst the most threatened living organisms worldwide, making riparian areas a conservation priority. Demographic analyses destined to improve our comprehension of the population dynamics of riparian species are crucial in this context. The present work analyses the spatio-temporal demographic dynamics of a presumably well-preserved White-throated Dipper (*Cinclus cinclus*) population from northern Spain. Using multistate models where we considered the effects of factors such as mean water flow in winter, age, sex, hydrographical basin of origin and hatching date, we found that the population had a constant annual dispersal rate ($\psi = 0.038$; 95% CI: 0.022–0.065). The mean apparent survival of Dippers from first-order clutches was 0.18 (95% CI: 0.12–0.22), whereas for those hatched in second-order clutches was 0.07 (95% CI: 0.03–0.15). The mean annual apparent survival for adults was 0.64 (95% CI: 0.56–0.70). Although apparent survival varied from year to year, we found no effect of the average winter flow on this parameter. Recapture probability (p) varied among basins, probably reflecting a heterogeneous sampling effort. In conclusion, using multistate models were found that Dippers from three adjacent river basins in northern Spain had a very short-range natal dispersal rate, and a breeding dispersal close to zero, a trait that could be different from findings in other zones of Spain, where dispersal rates seem to be much higher.

1. Introduction

Demographic analyses constitute a basic piece of knowledge necessary to comprehend causes explaining bird population dynamics (Croxall & Rothery 1991, Lebreton *et al.* 1992, Newton 1998, Lebreton 2001). For instance, population models are fed with the corresponding estimate of the different age-classes survival rates (Garcias & Tavecchia 2018), and quantifying the effect of the multiple sources that might shape variation in survival is crucial because this allows a proper evaluation of the direction and magnitude of environmental drivers on bird population dynamics (Loison *et al.* 2002, Prieto *et al.* 2019). Dispersal is also one key parameter driving demographic processes in birds (Oro *et al.* 2011, Delgado *et al.* 2021), for instance due to source-sink dynamics mediated by natal or breeding dispersal (Greenwood & Harvey 1982, Senar *et al.* 2002, Pfeiffer & Schaub 2023). From a conservation standpoint, most studies are usually done in relatively small areas where dispersal (*i.e.* emigration/immigration) can play a role. Thus, if dispersal is important, protecting only isolated small areas might be insufficient to maintain populations, and in these cases approaches to conservation should involve actions at broader spatial scales (Baillie *et al.* 2000).

Climate warming is causing dramatic changes worldwide, with river systems being one of the most drastically affected habitats (Pletterbauer *et al.* 2018). Predictive models suggest changes in the air and water temperature, and in the amount and/or regularity of precipitation (Chiu *et al.* 2013, Royan *et al.* 2015). These climate alterations trigger processes that can alter river morphology (Ashmore & Church 2001), riparian vegetation (Dwire *et al.* 2018), nutrient dynamics (Johnson *et al.* 2012) or distribution and abundance of animal species (Timoner *et al.* 2021). Consequently, highly specialised riparian species are amongst the most threatened living organisms worldwide, making these areas a conservation priority (Capon *et al.* 2013, Zhang *et al.* 2023).

The White-throated Dipper (*Cinclus cinlus*)—hereafter to simplify referred to as 'Dipper'—is a specialised small passerine bird associated with clean, well-oxygenated, fast-flowing streams living across much of Eurasia (Ormerod & Tyler 2005). Its dependence on such a well-preserved riparian ecosystem and its sensitivity to the pollution and alteration of the natural riparian systems have led to its consideration as a bioindicator (Ormerod *et al.* 1986, Ormerod & Tyler 1989, Ormerod *et al.* 1991, Vickery 1992, Nilsson *et al.* 2011, Morrissey *et al.* 2012). Studies on population dynamics of dippers are gaining increasing interest in the scientific community, given that their populations are suffering from the effects of climate change in many places worldwide, either due to droughts or an increasing number of extreme flooding episodes (Loison *et al.* 2002, Nilsson *et al.* 2011, Chiu *et al.* 2013, Sánchez *et al.* 2017).

The Cantabrian region in Spain constitutes, together with the Pyrenees, a capital bastion for the Dipper population in the Iberian Peninsula (Keller *et al.* 2020, Molina *et al.* 2022). Under the current climate change scenario, droughts and desertification are amongst the most serious threats to the conservation of Dipper populations in much of Spain (Galindo *et al.* 2003, Huntley *et al.* 2007). Therefore, Dipper populations breeding in those areas still maintaining well-preserved river basins might play a key role for the conservation of this species in southern Europe. In this context, all those studies aimed at determining the conservation status of Dipper populations, including analytical approaches to estimate demographic parameters such as survival or dispersal, are highly recommended. Although the Dipper is a relatively frequently ringed bird in Spain (Regla & Arizaga 2016), we know only one study in which survival is estimated (Sánchez *et al.* 2017). The average apparent annual survival of Dippers caught as adults in a nearby population (Gipuzkoa, Basque Country) was 0.56, and it varied annually slightly, in part explained by winter flooding episodes (Sánchez *et al.* 2017). Survival did not vary between sexes and the study, due to the nature of the used data set, was unable to estimate the survival of first-year birds (an essential parameter to feed population models) and did not test to what extent survival varied locally (*e.g.* between nearby river basins) or estimated dispersal. For this latter parameter, most analyses have been done by measuring directly distances from ring-recovery data (Tellería *et al.* 1999, Galindo *et al.* 2003, Campos *et al.* 2012, Regla & Arizaga 2016), a method which has often been questioned because the ringing effort is normally concentrated in very specific rivers or basins, what hampers from detecting longer-distance dispersal (*e.g.* Hernández *et al.* 2012). Although Dippers from Spain show on average short-range dispersal distances as compared to their northern European counterparts (Franks *et al.* 2022), there is still little knowledge of the characteristics of this trait for the Iberian Dipper populations.

The main goal of this study is to address the lack of information on Dipper population dynamics in Spain, contributing to investigate the environmental drivers that may influence variations in demographic parameters. In particular, we analysed the apparent annual survival and dispersal of an apparently well-preserved population of Dippers in northern Spain (Biscay, Basque Country, Cantabrian region), testing for the effects of factors such as mean water flow in winter (Chiu *et al.* 2013), age, sex, hydrographical basin of origin and hatching date. These parameters have been proved to affect Dipper population dynamics in previous studies (Bryant & Newton 1996, Loison *et al.* 2002, Middleton & Green 2008, Sánchez *et al.* 2017).

2. Material and methods

2.1. Study area and data collection

This study was carried out in three basins within the province of Biscay (Basque Country, Spain), from east to west: Artibai, Lea and Oka (Fig. 1). Overall, these basins cover an area of 458 km^2 with an accumulated length of *ca.* 90 km of rivers (tide-influenced stretches excluded). Most of the main rivers and their tributaries within the study area are protected under European regulations (Special Areas of Conservation: ES2130006, ES2130010 and ES2130011). Topographically, these three main rivers flow through valleys ranging from 0 to *ca.* 1000 m above sea level, though in the majority of the territory the altitudinal difference ranges from 0 to 200 m. The landscape is dominated by Atlantic native deciduous forest patches, timber plantations and countryside, with small scattered towns and farms.

We searched for nests during the breeding seasons of 2015 to 2022 (from mid-February to mid-May), trying to cover the whole study area and marking as many nestlings as possible. The population comprised from 54 to 68 pairs of adult, territorial Dippers. These were distributed equally and uninterruptedly throughout the three basins, from the sea level up to an altitude of

Fig. 1. River basins where the study was carried out. In the square right above, we show the location of these three basins within the province of Biscay (shaded in dark grey), belonging to the Basque Country (Spain). The small square shows the location of the Basque Country in the Iberian peninsula.

300 m. We estimate that we ringed 47.5% of the broods (n = 232 fledglings: Artibai=60, Lea=102, Oka=70). Given that the Dipper may lay a second clutch, each nest was monitored to determine whether the ringed nestlings came from the first or second clutch (in this last case we also included replacement clutches laid when the first one failed). During the subsequent breeding seasons we trapped adults using mist nets placed close to nests, captured when entering or leaving their nests to incubate or feed their offspring. Upon capture, each bird underwent ringing, and for adults, their sex was determined by assessing the presence of an incubating patch or employing the discriminant function as described by Arzak *et al.* (2014). Nestlings were ringed when they had an age of one to two weeks. Older nestlings were avoided because they tend to jump from the nest due to the manipulation, which would decrease their survival prospect.

The Basque Water Agency provided hydrological data. Because we wanted to assess the impact of extreme flooding in the months before the breeding season, we considered the mean values from November to February, just before the end of the interval between one season and the other (Sánchez *et al.* 2017). Dippers mostly feed on riparian macroinvertebrates (with a diet that include insects, molluscs, crustaceans and fish eggs and larvae) (Tyler & Ormerod 1994), Extreme flooding episodes, which in our sampling zones are more habitual in winter, can impact Dippers survival as they temporally hamper the access to food and reduce its availability by increasing the turbidity of the water and by favoring the washing of the river bed by strong currents. In particular, data were collected from three gauging stations located, respectively, in the basins of Lea (station of Oleta), Artibai (station of Berriatua) and Urdaibai (station of Muxika) (for details see Appendix 1).

2.2. Capture-mark-recapture models

We used multistate with only live recaptures models (Lebreton & Cefe 2002) to calculate the following parameters: apparent survival (ϕ: probability that a bird captured in time t is alive in t+1), recapture probability (p: probability of recapturing a bird which is alive at encounter occasion t+1) and transition probability (ψ, probability of moving from one of the states -in this work, river basin- to another one). Multistate models estimate local survival rates (apparent survival), since they cannot distinguish true mortality from permanent emigration. Models using a logit-link function were run in the software MARK 6.1 (White & Burnham 1999).

The original data sets (Dippers ringed either as nestlings or as adults—in their second year of life or later) were lumped into a single matrix with 868 rows (individuals) by 8 columns (years), where the birds ringed as nestlings or as adults were identified by considering two groups (a ‘marked as nestlings + marked as adults’ approach). In this matrix, we identified the river basin where the Dippers were captured or recaptured (A = Artibai, B = Lea, C = Oka). For instance, ‘A00B0BB0’ represents a bird ringed in A in 2015, not recaptured in 2016 and 2017, recaptured in B in 2018, not recaptured in 2019, recaptured in B in 2020 and 2021, and not recaptured in 2022.

Before starting to select models, we tested that the data fitted to the model assumptions. We used for that the software UCARE (Choquet *et al.* 2009). The global goodness-of-fit (GOF) for a matrix simplified to a single-site approach was significant ($\chi^2 = 94.25$, df = 33, P<0.001), due to the presence of transients (Z=5.925, P<0.001), and not trap-dependence (Z=–0.915, P = 0.360). Similarly, a multisite GOF test revealed a violation for the assumptions for the group of Dippers ringed as nestlings ($\chi^2 = 58.4$, df = 27, P<0.001), but not for those marked as adults ($\chi^2 = 2.26$, df = 10, P = 0.994). The presence of transients can be solved with matrices assuming age-dependence on CJS models (Pradel *et al.* 1997), considering the two-age class approximation.

Corrected small sample sizes Akaike values (AICc) were used for ranking the fit of alternative models to data (Burnham & Anderson 1998). Models with a ΔAICc < 2 were considered to fit the data equally well. Because models with additional unsupported parameters will be likely within 2 AICc units and these models are non-competitive unless the extra parameter leads to a reduction in AICc (Arnold 2010), we analysed in detail the *B*-parameters from all models having a ΔAICc < 2 from the top-ranked one in order to see if the parameters affected ϕ, but also the deviance. This is known as 'pretending variable', which is found when two models with similar AICc values and only one parameter of difference have an almost identical deviance, so the additional parameter is probably a 'pretending variable' with an artificial, not trustable, effect (Anderson 2008). Parameters with a 95% confidence interval (CI) including zero indicate a non-significant effect of the factor/covariate (Taylor *et al.* 2004) and the overlap with 95% CI of average survival estimates indicate a lack of significant difference between those means.

We ran a set of candidate models with various patterns in ϕ, *p* and ψ. Due to the huge amount of possible combinations (of thousands of models), we conducted a preliminary analysis to identify a global model structure with minimal or no estimability problems. Subsequently, we built a set of candidate models after fixing the best structure for parameter *p* (Burnham & Anderson 2002). These candidate models tested various hypotheses related to ϕ and ψ whilst *p* structure kept consistent.

Firstly, we built a first model assuming age-dependence on ϕ (considering two age

Table 1. M-array tables summarizing capture–recapture data from the Dipper Biscay population surveyed from 2015 to 2022. Data categories: Dippers ringed as nestlings or as adults, with sexes of the latter set segregated. Note that nestlings were ringed from 2015 onwards, whilst adults were ringed from 2017 onwards. The term R(*i*) refers to the number of Dippers released at each time (breeding season).

Year	R(*i*)	2016	2017	2018	2019	2020	2021	2022	Total
Nestlings									
2015	88	1	0	0	1	0	0	0	2
2016	50		6	5	0	0	1	0	12
2017	122			11	1	0	1	0	13
2018	174				15	1	3	0	19
2019	144					12	5	4	21
2020	129						8	5	13
2021	150							19	19
2022	28								0
Male									
2017	11			8	1	0	0	0	9
2018	14				9	0	0	0	9
2019	16					7	1	0	8
2020	17						9	1	10
2021	16							8	8
2022	10								0
Female									
2017	14			8	2	0	0	0	10
2018	16				7	2	0	0	8
2019	12					4	0	0	4
2020	15						3	0	3
2021	9							6	6
2022	9								0

categories: survival of first-years [*i.e.* during their first year of life] and of older birds [annual survival from the second year of life onwards], annotated as ϕ_{fy} and ϕ_{ad}), and constant ψ and p. We then checked whether p remained constant (ϕ_{fy}, ϕ_{ad}, p, ψ) or varied among basins [$p_{(basins)}$], given that the sampling effort was not homogeneous (we invested more effort in the Oka river basin than in the other two), between age classes [p_{fy}, p_{ad}], among years (*e.g.* time-dependence on p) [$p_{(year)}$] or taking into account interactions between basins, age classes and years. The model which considered an effect of river basin and age on p had a better fit than the rest of tested models, so we fixed the model [ϕ_{fy}, ϕ_{ad}, $p_{fy(basins)}$, $p_{ad(basins)}$, ψ] to test various hypotheses related to ϕ and ψ.

Secondly, we checked whether ψ was constant or varied between age classes (ψ_{fy}, ψ_{ad}), among basins [$\psi_{(basins)}$], in relation to clutch order [$\psi_{(clutch)}$] or considering a combination of both factors [$\psi_{(basins \times clutch)}$]. The model assuming age-dependence on ψ had a better fit to the data (Table 3), though it fitted to the data equally well than the one with constant ψ, suggesting a weak effect of age on ψ, also probably due to sample size constraints (only one adult was found to change of river basin; Table 2). Because of this, and given the small sample size for adult birds, we considered constant ψ for the models used to test effects on ϕ (next step). Time-dependence on ψ was ignored due to sample size constraints (for details see Tables 1 and 2).

Thirdly, starting from [ϕ_{fy}, ϕ_{ad}, $p_{fy(basins)}$, $p_{ad(basins)}$, ψ], we built various models testing for the effect of clutch order, basin, year and mean water flow in winter on ϕ. To test for the effect of flooding episodes on ϕ, we replaced year-dependence by the mean water flow measured during the months of November to February (Sánchez *et al.* 2017). Apart, and because the sex of most Dippers ringed as nestlings was ignored, we used a subset of the original matrix, comprised only by adults, in order to also test for the effect of the sex on ϕ. The alternative tested models in this case included constant-, time- (year) or sex-dependence on both/either ϕ and p. Due to sample size constraints, in this case we did not use multistate models, but Cormack-Jolly-Seber models with the data from the three sampling river basins pooled. The GOF test for this new dataset was not significant ($\chi^2 = 1.894$, df = 13, P = 0.999), nor the specific test to detect transients (Z=0.464, P = 0.642) or trap-dependence (Z<0.001, P = 0.999).

Table 2. Basic statistics of the number of Dippers ringed (also segregated by basins; A=Artibai, L=Lea, O=Oka) and recaptured (in a subsequent year of the ringing one). For those recaptured, we note whether they were recaptured within the same river basin where they were ringed (Recapt. no change) or in another river basin (Recapt. change). In this last case, we indicate the direction of the movement was done.

	Nestlings	Adults
Ringed	786	82
Basin: A	215	1
Basin: L	339	13
Basin: O	232	66
Recaptured	68 (8.65%)	53 (64.6%)
Recapt. no change	56	52
Recapt. change	12	1
Change: A to L	1	–
Change: A to O	2	–
Change: L to O	3	–
Change: O to A	1	–
Change: O to L	5	1

3. Results

From 786 Dippers ringed as nestlings, we only obtained 68 recaptures (8.65%). From them, 56 (82.4%) were recaptured within the same river basin where they were ringed, with only 12 dispersing to the nearby studied basins (for details see Table 2). The globally observed percentage of Dippers that moved outside their origin basin was on average 1.6% (referenced to the sum of Dippers ringed by basin), with this proportion being similar among basins ($\chi^2 = 2.56$, df = 2, P = 0.30). Once recruited in a new basin, birds were never recaptured in a third basin and they did not move again to the original one.

Models showed a higher fit to the data when dispersal rate (ψ) was age-dependent, though

Table 3. Top-ranked multistate with only live recaptures models used to test for the effect of several factors (age, year, winter flow, river basin) on survival (ϕ), recapture probability (p) and dispersal (ψ) across three river basins from the province of Biscay. Abbreviations: AICc=small sample sizes-corrected Akaike values; ΔAICc=AICc difference in relation to the top-ranked model within each case (candidate models on p, ψ or ϕ); np = number of parameters. For the column np, we show in parenthesis the number of real parameters that should be estimated (modified manually in MARK). This can be compared to the number of parameters actually estimated, as a result of sample size constraints.

Models	AICc	ΔAICc	np	Deviance
Candidate models on p				
ϕ_{fy}, ϕ_{ad}, $p_{fy(basins)}$, $p_{ad(basins)}$, Ψ	1022.02	0.00	9	303.25
ϕ_{fy}, ϕ_{ad}, $p_{(basins)}$, Ψ	1024.03	2.01	6	311.35
ϕ_{fy}, ϕ_{ad}, $p_{(basins \times year)}$, Ψ	1029.79	7.77	15(24)	298.71
ϕ_{fy}, ϕ_{ad}, p_{fy}, p_{ad}, Ψ	1044.29	22.27	5	333.64
ϕ_{fy}, ϕ_{ad}, $p_{(year)}$, Ψ	1045.49	23.47	10	324.68
ϕ_{fy}, ϕ_{ad}, p, Ψ	1050.61	28.59	4	341.98
Candidate models on ψ				
ϕ_{fy}, ϕ_{ad}, $p_{fy(basins)}$, $p_{ad(basins)}$, Ψ_{fy}, Ψ_{ad}	1020.80	0.00	10	299.98
ϕ_{fy}, ϕ_{ad}, $p_{fy(basins)}$, $p_{ad(basins)}$, Ψ	1022.02	1.22	9	303.25
ϕ_{fy}, ϕ_{ad}, $p_{fy(basins)}$, $p_{ad(basins)}$, $\Psi_{(clutch)}$	1024.05	3.25	10	303.23
ϕ_{fy}, ϕ_{ad}, $p_{fy(basins)}$, $p_{ad(basins)}$, $\Psi_{(basins)}$	1047.95	27.15	10(11)	327.13
ϕ_{fy}, ϕ_{ad}, $p_{fy(basins)}$, $p_{ad(basins)}$, $\Psi_{(basins \times clutch)}$	1074.45	53.65	10(14)	353.64
Candidate models on ϕ				
$\phi_{fy(year)}$, $\phi_{ad(year)}$, $p_{fy(basins)}$, $p_{ad(basins)}$, Ψ	1008.07	0.00	17(21)	272.86
ϕ_{fy}, $\phi_{ad(year)}$, $p_{fy(basins)}$, $p_{ad(basins)}$, Ψ	1014.12	6.05	12(15)	289.21
ϕ_{fy}, $\phi_{ad(flow)}$, $p_{fy(basins)}$, $p_{ad(basins)}$, Ψ	1016.75	8.68	10	295.94
$\phi_{fy(clutch)}$, ϕ_{ad}, $p_{fy(basins)}$, $p_{ad(basins)}$, Ψ	1017.11	9.04	10	296.30
$\phi_{fy(flow)}$, $\phi_{ad(flow)}$, $p_{fy(basins)}$, $p_{ad(basins)}$, Ψ	1018.68	10.61	11	295.82
$\phi_{fy(year)}$, ϕ_{ad}, $p_{fy(basins)}$, $p_{ad(basins)}$, Ψ	1018.88	10.81	15	287.80
$\phi_{fy(flow)}$, ϕ_{ad}, $p_{fy(basins)}$, $p_{ad(basins)}$, Ψ	1023.74	15.67	10	302.93
$\phi_{fy(basins)}$, ϕ_{ad}, $p_{fy(basins)}$, $p_{ad(basins)}$, Ψ	1024.76	16.69	11	301.90
ϕ_{fy}, $\phi_{ad(basins)}$, $p_{fy(basins)}$, $p_{ad(basins)}$, Ψ	1025.76	17.69	11	302.90
$\phi_{fy(basins)}$, $\phi_{ad(basins)}$, $p_{fy(basins)}$, $p_{ad(basins)}$, Ψ	1028.06	19.99	12(13)	303.15

the fit to the data was as good as for the models assuming constant ψ (Table 3; see methods for more details). Thus, our top-ranked model provided a mean dispersal of 0.05 (95% CI: 0.026–0.086) for the first-year birds, and of 0.01 (95% CI: 0.002–0.070) for the adults (note that the 95% CI of the two age classes overlap). The second model provided a mean dispersal of 0.038 (95% CI: 0.022–0.065), *i.e.* on average 4% of Dippers moved outside their original basin.

Recapture probability (p) varied among basins and between age categories. Thus, models supported decreasing mean values from west to east (being lower in Artibai than in the other two basins), and for Dippers recaptured one year after having been ringed as nestlings than in older birds (Fig. 2).

The top-ranked model showed time-dependence on both ϕ_{fy} and ϕ_{ad} (Table 3), albeit a detailed exam of the parameter estimates showed that the model was unable to estimate most of the annual values for adults, clearly because of the lack of a sufficient amount of data (for details see also Table 1). For first-years, a plot of their annual survival rates together with their 95% CI indicate that, in fact, most of the variation was capitalized by the annual survival rates obtained for the nestlings ringed in 2015 (ϕ_{fy}=0.032, 95% CI: 0.008–0.116) and 2016 (ϕ_{fy}=0.270, 95% CI: 0.152–0.430), whilst for the rest of the years the mean annual survival remained relatively constant, around a mean of 0.16 (Fig. 3). Models assuming an effect of the mean water flow in winter on survival were lower-ranked and hence did not fit to the data as well as the models assuming time-dependence. Other models that were ranked also very high were those which included an effect of the clutch order on ϕ_{fy}. Thus, the mean apparent survival of Dippers from first-order clutches was 0.18 (95% CI: 0.12–0.22), whereas for those hatched in second-order clutches was 0.07 (95% CI: 0.03–0.15). The mean annual survival for older birds (ϕ_{ad}) was 0.64 (95% CI: 0.56–0.70).

For the data subset of adults, we observed that a model assuming sex-dependence on ϕ, constant *p* (AICc=237.71, deviance=46.36) fitted to the data as well as the one with constant ϕ (237.90, deviance=48.64). This slight difference must be interpreted as a weak, statistically null effect of sex on survival. Average survival for males was 0.82 (95% CI: 0.56–0.94), whereas in females was 0.52 (95% CI: 0.40–0.64), and *p* was 0.84 (95% CI: 0.70–0.93).

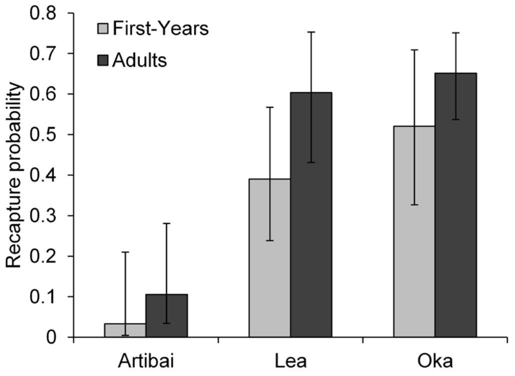

Fig. 2. Recapture probability (*p*; we show mean values ± 95% confidence interval) of Dippers ringed in three river basins (Artibai, Lea and Oka) from Biscay either as nestlings (first-years) or as adults. Estimates obtained from the top-ranked model (the one with the lowest AICc) shown in Table 3.

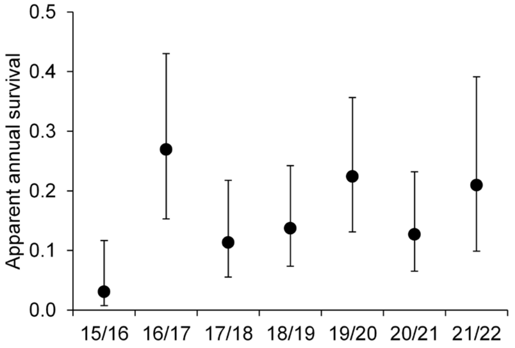

Fig. 3. First-year annual apparent survival of Dippers ringed as nestlings in Biscay. We show mean values (±95% confidence interval) obtained from the top-ranked model shown in Table 3.

4. Discussion

This is the first study estimating survival in a Dipper population of Biscay, and to the best of our knowledge the second one for Spain (Sánchez *et al.* 2017). Moreover, we used for the first time multistate models to estimate dispersal rates among river basins, an approach that is statistically more robust than assessing them directly from the raw data, because we control for the effect of other parameters, including recapture rate (Senar & Conroy 2004). Dippers from the three studied river basins had very low annual dispersal rates, with most being recaptured within the same river basin where they were ringed either as nestlings or adults. For adults, indeed, only one bird out of 53 was found to change basin. Our results suggest that the population had a very short-range natal dispersal rate, and a breeding dispersal close to zero, a trait that could be different from findings in other zones of Spain, where dispersal rates seem to be much higher (Hernández *et al.* 2018).

The mean dispersal rate among the three studied river basins was 4%, with models ignoring local variation among basins. Note that this estimation is higher than the observed 1.6% dispersal. This is caused by an imperfect detection of individuals. Indeed, the advantage of the use of multistate models is that we also estimated the detection probability (p) and, by doing so, we obtained a more robust estimate of dispersal. As the amount of recaptures of adult birds was nearly zero, and since birds did not move to third river basins once they were recaptured, the estimated dispersal can be considered as a true natal dispersal value for the studied Biscayan population. Although we cannot reject that the assessed 4% rate could be biased to a sample size limitation (*e.g.* models showed problems of convergence to estimate parameters in more complex contexts) and by the fact that our study was based on a data set of capture-recaptures obtained in a relatively small zone, so we could still ignore certain amount of dispersal to further distant basins, evidence supports that, overall, dispersal was truly low for our population (see below for more discussion). The biological conservation status of the three studied river basins was good, according to indicators of the composition and abundance of benthic aquatic macroinvertebrates, aquatic plant species or fish, as stated by European laws (López *et al.* 2021). Therefore, the lack of a clear flow from a given basin to others (*i.e.* a source–sink scenario) could also respond to the lack of an environmental variation promoting this potential flow (Senar *et al.* 2002).

Our estimated mean dispersal rate of *ca.* 4% is similar to the *ca.* 3% observed for all Spain using directly ring-recovery data (Hernández *et al.* 2018). However, this last number should be higher in case of applying multi-state models that control for aspects like recapture rate, which is likely to be very low for those birds moving outside their natal river basins (Regla & Arizaga 2016). Noteworthy, our estimated dispersal through models doubled the observed one. In this scenario, the dispersal for the studied population would be lower than the one possibly existing in other parts of Spain.

According to Hernández *et al.* (2018), ring-recovery analyses may underrepresent the true magnitude of the genetic flow between river basins in Spain, assessed to be *ca.* 14%. In that work, however, authors did not include any sample from the Cantabrian basins (northern slopes of the Cantabrian mountains), where due to the occurrence of more stable hydrological conditions Dippers could show lower dispersal rates than their southern (Mediterranean) counterparts. Noteworthy, Hernández *et al.* (2018) observed that the dispersal was smallest for the Dippers sampled in the southern slopes of the Cantabrian mountains. Moreover, we calculated an annual dispersal rate, whilst Hernández *et al.* (2018) pooled data from many years, hence they obtained some kind of accumulated (‘historical’) dispersal within each population, which is likely to be higher than an annual estimation obtained with a sample collected over eight consecutive years. We consider that our three-basin approach provides a robust design to estimate dispersal, but it would be useful for the future to (1) replicate our study in other basins and (2) to do genetics in order to estimate the genetic flow between basins and test the hypothesis that the Cantabrian populations might show lower dispersal rates than their Mediterranean or Pyrenean counterparts.

As expected, first-year survival was lower (almost 80%) than adult survival. This is because most bird species tend to show lower apparent survival rates in their first-year, either due to higher dispersal rates or because they are less experienced and then more vulnerable to predators and other causes of mortality (Newton 1998). Moreover, birds from first broods had a higher survival prospect than those hatching in second clutches, a phenomenon also reported in many other bird species (*e.g.* Parejo & Danchin 2006, Galarza & Arizaga 2014). There is a very large body of studies dealing with this behaviour (*e.g.* see for a review Newton 1998), and the occurrence of second clutches in short-lived species is ultimately driven by trade-offs between the current reproductive investment and the breeders’ future fitness assuming intra-generational costs (Dawkins & Ridley 1986). For our particular case, it would be interesting to address a finer comprehension about under which circumstances Dippers lay second clutches and to what extent these are critical to keep a sustainable (either stable or growing) population.

Female apparent survival was on average 0.3 points lower than males (0.52 versus 0.82), but the 95% confidence interval showed a slight overlapping, indicating that the difference was non-significant. We attribute this lack of significance to relatively small sample sizes, possibly linked to an also high variability of this parameter. Other studies dealing with larger data sets, however, were equally unable to detect sex differences in survival (Loison *et al.* 2002, Sánchez *et al.* 2017). If this difference between sexes would have biological significance within the survey area, it may be due to either lower survival rates in females (*e.g.* due to higher predation rates than males during the incubation period) and/or higher dispersal in females. Regarding this last possibility, it must be acknowledged that females from our population had slightly longer natal dispersal distances than males (Galarza *et al.* 2023), but anyway most Dippers ringed as nestling, including females, were recaptured at less than 5 km from their natal site. Given that our entire sampling region covered by far more than 5x5 square kilometres, it is unlikely that presumably lower apparent survival rates in the females may be due to emigration. This hypothesis is in line with findings obtained for all Spain using ring-recovery data (Regla & Arizaga 2016).

Overall, we found no effect on mean water flow regimens during the winter on annual survival, as observed in other cases, both in the Brown Dipper (Chiu *et al.* 2013) and the White-throated Dipper (Sánchez *et al.* 2017), although in this last case differences were subtle. It is possible that flooding episodes within the study area had a negligible effect on Dippers (*e.g.* birds could find alternative feeding sources during the days/weeks when their main used streams remained flooded; Chiu *et al.* 2013). Future research, focusing also on breeding parameters (such as clutch size or productivity), will be necessary to disentangle more finely whether the current flow regimens of the Cantabrian rivers have a significant impact on Dippers populations and, therefore, estimate more accurately the degree of vulnerability of such populations to climate warming.

Koskikaran (*Cinclus cinclus*) eloonjääminen ja levittäytyminen Pohjois-Iberian populaatiossa

Jokiympäristöt ovat erityisen herkkiä ilmastonmuutoksen vaikutuksille, ja monet niissä elävistä lajeista kuuluvat maailman uhanalaisimpiin. Tästä syystä jokivarsien suojelu on ensiarvoisen tärkeää. Demografiaan perustuvat analyysit voivat syventää ymmärrystämme jokivarsien lajien populaatiodynamiikasta ja edistää suojelutoimia. Tässä tutkimuksessa tarkastelimme koskikaran (*Cinclus cinclus*) populaatiodynamiikkaa ajallisesti ja alueellisesti Pohjois-Espanjassa. Tilastollisissa malleissamme huomioimme talvien keskimääräisen virtaaman, yksilön iän, sukupuolen, syntyperän valuma-alueen sijainnin sekä kuoriutumispäivän. Tuloksemme osoittivat, että populaation vuosittainen levittäytymisaste pysyi vakiona (ψ=0.038; 95% luottamusväli: 0.022–0.065). Ensimmäisen poikueen poikasten keskimääräinen eloonjäämisaste oli 0.18 (95% lv: 0.12–0.22), kun taas toisen poikueen poikasten eloonjäämisaste oli 0.07 (95% lv: 0.03–0.15). Aikuisten keskimääräinen vuosittainen eloonjäämisaste oli 0.64 (95% lv: 0.56–0.70). Vaikka eloonjäämisaste vaihteli vuosittain, talvivirtaamalla ei havaittu olevan merkittävää vaikutusta siihen. Uudelleenpyyntitodennäköisyys (p) vaihteli valuma-alueiden välillä, mikä saattaa johtua näytteenoton heterogeenisyydestä. Yhteenvetona voidaan todeta, että Pohjois-Espanjan kolmella vierekkäisellä valuma-alueella koskikaran syntymälevittäytyminen oli vähäistä ja aikuislevittäytyminen lähes olematonta. Tämä voi poiketa muista Espanjan alueista, joissa levittäytymisasteet ovat raportoidusti korkeampia.

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Appendix 1.

Mean discharge (calculated for the months of November to February of the next year, unit: m^3/s) in gauging station located in the basins of Urdaibai, Artibai and Lea (Bizkaia).

	2014/15	2015/16	2016/17	2017/18	2018/19	2019/20	2020/21	2021/22	Average
Muxika (Urdaibai)	206.6	122.1	93.0	282.2	96.1	154.8	190.3	212.5	169.7
Berriatua (Artibai)	756.0	396.8	334.5	1011.7	378.6	532.8	605.3	741.1	594.6
Oleta (Lea)	667.8	419.0	349.7	806.6	316.3	476.5	615.4	686.6	542.2
Total	1630.4	937.9	777.1	2100.5	791.0	1164.1	1411.1	1640.1	1306.5

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Assessing avian incubation behavior in response to environmental pollution with temperature-humidity loggers

Noé Freyssinge, Maria Perkkola, Lyydia Leino, Miia Rainio & Tapio Eeva*

N. Freyssinge, M. Perkkola, L. Leino, M. Rainio, T. Eeva, Department of Biology, University of Turku, FI-20014 Turku, Finland
** Corresponding author's e-mail: teeva@utu.fi*

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The negative impact of environmental pollution on avian physiology and breeding success is well documented. However, pollution-related behavioral changes during reproduction remain underexplored, despite behavior often being one of the earliest indicators of environmental disturbances and having significant life-history consequences. For example, altered food availability in a polluted environment could potentially perturb the incubation behavior of income breeders. These birds typically alternate between staying in the nest and heating eggs (on-bout) and taking foraging trips (off-bout). In this two-year study (2020 and 2022), we investigated how the incubation behavior of an insectivorous passerine, the pied flycatcher (*Ficedula hypoleuca*), varied with environmental pollution levels around a Cu-Ni smelter. Additionally, we compared two different metrics – temperature and humidity within the nest – to evaluate their use as indicators of incubation rhythm. We found that temperature- and humidity-based incubation rhythm parameters correlated, but those based on humidity matched better the true incubation behavior documented by simultaneous video recording. This was because the humidity curve showed a more immediate and intensive response to the female's incubation behavior. Birds in the polluted area took slightly more (11%) but shorter (11%) off-bouts, possibly reflecting smaller energetic constraints or better food availability in the polluted area. However, we found no difference in total incubation intensity between polluted and control areas, with *F. hypoleuca* females incubating their eggs 75% of the daytime in both environments. Hence, incubating females in the polluted area did not allocate more time for gathering their energy reserves than the birds in the control area, and there was also no difference in the hatching success. Our study is the first to use humidity variation to record incubation rhythm, and our results indicate that measuring humidity inside the nest is a promising technique to test and develop further. For example, further studies are needed to test if this method would work in different types of nests. From an environmental protection standpoint, our results also contribute valuable insights to the relatively limited information on pollution-related behavioral changes.

1. Introduction

Environmental pollution, such as industrial emissions, can alter the habitat and the quality of food resources available to birds, potentially leading to both direct and indirect effects on their reproduction (Morrison 1986, Furness & Greenwood 1993, Eeva *et al.* 2005, Belskii & Belskaya 2013). The influence of industrial emissions becomes particularly apparent during breeding, since *e.g.* metal emissions and acidifying compounds can affect the vegetation and invertebrate numbers, reducing the amount of birds' prey during the period when food consumption is at its highest (Belskii *et al.* 1995, Eeva *et al.* 1997). So far, studies have mainly focused on reproductive output or physiological effects caused by pollution, while there is relatively little information about the potential impacts of environmental pollution on birds' behavior during reproduction, which could partly explain the links between pollution and reproductive success (Sanderfoot & Holloway 2017). For example, behavioral changes could reveal secondary effects of pollution that might not be immediately apparent through physiological measurements but could be important early warning signals from the conservation point of view. One reason for the small amount of behavioral research is that behavioral studies tend to require extensive field effort. However, recent technological advances and the miniaturization of data loggers have facilitated some behavioral studies, such as the measurement of birds' incubation behavior, which is a critical aspect of parental care in birds and can affect the development of embryos (Smith *et al.* 2015, Hope *et al.* 2022).

Almost all birds incubate their eggs by warming them to reach the required temperature with the heat being transferred via an abdominal skin area called the brood patch. This extra cost, in terms of heat loss and time, may be energetically demanding for the parents (*e.g.* Bryan & Bryant 1999, but see Ilmonen *et al.* 2002, Nord *et al.* 2010). In order to compensate for the increased energy requirements during this period, incubating birds need to allocate more time for foraging. Depending on the species, the incubating bird may either forage itself or the other parent may partly or fully feed the incubating partner (Koski *et al.* 2020). Incubation intensity largely determines the early developmental trajectory of bird embryos (DuRant *et al.* 2013). Ectothermic bird embryos need an optimal developmental temperature (36–38°C; Tieleman *et al.* 2004), which is not often matched by the environment (Camfield & Martin 2009). This challenge for birds is accentuated when only one parent incubates (Hu *et al.* 2024). For instance, over 60% of Passeriformes families demonstrate female-only incubation (Deeming 2002). Consequently, uniparental incubation patterns reflect a trade-off between self-maintenance (foraging) and the temperature requirement of the embryos (Cooper & Voss 2013). The alternating periods, where females leave the clutch to obtain food (off-bout) and return to warm the eggs (on-bout), are called the incubation rhythm (von Haartman 1958).

Industrial emissions can restrict food availability by disrupting food chains. This can occur through the accumulation of toxic substances in the environment, which could harm or reduce populations of key species within the ecosystem, ultimately leading to a decrease in the food supply for higher trophic levels. This may pose a problem not only for growing nestlings but also for incubating parents (Eeva *et al.* 1997). In normal conditions, birds that take many off-bouts also tend to take shorter off-bouts to keep incubation temperatures more stable (Cooper & Voss 2013). However, in low-quality territories, birds are more likely to take more foraging trips and have longer off-bouts and shorter on-bouts, which increases egg temperature variation (DuRant *et al.* 2013, Koski *et al.* 2020). Polluted sites may represent such low-quality territories, where vegetation and invertebrates suffer from pollution exposure with negative consequences to insectivorous birds (Kiikkilä 2003, Eeva *et al.* 2005).

Point sources of pollution provide a good opportunity to test behavioral effects between polluted and relatively unpolluted environments. A long-term follow-up study around a Finnish copper-nickel smelter, a point source of metal pollution, has revealed pollution-related reductions in breeding parameters and physiological changes in some small insectivorous passerines, such as the pied flycatcher (*Ficedula hypoleuca*)

(Eeva & Lehikoinen 1995, Espín *et al.* 2017). In this and other similar environments, the composition and nutritive quality of prey species varies depending on the level of pollution (Eeva *et al.* 2005, Belskii & Belskaya 2013). To study the impact of pollution on birds' breeding behavior, we explored whether the incubation rhythm and intensity of *F. hypoleuca* females differ between the polluted sites close to the smelter and relatively unpolluted control sites farther away. We also took into account several other parameters that could potentially influence the incubation rhythm, such as ambient temperature, time of day, and phase of incubation. In addition, we tested a potential new method to study birds' incubation behavior: incubation rhythm is often studied by measuring incubation-dependent temperature variation in the nest, but here we test if humidity variation could be used for the same purpose. Testing another method was motivated by our prior pilot study (T. Eeva, unpublished), which suggested that the humidity curve may even show a faster and stronger response than the temperature curve for tracking the incubation rhythm.

We expected that the indirect effects of heavy metal pollution, such as habitat deterioration and related scarcity of suitable food, which have been documented in our study area (Eeva *et al.* 2005), could affect birds' incubation rhythm. In particular, we hypothesized that, in the polluted areas, birds might take more and/or longer off-bouts to find enough food, due to a trade-off between fueling and incubation intensity. Furthermore, we expected that measuring humidity could provide a novel means to measure incubation rhythm and potentially provide better-quality data than temperature.

2. Material and methods

2.1. Study area

One of the main sources of local air pollutants in Finland is a factory complex located in the center of Harjavalta town (61°20'N, 22°10'E). Arsenic, copper, nickel, lead, and zinc are common pollutants in the area (Kiikkilä 2003). Elevated heavy metal concentrations occur in the soil and biota of the polluted area but decrease exponentially with increasing distance to the smelter, approaching background levels at sites further than five kilometers from it (Eeva & Lehikoinen 1996). Based on this information, nine study sites were established along an air pollution gradient in three main directions (SW, SE, and NW) around the town (Fig. 1). Five sites were classified as "controls" (>5 km from the factory complex) and four as "polluted" (<2.5 km from the factory complex) and these distance classes are used in the statistical analyses. Each site contains between 20–60 wooden nest boxes attached to a tree. The design of nest boxes has been described by Lambrechts *et al.* (2010). Special attention was paid to select study sites which represent similar habitat type, *i.e.* relatively barren forests dominated by Scotch pine (*Pinus sylvestris*), which forms mixed stands with spruce (*Picea abies*), and birches (*Betula spp.*). However, vegetation near the smelter has suffered from the long-term pollution and *e.g.* the ground layer vegetation cover is patchy or lacking at more heavily polluted locations (Kiikkilä 2003).

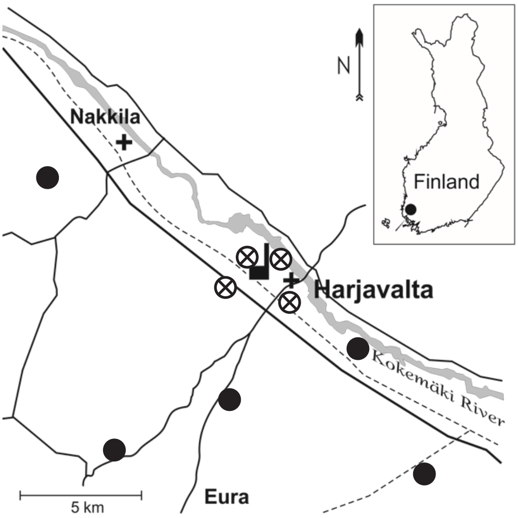

Fig. 1. Location of nine study sites, with the factory complex in the center (black dots = control site, crossed dots = polluted site).

2.2. Study species

Like many other long-term population studies in birds, pollution-related studies have mainly focused on hole-breeding birds such as *F. hypoleuca* (Çelik *et al.* 2021). This migratory and insectivorous species, which typically lays only one clutch per season, breeds in a wide area in northern Eurasia (Cramp 1988). The female normally lays one egg per day until having a clutch size of 5 to 8 eggs, and, after laying the last egg, starts the incubation period of *ca.* two weeks (Lundberg & Alatalo 1992). Incubating females forage themselves, but the male also feeds the female, and high contribution by a male may increase the female's body mass and nest attendance, although this is condition-dependent (von Haartman 1958, Lifjeld & Slagsvold 1986, Cantarero *et al.* 2014). In our study, however, the male's feeding activity could not be estimated. Typical prey includes spiders, caterpillars, and winged insects (*e.g.* moths *Lepidoptera*, beetles *Coleoptera,* and sawflies *Symphyta,* depending on the environment) (Eeva *et al.* 2005). This species also readily accumulates heavy metals, and a few weeks after the arrival from their wintering grounds in Africa, female birds show increased tissue concentrations of metals in polluted locations (Eeva & Lehikoinen 2004, Berglund *et al.* 2011).

2.3. Measurements of incubation rhythm

In 2020 and 2022, all nest boxes were inspected at least once per week (starting at the end of April) to record basic breeding data such as timing of breeding, clutch size, and number of hatchlings. When we encountered a nest with warm eggs (*i.e.* a female had started to incubate), a high-resolution hygrochron iButtons® DS1923-F5 (Maxim Integrated Products 2020) were placed inside the nest materials in the summer of 2020 (n = 28 nests) to measure incubation rhythm by recording temperature and relative humidity. Measurements were not taken on rainy days. Loggers were placed underneath the eggs within the nest lining layer, since preliminary studies have shown that eggs can break during the incubation period if loggers are placed among them (Schöll *et al.* 2020). A plastic key ring mount (iButton, DS9093AB+) was attached to each logger to avoid displacement of the small loggers in the nest. Humidity loggers were not available in 2022, and we used temperature iButtons DS1922-F5 instead (n = 44 nests). The loggers were programmed to measure temperature (°C) and relative humidity (% RH) at intervals of 30 seconds with a resolution of 0.5 °C (2020) or 0.063 °C (2022) for temperature and 0.6% RH (2020) for humidity. For logistic reasons, the logger installation time varied from 8:25 am to 15:49 pm, and the recording period length varied from 4 h 45 min to 10 h 25 min (mean ± SD: 7.8 ±1.4 h). For the same reason, the estimated phase of incubation varied from incubation day 1 (= 1st incubation day) to day 13 (mean ± SD: 7.3 ± 2.6 days). Because clutch size is known to affect the egg cooling rate, which is faster in smaller clutches (Boulton & Cassey 2012), we standardized the sampling by selecting focal nests of primarily 6 or 7 eggs, although two nests with smaller clutches were measured when suitable nests were not available (removing those nests from our analyses did not change qualitatively the results). Female birds were also trapped for ringing and age determination, which was based on their plumage characteristics (Svensson 1992). However, age-related differences in plumage are relatively small, and we have estimated that <5% of age determination can be erroneous (Eeva *et al.* 2018). Females were usually trapped a few days before the incubation rhythm measurements, but never on the same day right before the measurements, to avoid disturbance.

Another logger was placed on the outer back wall of the nest box, recording the ambient temperature (2020 and 2022) and humidity (2020 only) every 30 seconds. This was done because, in the data analysis phase, the ambient temperature and humidity were used as background values to take into account the ambient changes during the measurement period. Furthermore, ambient temperature was used in statistical models as an explanatory variable. Finally, we verified the iButton measurements inside one nest by simultaneously video recording the entrance of the nest box, allowing a comparison of visually documented incubation rhythm with the iButton data (see also Bueno-Enciso *et al.* 2017). The observations and measurements were made under the licenses from the Finnish Centre for Economic Development, Transport and the Environment (VARELY/3622/2017, VARELY/6817/2021).

2.4. Data handling and statistics

2.4.1. Calculation of incubation rhythm parameters

We calculated the off-nest bout frequency (variable BPerH; number of off-bouts/h), mean duration of on-bouts (MOnDur; min), mean duration of off-bouts (MOffDur; min), total on-bout duration (TOnDur; min/h; hereafter "incubation intensity") and mean ambient air temperature (°C) during the measurement period by using NestIQ v.0.2.5 software (Hawkins & DuRant 2020). Following the previously used parameters for investigating incubation behavior of *F. hypoleuca*, we set the detection threshold to a 1°C decrease in temperature and a 1% decrease in humidity lasting at least 4 minutes (Koski *et al.* 2020). Note that on- and off-bout duration times are not opposite or mutually constrained measures, and they can vary independently. Considering the possible disturbance to the natural incubation rhythm because of installing the logger in the nest, we excluded data of the first on-bout/off-bout incubation cycle after visiting the nests. Five low-quality measurements were discarded from further analyses (2020 n = 3, 2022 n = 2). A possible reason for low-quality measurements was placing the logger too deep in the nest material, and in one case, logger failure. The final sample number was 67 measurement periods (25 nests in 2020 and 42 nests in 2022). Age determination was missing for three females, decreasing the sample number in statistical tests where age was included. Each nest was measured only once. Statistical tests were performed in SAS 9.4 software (SAS Institute Inc. 2013).

2.4.2. Comparison of temperature- vs. humidity-based measures (2020)

First, we tested correlations among the measures produced by two different measurement techniques in the dataset of 2020. Because some of the variables (temperature-based BPerH and MOnDur, humidity-based MOnDur) showed deviations from normal distribution, we used Spearman's rank correlation tests. Second, we compared temperature-based and humidity-based estimates with pairwise t-tests. Normality of distributions was confirmed by Kolmogorov-Smirnov tests. Finally, we inspected one video recording of a pied flycatcher nest by manually determining all on- and off-bout durations and the number of bouts. From this information, we explored temporal match of temperature- and humidity-based data with video-based observations.

2.4.3. Variation in temperature-based incubation rhythm parameters (2020 and 2022)

Variation in the four incubation rhythm parameters was studied with linear (LM) and generalized linear (GLM) models. For off-bout frequency, we used GLM with Poisson error distribution, while the other response variables were tested with LM with normal error distribution. Furthermore, we tested differences in hatchability of eggs between polluted and control areas with GLM, where the hatching probability of eggs was modeled with binary error distribution (using events/trial syntax of SAS). Model fits were confirmed by checking the overdispersion parameter (Pearson Chi-square/df) for the GLM models and normality of model residuals for LMs. The main explanatory factors were area (polluted vs. control) and year (2020 and 2022). Their interaction effect was non-significant in all models, and we did not include the interaction term in the final analyses. Instead, we tested other factors which may affect avian incubation. First, the ambient temperature outside the nest box has been shown to affect the incubation intensity, which was higher in cool conditions (Conway & Martin 2000, Arct *et al.* 2022). Second, the age of the female (two categories: young vs. old) was considered as a potential covariate of foraging efficiency (Joyce *et al.* 2001, Cauchard *et al.* 2021). Finally, time of measurement (at start) and phase of incubation (estimated number of days incubated) were included in the models as possible confounding factors (Cooper & Voss 2013, Hope *et al.* 2022). Although the length of measurement periods also varied, we did not include it in the statistical models because there was no *a priori* expectation that it would affect the incubation rhythm on the top of the effect of time of day. Since the exact day of the start of incubation was not always known, we calculated this estimate from the laying date and egg number, with the defaults of one egg laid per day and incubation started after the last egg, which is the norm in this species although *e.g.* laying gaps may cause extra variation in this estimate (Koski *et al.* 2020, Glądalski *et al.* 2020). Laying date was also first considered as a covariate but since it correlated significantly with ambient temperature ($r = 0.49$, $n = 67$, $p < 0.0001$), we did not include it in the models to avoid collinearity between explanatory variables. The categorical variables area and year were retained in all models, while non-significant covariates were removed or left in the model by using model AIC value as a criterion (Burnham *et al.* 2011).

3. Results

3.1. Comparison of humidity- vs. temperature-based data (2020 dataset)

Off-bout frequencies (BPerH) based on temperature and humidity correlated positively ($n = 25$, $\rho = 0.69$, $p < 0.0001$). The temperature-based data showed lower off-bout frequencies ($\mu \pm SD = 2.78 \pm 0.50$ bout/hour) than humidity-based data ($\mu \pm SD = 3.49 \pm 0.78$ bout/hour) (paired t-test, $df = 24$, $t = -5.87$, $p < 0.0001$; Fig. 2a).

The mean off-bout duration (MOffDur) showed a significant positive correlation ($n = 25$, $\rho = 0.55$, $p = 0.0041$) between temperature- and humidity-based values. Temperature-based data showed 21% longer off-bout duration times ($\mu \pm SD = 5.06 \pm 0.59$ min) than humidity-based data ($\mu \pm SD = 4.19 \pm 0.75$ min) (paired t-test, $df = 24$, $t = 6.45$, $p < 0.0001$; Fig. 2b).

The two measures of mean on-bout duration (MOnDur) correlated positively ($n = 25$, $\rho = 0.66$, $p = 0.0003$). Mean on-bout duration based on temperature data ($\mu \pm SD = 15.7 \pm 4.10$ min) was higher than that based on humidity data ($\mu \pm SD = 12.6 \pm 4.66$ min) (paired t-test, $df = 24$, $t = 4.79$, $p < 0.0001$; Fig. 2c), indicating that values based on temperature and humidity are well correlated but temperature produces 25% higher values for the nest attendance time. Mean off-bout duration did not correlate with the mean on-bout duration for either method ($p > 0.6$ in both), indicating that these two measures varied independently.

Incubation intensity (TOnDur) showed a significant positive correlation ($n = 25$, $\rho = 0.57$, $p = 0.0027$) between temperature- and humidity-based values. There was no significant difference between temperature-based ($\mu \pm SD = 45.9 \pm 3.20$ min/h) and humidity-based incubation intensities ($\mu \pm SD = 45.4 \pm 3.67$ min/h) (paired t-test, $df = 24$, $t = 0.92$, $p = 0.37$; Fig. 2d). The overall mean temperature below the nest cup was 27.0 ± 2.36 °C, and mean relative humidity 38.4 ± 6.98% ($n = 25$ nests).

3.2. Comparison of iButton data with video-based values (2022)

Temporal variation in temperature- and humidity are generally in good agreement with simultaneous video-based observations of the incubation rhythm (Fig. 3). However, differences between nest entry and exit times given by NestIQ and those revealed by direct video observations indicated that humidity reacted much faster than temperature to female movements: mean delay after entry was 29.5 s for humidity and 107.9 s for temperature. In other words, humidity starts to increase soon after the bird enters the nest, while temperature shows a longer lag (Fig. 3). At the moment of exit, both lags are shorter than at entry, but humidity response is still much faster (2.07 s) compared to temperature (77.3 s).

Finally, we compared how well the logger-based incubation rhythm parameters given by NestIQ match the values measured from the video recording (Table 1). The bout number estimates were similar, except that humidity showed one more on-bout observation (the last one shown in Fig. 3). Humidity- and temperature-based on-bout duration estimates were slightly shorter while off-bout duration estimates were longer, especially for the temperature (Table 1). Taken together, humidity-based estimates of bout numbers reflect well the temperature-based estimates but, since humidity curve tracks faster the true incubation rhythm, the humidity-based off-bout durations match better with true values and result in a less biased estimate.

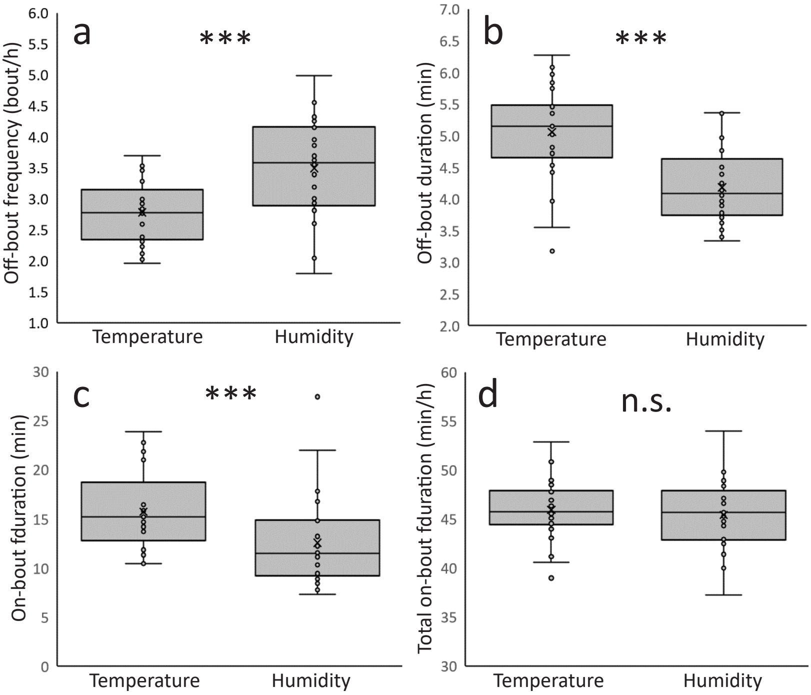

Fig. 2. Boxplots (min, max, median, 1st and 3rd quartiles, mean shown by ×) of four incubation parameters from the 2020 dataset based on temperature and humidity measurements. Mean off-bout frequency (bout/hour; a), mean off-bout duration (min; b), mean on-bout duration (min; c) and incubation intensity (min/h; d). Pairwise T-tests for between-group differences n = 25 nests): n.s. = not significant, *** = p < 0.001.

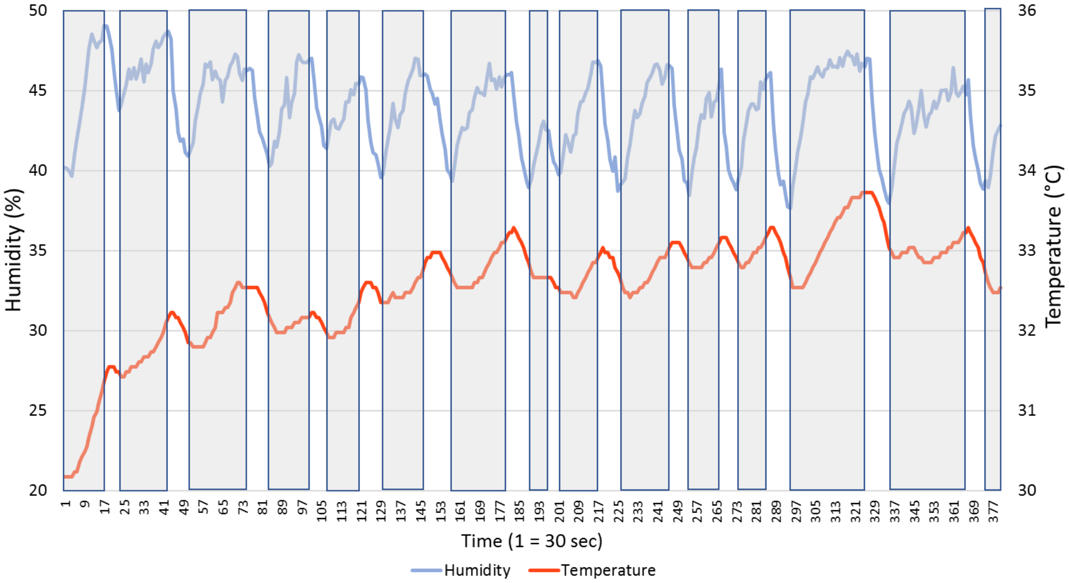

Fig. 3. Graphs of relative humidity and temperature recorded by iButton superimposed with on-bout periods (grey frames) obtained by video recording indicating that the female was inside the nest box. One unit on the x-axis equals 30 seconds (video length 3.1 h). Blue (upper line) = humidity, red (lower line) = temperature.

Since the NestIQ software detects bout transitions based on changes in temperature and humidity, with larger fluctuations being more readily detected, we calculated the coefficients of variation (CV) for both measures in each nest to assess their variability. Humidity exhibited a CV 4.4 times higher than that of temperature (CV for temperature = 3.3%, CV for humidity = 14.5%; paired t-test, df = 24, t = −12.6, $p < 0.0001$), indicating significantly greater fluctuations in the humidity data.

3.3. Pollution effects based on temperature data (2020 and 2022)

The median values of the temperature-based incubation rhythm parameters for polluted and control areas are shown in Fig. 4. Off-bout frequency was 11.0% higher and off-bout duration 10.9% shorter in the polluted area, while there were no significant differences in the other parameters between the areas (Table 2, Fig. 4). None of the parameters were dependent

Table 1. Four incubation parameters compared between three measurement methods: video recording, humidity logger and temperature logger (mean ± SD). Percentages in parenthesis were obtained comparing humidity- or temperature-based values with ones obtained from the video recording.

	Off-bout frequency	Mean off-bout duration (min)	On-bout frequency	Mean on-bout duration (min)
Video	14	3.05 ± 0.83	15	9.77 ± 3.76
Humidity	14	3.21 ± 0.97 (+5%)	15	8.67 ± 3.37 (−13%)
Temperature	14	3.96 ± 1.85 (+30%)	14	8.57 ± 4.40 (−14%)

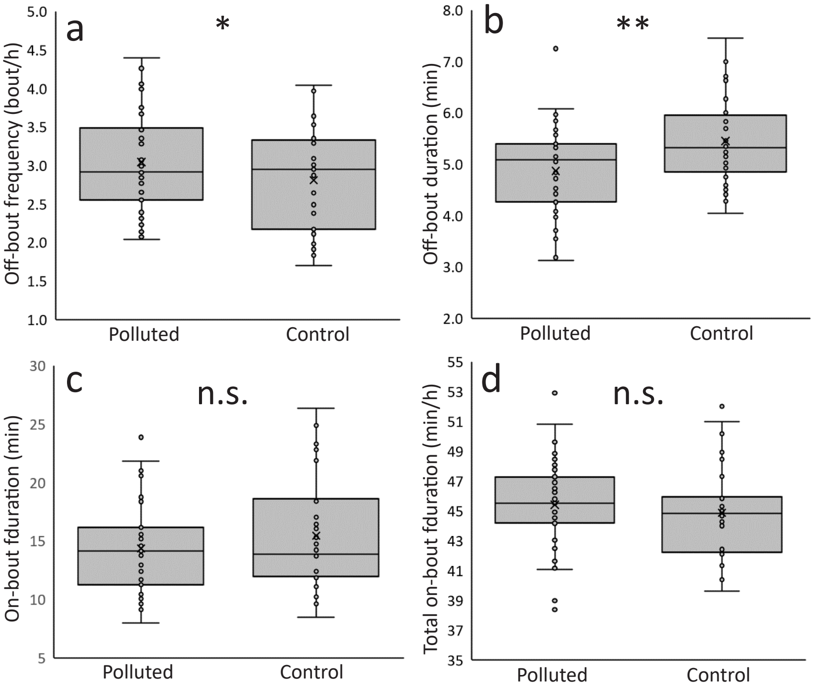

Fig. 4. Boxplots of four incubation parameters in polluted and control areas. Seasons 2020 and 2022 combined (n = 67 nests). Mean off-bout frequency (bout/hour; a), mean off-bout duration (min; b), mean on-bout duration (min; c) and incubation intensity (min/h; d). Linear model results for differences among areas: n.s. = not significant, * = $p < 0.05$, ** = $p < 0.01$ (see Table 2).

on the year of measurement or female age (Table 2). The mean off-bout duration increased, whereas on-bout duration and incubation intensity decreased with increasing ambient temperature (Table 2, Fig. 5). On-bout duration and incubation intensity slightly increased with time of day (Table 2). Furthermore, the off-bout frequency increased but the on-bout duration and incubation intensity decreased with advancing incubation phase (Table 2). The overall mean incubation intensity was 45.2 ± 3.12 min/h ($n = 67$). Hatching probability of eggs did not significantly differ between the areas (polluted 0.92; control 0.87; GLM: $F_{1,65}=0.89$, $p = 0.35$). Ambient temperatures at the time of measurements increased on average 0.53 °C per day (LM: $F_{1,63}=37.2$, $p < 0.0001$) and were 1.5°C higher in 2020 than in 2022 (LM: $F_{1,63}=6.48$, $p = 0.013$) but did not differ significantly between the areas (polluted: 20.0 °C; control: 19.6 °C).

4. Discussion

4.1. Humidity vs. temperature as measures of incubation rhythm

Our study suggests that relative humidity is a good alternative to temperature for measuring incubation rhythms. Temperature-based data showed lower off-bout frequencies and longer off- and on-bout duration times than humidity-based

Table 2. Linear models[1] to explain variation in four incubation rhythm related parameters of *Ficedula hypoleuca*: off-bout frequency (BPerH), mean off-bout duration (MOffDur), mean on-bout duration (MOnDur) and incubation intensity (TOnDur). N=67 nests.

Source of variation	BPerH		MOffDur		MOnDur		TOnDur	
	Est.	F_{df}	Est.	F_{df}	Est.	F_{df}	Est.	F_{df}
Intercept	2.458		3.227		19.57		52.31	
Area [Control]	−0.302	$4.17_{1,63}$*	0.60	$8.33_{1,63}$**	0.87	$0.74_{1,61}$	−0.75	$1.32_{1,61}$
Year [2020]	−0.223	$2.09_{1,63}$	−0.10	$0.23_{1,63}$	1.00	$0.87_{1,61}$	1.06	$2.41_{1,61}$
Female age [Old]	−0.171	$1.11_{1,57}$	0.065	$0.08_{1,57}$	0.87	$0.59_{1,57}$	0.80	$1.26_{1,57}$
Ambient temperature (°C)	0.039	$2.35_{1,61}$	0.085	$5.48_{1,63}$*	−0.36	$4.17_{1,61}$	−0.49	$19.0_{1,61}$***
Measurement time (hour)	−0.078	$3.05_{1,62}$	−0.032	$0.26_{1,61}$	0.66	$4.66_{1,61}$*	0.48	$5.96_{1,61}$*
Incubation phase (days)	0.096	$11.5_{1,63}$**	−0.061	$2.33_{1,62}$	−0.74	$12.9_{1,61}$***	−0.35	$7.15_{1,61}$*

[1] Model reduction is based on AIC values. Terms left in the final model are bolded. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

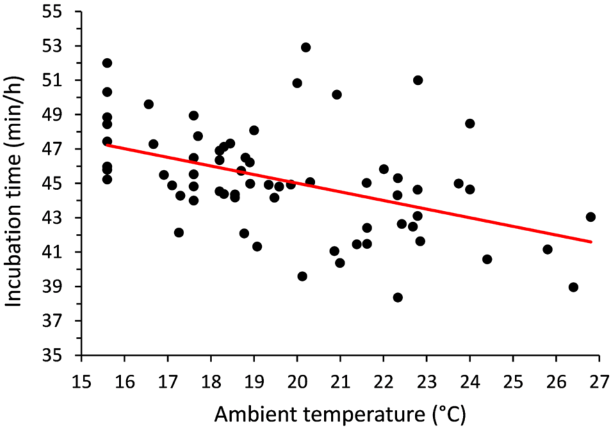

Fig. 5. The association between incubation intensity (incubated minutes per hour) and ambient air temperature (measured by a logger on the outer back wall of the nest box). Linear regression line. N = 67 nests.

data. This is because humidity gave a stronger and faster signal as a response to female's incubation behavior, whereas all changes of bouts (most likely those of short duration) could not be detected from the temperature curve. Even though humidity-based and temperature-based values were positively correlated, the video-observations suggest that the humidity-based values reflect better the female movements. However, lower bout frequency and higher bout duration in the temperature-based data have opposite effects on total incubation time, and, at the end, the two methods still gave very similar total incubation intensities. A reason to the higher sensitivity of humidity measure is likely the higher relative variation in the humidity data. In practice, higher variation means stronger peaks in the humidity graph, from which the inflection points will be more easily detected by the NestIQ software.

The justification to measure temperature variation is straightforward, but it is less clear what is the exact mechanism producing behavior-related variation in relative humidity inside the nest. When an incubating female settles in the nest cup, her warm body and possibly breathing are likely to cause an increase in the relative humidity, which is detected faster by the data logger than the temperature, probably because humidity can move fast with air through convection and diffusion whereas heat can move more slowly by conduction through nest materials and the logger capsule. Furthermore, if humidity is evaporated from warming nest materials, this can slow down the increase of temperature because of counteractive evaporative cooling effect. However, further studies are needed to find out whether most of the humidity derives from nest materials (Biddle *et al.* 2019), eggs (Ar & Rahn 1980) or female itself (Dawson 1982). These alternatives could best be tested with experimental studies (*e.g.* by placing an artificial heat source inside an artificial bird nest).

As far as we know, our study is the first to measure humidity variation to record incubation rhythm, and our results suggest that measuring humidity within the nest is a promising technique to test and develop further. A major disadvantage of this technique is perhaps the higher price of humidity loggers, and we do not know if it would work well with other bird nest types (*e.g.* open nests or ground nests) or nest materials. At least in the case of cavity-breeding *F. hypoleuca,* the humidity-based measurements match better with true incubation behavior, which would enable more precise time-budgets for studying female behavior. Humidity-based measurements will also likely be less sensitive to logger position inside the nest material than temperature measurements. We recommend further testing of the humidity method across different species, habitats, and nest types. However, it may be more crucial to avoid conducting tests in rainy conditions with open nest types.

4.2. Pollution effects based on temperature data

We found that birds in the polluted area took slightly more (11%) but shorter (11%) off-bouts. Because these variables have an opposite effect on incubation intensity, there was no difference in total incubation intensity between polluted and control areas, *F. hypoleuca* females incubating their eggs *ca.* 75% of daytime in both environments. This estimate matches well with what has been found for this species earlier (Lundberg & Alatalo 1992). However, we did not measure possible differences in the birds' daily activity vs. roosting rhythm, which could also affect the total incubation times (see Hope *et al.* 2022). In any case, our results indicate that incubating females in the polluted area do not allocate more time for gathering their energy reserves than the birds in the control area. This could mean that, during the incubation period, *F. hypoleuca* females have similar opportunities to gain enough food and meet their energetic demands in both areas either by their own foraging or supplemental feeding by a male. This species also performs well with rather variable diets (Eeva *et al.* 2005). A recent study from the same area found that the body mass of incubating *F. hypoleuca* females was even slightly higher in the polluted area (Rainio *et al.* 2017). This suggests relatively good food availability in the polluted area, although birds can also maintain higher fat reserves when the availability of food is unpredictable (*e.g.* Lima 1986, Ekman & Hake 1990). Shorter off-bouts might then be explained by smaller energetic constraints in the polluted area.

Consistent with our results, shorter off-bouts were also observed in urban great tits, *Parus major*, which spent more time incubating than those in more remote forest habitats, possibly due to differences in food availability or male investment in female feeding (Amininasab *et al.* 2017, Hope *et al.* 2022). We did not record males' food provisioning efforts during the incubation period, but earlier studies in our study area indicated that males at least fed their nestlings with the same frequency and similar food loads in polluted and control areas (Eeva *et al.* 2005, Mari *et al.* 2024). Urban blackbirds (*Turdus mandarinus*) and house wrens (*Troglodytes aedon*) again showed more, albeit shorter incubation periods than rural birds (Heppner & Ouyang 2021, Ma *et al.* 2023). All these studies suggest that urban birds incubate with different rhythm and often with higher bout frequency than rural birds. One possible explanation for this could be an increased anthropogenic disturbance in urban environments (Price 2008). However, birds can also adapt to human disturbance. For instance, urban *P. major* females exhibit bolder behavior during incubation, often remaining on their nests despite disturbances, in contrast to those in non-urban forests (Vincze *et al.* 2016, 2021).

We also found that *F. hypoleuca* females increased their bout frequency and decreased their incubation intensity over the course of their approximately two-week incubation period. In accordance with this, also black-capped chickadees (*Poecile atricapillus*) showed increased bout frequencies with advancing phase of incubation, likely to keep the egg temperatures more stable for the large embryos (Cooper & Voss 2013). Instead, contrary to chickadees, *F. hypoleuca* females decreased incubation intensity, which might be explained by warming weather during the *F. hypoleuca* incubation period, allowing less intensive incubation with advancing spring and higher temperatures (Lundberg & Alatalo 1992, Amininasab *et al.* 2017).

In general, and especially after the decreased emissions of pollutants in recent decades, the breeding success of *F. hypoleuca* is currently relatively good in the polluted area of Harjavalta, and important breeding parameters like clutch size, hatching success, and fledgling numbers approach the values of the control area (Eeva & Lehikoinen 2015, Espín *et al.* 2016). Still, breeding success remains lower in the polluted area, and especially when there are other simultaneous stress factors during the breeding, such as harsh weather conditions (Eeva *et al.* 2020). Cold weather during the laying and incubation periods reduces hatchability of eggs in *F. hypoleuca*, and more intensive incubation behavior is likely to be adaptive at lower temperatures (Eeva & Lehikoinen 2010, Eeva *et al.* 2020). The weather during the incubation periods of *F. hypoleuca* was relatively favorable in the breeding seasons 2020 and 2022, and we found no major pollution-related differences in the incubation behavior. It is, however, possible that such differences could arise under more extreme weather conditions.

Kirjosiepon haudontakäyttäytymisen vertailu saastuneen ja puhtaamman ympäristön välillä pesään sijoitettavien lämpötila-kosteusloggereiden avulla

Ympäristön saastumisen aiheuttamia käyttäytymismuutoksia on tutkittu melko vähän, vaikka muutokset eläinten käyttäytymisessä saattavat olla varhainen merkki ympäristön heikentymisestä ja niillä voi olla merkittäviä seurauksia eläinten lisääntymiseen. Esimerkiksi huonontunut ravinnon saatavuus saastuneessa ympäristössä saattaa haitata lintujen haudontaa. Monilla lajeilla emolinnut vuorottelevat tyypillisesti pesässä hautomisen ja ravinnonhakumatkojen välillä. Tämän kaksivuotisen (2020 ja 2022) tutkimuksen tavoitteena oli selvittää pienten, linnunpesään sijoitettavien lämpötilaloggereiden avulla, onko hyönteisiä syövän kirjosiepon (*Ficedula hypoleuca*) haudontarytmi erilainen metallien saastuttamalla alueella kuparisulaton ympäristössä verrattuna puhtaampiin vertailualueisiin. Lisäksi testasimme kahden erilaisen mittarin – lämpötilan ja ilmankosteuden – toimivuutta haudontarytmin indikaattoreina. Havaitsimme, että vaikka lämpötilaan ja kosteuteen perustuvat haudontarytmiä kuvaavat tunnusluvut korreloivat, kosteuteen perustuvat arvot vastasivat paremmin samanaikaisella videotallennuksella dokumentoitua todellista haudontakäyttäytymistä. Tämä johtui siitä, että loggereiden mittaama kosteuskäyrä reagoi lämpötilaa nopeammin ja voimakkaammin lintujen haudontakäyttäytymiseen. Saastuneen alueen linnut pitivät hieman useampia (11%) mutta lyhyempiä (11%) haudontataukoja, mikä saattoi johtua pienemmästä energiatarpeesta tai paremmasta ravinnon saatavuudesta saastuneella alueella. Haudonnan kokonaisintensiteetissä ei kuitenkaan ollut eroa saastuneen ja kontrollialueen välillä, ja siepponaaraat käyttivät munien hautomiseen 75% ajastaan molemmissa ympäristöissä. Hautovat naaraat eivät siis käyttäneet saastuneella alueella enemmän aikaa energiavarantojensa täydentämiseen, eikä munien kuoriutuvuudessakaan ollut eroa suhteessa vertailualueeseen. Ilmankosteutta ei ole tätä tutkimusta aiemmin käytetty lintujen haudontarytmin mittaamiseen ja tulokset osoittavat, että menetelmä toimii hyvin. Lisätutkimuksia tarvitaan esimerkiksi sen testaamiseksi, toimisiko tämä menetelmä erityyppisissä linnunpesissä. Ympäristönsuojelun näkökulmasta tulokset tuovat arvokkaan lisän suhteellisen niukkaan tietoon käyttäytymisen muutoksista saastuneessa ympäristössä.

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Home range sizes and nychthemeral habitat uses by the Northern Shoveler (*Spatula clypeata*) on prenuptial stopovers in Vendée marshes, western France

Axelle Moreau*, Clément Rousseau, Pierrick Bocher, Christine Dupuy & Sébastien Farau

A. Moreau, C. Rousseau, S. Farau, Fédération Départementale des Chasseurs de la Vendée, Les Minées, Route de Château Fromage, 85010 La Roche-sur-Yon, France
A. Moreau, P. Bocher, C. Dupuy, Littoral Environnement et Sociétés (LIENSs), UMR 7266, CNRS-La Rochelle University, 17000 La Rochelle, France
** Corresponding author's e-mail: amoreau@chasse85.fr*

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The wetlands of Marais breton (MB) and Marais poitevin (MP) on the French Atlantic coast are commonly used by several duck species, especially as stopover sites during the prenuptial migration. Understanding the ecological requirements of Anatidae at spring stopover sites is important to define appropriate management actions that might have a carry over effect on the subsequent reproduction success. This study focused on the Northern Shoveler (*Spatula clypeata*), a species that regularly visits the two marshes during spring and fall migrations and is highly dependent on freshwater invertebrates as the food resource. Fifteen Northern Shovelers were equipped with GPS/GSM tags and monitored during their stopover in both marshes in 2020 and 2021. The aims of the study were to understand the habitat use on stopover sites and relate home range (HR) size with characteristics of the feeding habitats (such as freshwater invertebrates' density and diversity). The HR area of the studied individuals was mainly constituted of ponds in MB (83% of the HR) and wet meadows in MP (71% of the HR). The Northern Shovelers equipped with tag spent more than 72 consecutive hours in 31 wetlands, using them during the day, at night or all day. The diurnal visited sites were deep ponds that were sparsely vegetated and dominated by microcrustaceans, whereas the nocturnal visited sites were wet meadows or ponds with high aquatic vegetation cover and high invertebrate taxonomic diversity. The 31 described sites appeared to be rich in freshwater invertebrates, with no significant difference in invertebrate densities between the diurnal and nocturnal sites. HR sizes were highly homogenous between the two study sites (MB and MP), between sexes or between age classes. In conclusion, according to this study, an appropriate HR for the Northern Shoveler at spring stopover is 8.49 ± 5.95 km² (mean ± standard error).

1. Introduction

Migratory birds are dependent on different sites throughout their annual cycle, such as the wintering and breeding grounds or staging sites during the post and prenuptial migrations. Habitat selection and use are guided by several factors (Dow & Fredga 1985, Safine & Lindberg 2008, Holopainen *et al.* 2015) such as food availability, intra- and interspecific competition, predation, vegetation structure (especially for breeding birds), and extreme natural events (*e.g.* drought, storm). Migratory birds need to leave their wintering and then staging sites with an appropriate body condition to successfully migrate and prepare for breeding. Migratory Anatidae, are mostly considered as 'income' breeders' (Ganter & Cooke 1996, Gauthier *et al.* 2003), *i.e.* they rely on exogenous resources to fuel their migration. Hence, they need to stop repeatedly on their way to their breeding grounds to forage. At stopover sites, they require foraging areas as well as resting places (Arzel 2006). Various studies have highlighted the crucial role of stopover areas for the survival of birds, although they are inhabited for only a short time during the annual cycle (Moore *et al.* 1990).

It is important to understand home ranges of waterfowl to direct appropriate management action plans in the face of overall degradation of suitable habitats in their flyway route (Legagneux *et al.* 2009, Ma *et al.* 2010). The home range is defined as the interaction between animals and their environment, and its size is a direct result of movement driven by habitat selection and other external factors (Börger *et al.* 2008). Hence, the home range size of migratory animals might vary seasonally pending on the conditions encountered along the migratory route (Legagneux *et al.* 2009, Verheijen *et al.* 2024). Furthermore, at a small spatial scale, *i.e.* over a defined area such as a stopover area, habitat selection and resource use influence home range size (Johnson 1980, Van Moorter *et al.* 2016). Home range size could also be affected by social interactions and intrinsic factors such as sex, age and health status (Börger *et al.* 2008). The habitat and the internal state of the individual can change through time and cause the size variation of the home range.

The Northern Shoveler (*Spatula clypeata*, hereafter Shoveler) is a migratory dabbling duck common throughout the Holarctic region (Cramp & Simmons 1977). This species overwintering grounds range from Western Europe to West Africa and it breeds throughout most of the Nearctic and Palearctic. The Vendée wetlands, in western France, are the major wintering and breeding sites in France. Trolliet *et al.* (2016) estimated a breeding population of approximately 1,600 pairs in the Marais breton (MB) representing 80% of the French breeding population in 2015 (Trolliet *et al.* 2016). Further south, the Marais poitevin (MP) is also an important stopover and breeding site for waterbirds (Duncan *et al.* 1999). In 2010, 44 breeding pairs of Northern Shoveler were estimated in MP (Guéret 2010).

Factors that influence Shovelers' use of wetlands include habitat availability, disturbance, predation but also the diversity, density, spatio-temporal dynamics (Matsubara *et al.* 1994, Guillemain *et al.* 2000) and accessibility (Bolduc & Afton 2004) of their main food resource *i.e.* freshwater invertebrates. In addition, Shovelers select foraging sites according to prey availability, prey size and energy values to maximise the net energy intake (Crome 1985, Tietje & Teer 1996). The bill with its spoon-shaped morphology and high-density, closely spaced lamellae, *i.e.* 21.48 ± 2.41 lamellae/cm^2 (Nudds & Bowlby 1984), is an adaptation to sieving. Shovelers filter the surface of the water to collect food giving them a specific food niche compared with other Anatidae species. The Shoveler's diet mainly consists of small freshwater invertebrates (Pirot & Pont 1987, Ankney & Afton 1988, Baldassarre & Bolen 2006) and, particularly, swimming microcrustaceans such as Cladocera and Ostracoda (DuBowy 1985, Pirot & Pont 1987, Baldassarre & Bolen 2006). Improved knowledge of Shovelers' ecology during prebreeding migration will help to determine their ecological requirements in terms of habitat and feeding.

In the present study, Shovelers were equipped with GPS-GSM tags in the MB and MP . The birds were monitored for two weeks during their prenuptial migration period in order to define their stopover requirements, which are important to understand for conservation and management purposes. We hypothesize that: (1) the home range (HR) sizes of the Shoveler in the MP are larger than in the MB considering the lower density of ponds and the greater distance between them; (2) sex does not influence the HR size at stopover sites; and (3) environmental variables such as water level, presence of aquatic and riparian vegetation or water surface area, as well as invertebrate communities, energy values and size classes, contribute in shaping the size of the HR and determine movements of birds between sites.

2. Material and methods

2.1. Study sites

This study was carried out on the two large wetlands the MB (N2000 FR5212009 and Ramsar 2283) and the MP (N2000 FR5200659) (Fig. 1). MB and MP cover areas of approximately 32,000 ha (Trolliet *et al.* 2016), and 96,000 ha (Duncan *et al.* 1999), respectively. The sampling for aquatic invertebrate's areas in the two regions were limited to freshwater marshes used by the Shovelers equipped with the GPS-GSM tags. Overall, 31 sites were sampled between 1st March and 30st April 2021.

2.2. Capture and tagging

During the prenuptial migration period, Shovelers were captured using cage traps and attracted with live male or female Shovelers as decoys. A camera (NATURACAM – STDX2) was positioned near each trap to monitor the presence of birds in the traps, which were caught every day from the 1st of March to the 17th of March 2020, and from the 1st of March to 10th of April, 2021. In 2020, the capturing effort was stopped on the 17th of March due to the COVID-19 lockdown. In total, eight individuals were caught in the MB and 7 in the MP. All Shovelers were equipped with a GPS-GSM tag (Ornitela, OrniTrack-E10, 10 g, solar-powered GPS-GSM); these included 2 F juv (female juvenile; less than two calendar years), 2 F ad (adult; more than two calendar years), 6 M juv (male) and 5 M ad (see details in Supplementary Material Table S1). The GPS-GSM tags were attached as backpacks using a harness made of Teflon straps with rubber tubing (Klaassen *et al.* 2008, Lameris *et al.* 2017, 2018). The equipment (GPS-GSM tag, harness, and metal ring) weighed less than 3% of the body mass and we assume that the use of the GPS did not cause significant impact on ducks movements

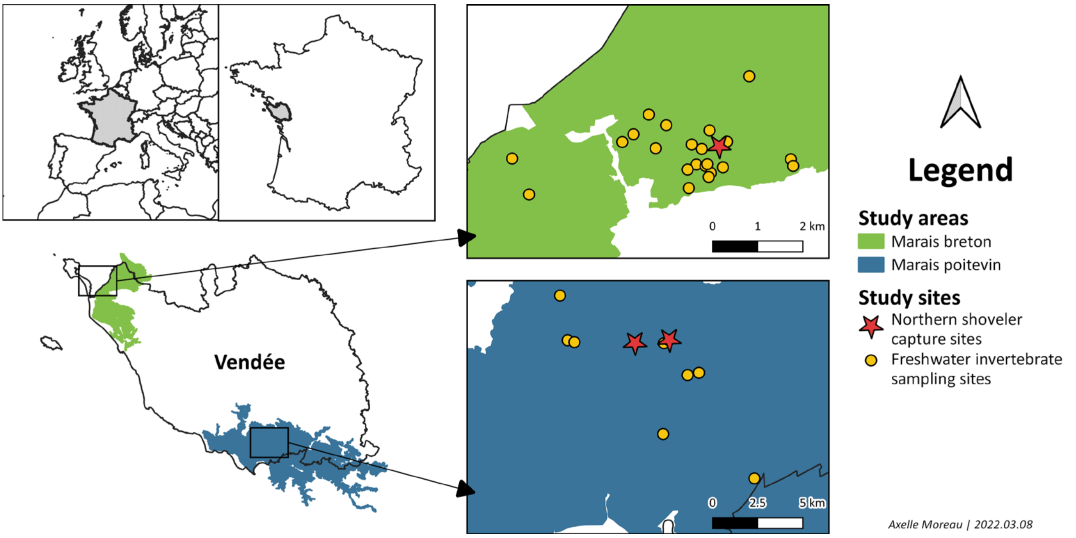

Fig. 1. Locations of the 31 sampling sites in the Marais breton (MB) and the Marais poitevin (MP) on the French Atlantic coast, France.

and behaviour. The Shovelers were captured and handled according to ethical rules edicted by French legislation (Authorization from Ministry of Ecological Transition by Research Center on the Biology of Bird Populations PP: 1821).

The location of the individuals were recorded during the prenuptial period from the 1st of March to the 30th of April in 2020 and 2021 with a frequency of 5 minutes. The location of the 15 individuals was then recorded for (14 days ± 2 days; mean ± standard error) (Table S1). No fundamental differences were observed in precipitation or hydrology between years (2020 vs. 2021) or temporal patterns within a year (*i.e.* early vs. late spring) (Moreau A., pers. comm.). None of the studied individuals attempted to breed in the studied areas.

2.3. Trophic resources at the feeding sites

The tagged individuals spent more than 72 consecutive hours in 31 sites. These sites were classified into three categories according to the habitat type: wet meadow, pond, and channel (Supplementary Material Fig. S1). From the 1st of March to 10th of April 2021, freshwater invertebrates were sampled at each site using a plankton net (mesh of 200 µm, frame size of 35.5 x 15.0 cm) on a transect of 2 m at a depth of 35 cm, which corresponded to the Shovelers' maximum feeding depth capacity (Pöysä 1983). The net contents were preserved in 70% ethanol (Balcombe *et al.* 2005) and quickly analysed at a laboratory. Invertebrates were sorted, counted and identified using a binocular magnifier (Euromex, Series Z, 7-45 x) to the family level except Copepoda, subclass; Cladocera, superorder; Hydrachnidia, suborder; and Ostracoda, class (Thorp & Rogers 2011).

2.4. Environmental parameters measurement

The feeding sites were characterized by the following continuous environmental variables: the sediment depth (in cm), water level (in cm) (both were measured with a graduated stake), salinity (in psu, using a multiparameter probe VWR MU 6100 H Multimeter), percentage cover of riparian helophytes (*i.e.* palustrine plant that lives in the mud but whose leaves are above the waterline) and of emerged and submerged aquatic vegetation (vegetation were characterized empirically). Three environmental variables were categorized into three classes: sediment type (class 1: loamy sediment; 2: loamy/muddy; 3: muddy), slope (class 1: < 5% soft slope; 2: 5%–10% moderate slope; 3: > 10% steep slope), and habitat type (class 1: meadows; 2: ponds; 3: channels). The water surface area of each study sites was measured using Satellite images via the geographic information system QGIS (QGIS Development Team 2009).

2.5. Home range and movement analysis

The time of the day during which the individuals were recorded on a study site was used to categorize the sites into 3 classes: only daytime use (from sunrise to sunset), only nighttime use (from sunset to sunrise) and all day use. Individuals were considered flying when GPS data indicated a speed greater than 14.4 km/h (Bengtsson *et al.* 2014); the corresponding locations were excluded from the analysis. GPS coordinates with less than 5 satellites (Hulbert & French 2001), HDOP value of less than 5 (Rempel & Rodgers 1997), and altitude greater than 15 m were excluded from the analysis. Shovelers always used water for feeding and the water edges for resting, so points on land have been excluded from the analysis. Finally, the first day after capture and tagging was excluded from the analysis in case birds did not behave normally due to recent handling (Bengtsson *et al.* 2014).

The HR and the minimum convex polygon (MCP) were calculated for each individual using the 'adehabitatHR' package (Calenge 2006) on R software (R Core Team 2022). For the HR calculation, based on the kernel density method (Worton 1989), 95 % of the GPS point are used whereas, for the MCP calculation, 100% of the GPS points are used (Legagneux *et al.* 2009). The cumulative number of sites visited over the 15-day period in the HRs was calculated per individual. The proportion of habitat type (+/- standard error) used within the HRs (wet meadows, ponds, channels) was estimated for each individual.

2.6. Statistics

Statistical analyses were conducted using R software (R Core Team 2022) and considered significant when the p-value was below the 5% threshold. The MCP and HR sizes were compared between individuals per sex and age at the MB and MP using the nonparametric Wilcoxon test. The cumulative number of sites used per day by the Shovelers were compared in MB and MP using the nonparametric Kruskal-Wallis test. The proportion of habitat type used within the HRs (wet meadows, ponds, channels) were compared in MB and MP using the nonparametric Wilcoxon test. A principal component analysis (PCA) was conducted to characterize the different habitats in the sampled sites (R packages: 'FactoMineR' (Husson *et al.* 2024) and 'Hmisc'(Harrell 2024)). In addition, the invertebrate densities at the diurnal sites, all day sites, and nocturnal sites were compared using the nonparametric Kruskal-Wallis test. To detect the differences in invertebrate community composition depending on the daily use of the sites, a nonmetric multidimensional scaling (NMDS) was conducted to visualize the degree of overlap between communities. This analysis focused on the density of freshwater invertebrate taxa per cubic metre in each site. The 'vegan' package (Oksanen *et al.* 2024) was used for the analysis. Only groups of freshwater invertebrates with ≥10% occurrence on all the sampled sites were retained for the analysis (Davis & Bidwell 2008). The two deleted groups (Asellidae and Mysidae), with < 10% occurrence, are not considered to be important groups in the Shoveler diet.

3. Results

3.1. Home range, number of sites frequented and habitat use

The size of the minimum convex polygons (MCPs) for the 15 individuals ranged from 9.0 to 2,846.4 ha, and the estimated home ranges (HR) ranged from 2.9 to 25.4 ha (Table S1). The mean MCP areas of the individuals from MB (78.7 ± 54.1 ha, n = 8) were significantly lower than those from MP (738.0 ± 10,003.0 ha, n = 7; Wilcoxon test, $p < 0.05$) while the mean HR sizes did not differ (MB = 6.2 ± 2.9 ha, n = 8; MP = 11.2 ± 7.6 ha, n = 7; Wilcoxon test, $p > 0.05$) (Fig. 2). The MCP size did not differ between males

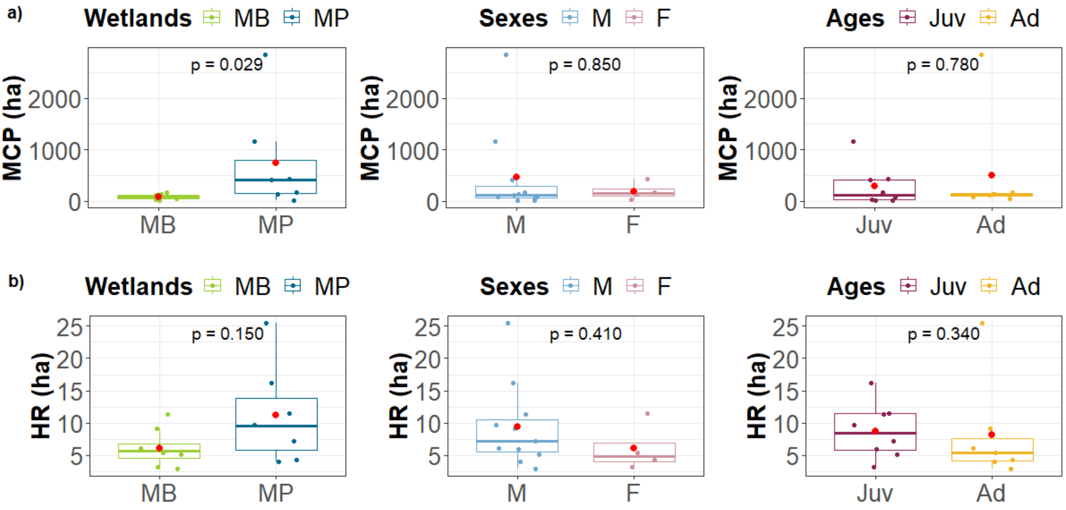

Fig. 2. Mean comparison (Wilcoxon Test) of a) the Minimum Convex Polygons (MCP) and b) the Home Range (HR) size between individuals from the Marais breton (MB, n = 8) and Marais poitevin (MP, n = 7), between sexes (males (M), n = 11 and females (F), n = 4, and between juveniles (juv, n = 8) and adults (ad, n = 7). The red dot corresponds to the mean value.

and females (M = 459 ± 859 ha, n = 11; F = 185 ± 171 ha, n = 4; Wilcoxon test, $p > 0.05$) or between juveniles and adults (juv = 286 ± 393 ha, n = 8; ad = 500 ± 1035 ha, n = 7; Wilcoxon test, $p > 0.05$) (Fig. 2). Moreover, the HR size did not differ between males and females (M = 9.4 ± 6.5 ha, n = 11; F = 6.1 ± 3.7 ha, n = 4; Wilcoxon test, $p > 0.05$) or between juveniles and adults (juv = 8.8 ± 4.2 ha, n = 8; ad = 8.2 ± 7.8 ha, n = 7; Wilcoxon test, $p > 0.05$) (Fig. 2).

Over the 15-day study period, the cumulative number of sites visited by the individuals increased rapidly at the MB but increased slowly at the MP (Fig. 3a). In addition, the number of sites used per day at the MB was greater than MP (Fig. 3a). However, the mean surface size of each habitat type at MP were significantly greater than those at MB, *i.e.* ponds (MB = 0.8 ± 0.8 ha, n = 56; MP = 2.5 ± 3.9 ha, n = 10; Wilcoxon test, $p < 0.05$) and wet meadows (MB = 0.2 ± 0.2 ha, n = 29; MP = 2.1 ± 2.3 ha, n = 23; Wilcoxon test, $p < 0.05$), except for channels (MB = 0.1 ± 0.1 ha, n = 4; MP = 2.4 ± 3.2 ha, n = 2; Wilcoxon test, $p > 0.05$) (Fig. 3b). Finally, the spatial distribution showed that Shovelers used some sites only during daytime for resting or foraging, others only during nighttime for foraging, and some during both day and night (Supplementary Material Fig. S2).

Besides the significant differences in MCP sizes and number of sites visited, the utilization of habitat types also differed significantly between both marshes and individuals (Fig. 4, Table S1). In the MB, HRs mainly consisted of ponds (83 ± 15% of the HR area on average, n = 8), wet meadows were the 2nd most used habitat type (16 ± 15%, n = 8) and channels were very little used (1 ± 1%, n = 8). At the MP, HRs mainly constituted of wet meadows (71 ± 37%, n = 7) and secondly of ponds (26 ± 33%, n = 7). As in the MB, channels were rarely used in MP (3 ± 7%, n = 7).

3.2. Foraging habitat

The environmental characteristics of the sites were analysed using PCA (Supplementary Material Fig. S3). On Axis 1 (39%), the sediment depth, habitat type, sediment type, and slopes were negatively correlated with the emerged aquatic vegetation (Fig. S3 and confirmed by the Spearman correlation values which are –0.41, –0.51, –0.61 and –0.50 respectively).

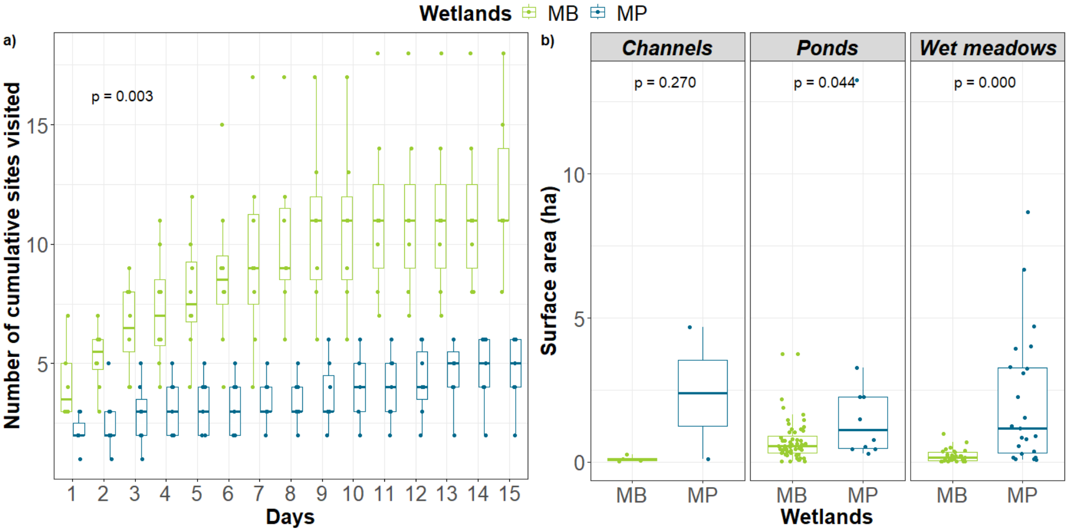

Fig. 3. (A) Mean comparison (Kruskal-Wallis test) of the cumulative sites in each wetland visited by the 15 Shovelers over the study period. (B) Mean comparison (Wilcoxon Test) of the surfaces used by the Shovelers at the three main habitats in the MB and MP.

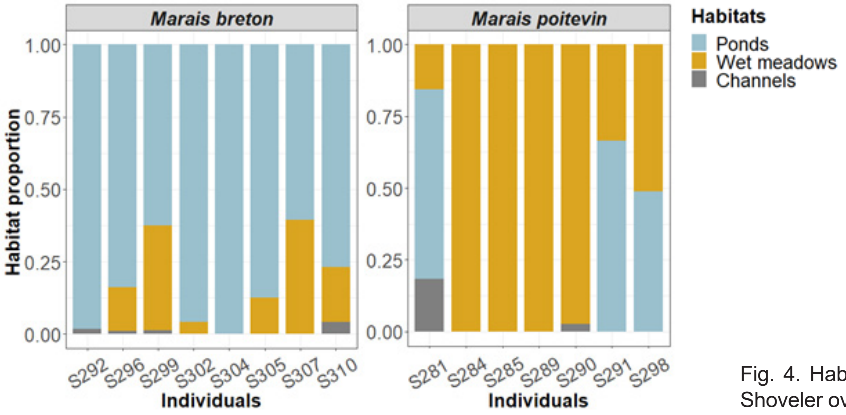

Fig. 4. Habitat proportion for each Shoveler over the study period.

On Axis 2 (17.2%), the variables water level, submerged aquatic vegetation, and water surface area contrasted with the invertebrate density (Fig. S3 and confirmed by the Spearman correlation values which are –0.33, –0.28 and –0.22 respectively). The other variables could not be interpreted ($\cos^2 < 0.4$ on the two axes).

Diurnal sites (Fig. S3 and Supplementary Material Table S2) were mainly defined by a deep water level (40.9 ± 11.1 cm), high sediment height (10.7 ± 10.7 cm), steep slopes, muddy sediment, low cover of aquatic vegetation, and a site typology corresponding to a pond. In contrast, the nocturnal sites (Fig. S3 and Table S2) were characterized by a low water level (28.2 ± 21.7 cm), low sediment height (6.3 ± 6.5 cm), loamy/muddy sediment, soft slopes, a significant cover of aquatic vegetation, and a site typology corresponding to wet meadows. Sites that were frequented at both day and nighttime were not specifically characterized by one or more environmental variables.

3.3. Trophic resources

Among the 15 taxa of freshwater invertebrates inventoried from the study sites, 12 (occurrence of ≥10% on all sites) were retained for the analysis. Five taxa were widespread (present in more than 50% of the samples). These included Copepoda and Cladocera (100% occurrence), Diptera and Hemiptera (84% occurrence), and Ostracoda (61% occurrence). The size class 0.1 to 2.5 mm was the most dominant *i.e.* 51% of the taxa and 98% of the individuals at each site.

The invertebrate densities for all taxa combined ranged from 3,387 to 113,315 individuals/m^3 (Table S2). There was a significant difference in taxon density according to the daily use in the MB, the density in diurnal sites were lower than the density in nocturnal sites (Diurnal site = 16,106 ± 13,241 ind/m^3, $n=9$; Nocturnal site = 37,698 ± 31,316 ind/m^3, $n=9$; Wilcoxon test, $p>0.05$) (Fig. 5 and Supplementary Material Table S3). However, there was no significant difference in the density of freshwater invertebrates based on the daily use of the sites in the MP (Diurnal site = 31,899 ± 13,148 ind/m^3, $n=3$; Nocturnal site = 23,795 ± 15,468 ind/m^3, $n=4$; All day site = 19,585 ± 16,419 ind/m^3, $n=2$; Wilcoxon test, $p>0.05$) (Fig. 5 and Table S3). Moreover, there was a significant difference in taxon diversity according to the daily use in the MB, diurnal sites were less diversified than the other sites (Diurnal site = 4.3 ± 1.2 taxa per site, $n=9$ sites; Nocturnal site = 6.6 ± 1.7 taxa, $n=9$; All day site = 7.8 ± 2.6 taxa, $n=4$; Wilcoxon test, $p<0.05$) but, not in the MP (Diurnal site = 6.7 ± 0.6 taxa, $n=3$; Nocturnal site = 5.5 ± 2.1 taxa, $n=4$; All day site = 5 ± 0 taxa, $n=2$; Wilcoxon test, $p>0.05$) (Fig. 5 and Table S3), which was confirmed by the NMDS plot (Supplementary Material Fig. S4). Microcrustaceans (Cladocera and Copepoda) as well as Odonata, Amphipoda, Hydrachnidia, and Hemiptera were present in all the sites.

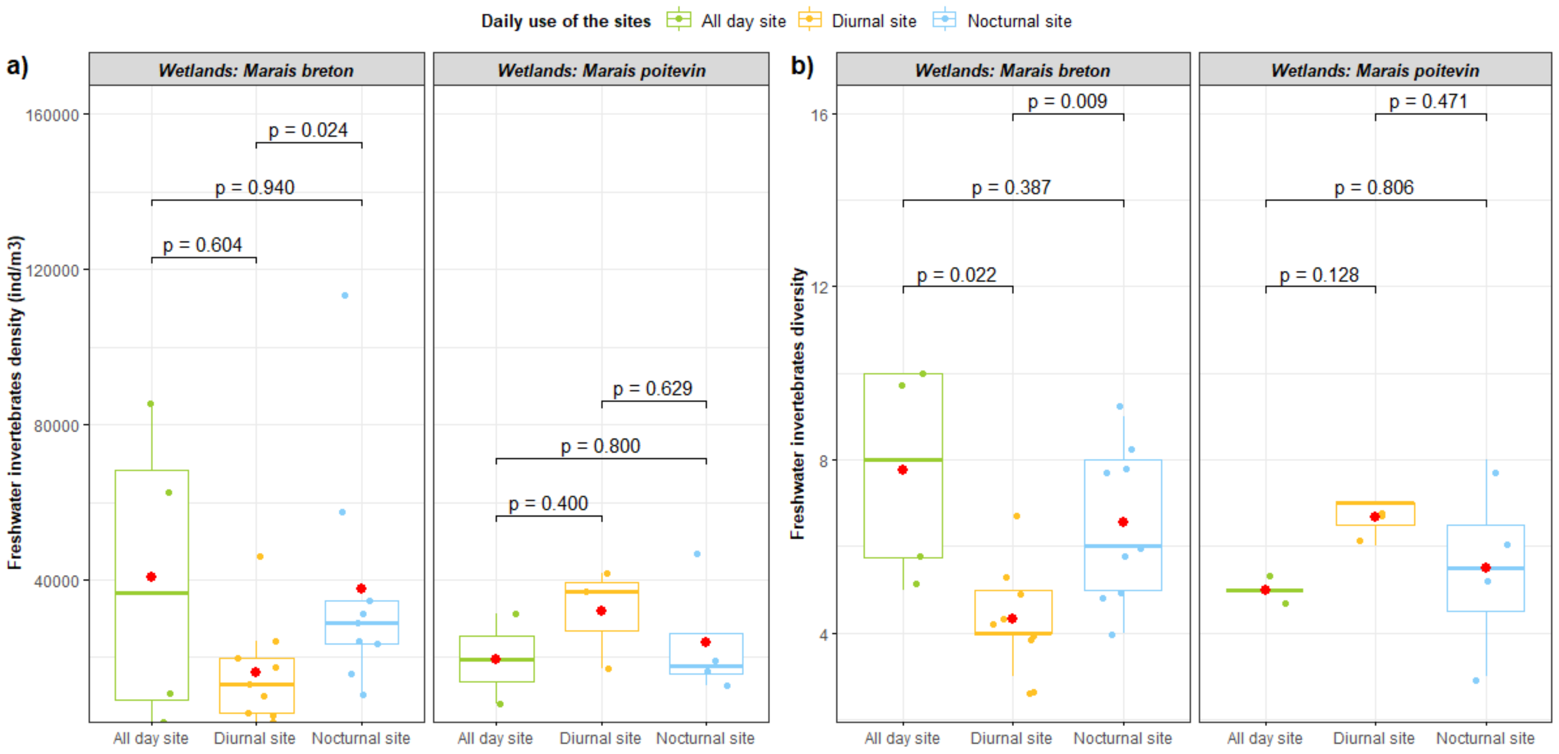

Fig. 5. Mean comparison (Wilcoxon Test) of the freshwater invertebrates a) density and b) diversity, in MB and MP, depending on daily use of the sites, i.e. diurnal site (MB, n = 9; MP, n = 3), all day site (MB, n = 4; MP, n = 2), nocturnal site (MB, n = 9; MP, n = 4).

4. Discussion

This study highlighted that the home range (HR) sizes of Shovelers did not differ between individuals from the MB and MP, between males and females or between juveniles and adults. The proportion of the type of habitat used differed between individuals in both marshes. Invertebrate densities did not differ between the diurnal and nocturnal sites.

4.1. Home range, number of sites and habitats used

Heitmeyer and Vohs (1984) defined that the Shoveler preferentially uses small marshes and muddy ponds, which is consistent with the results of the present study, wherein the HR of more than half of the individuals studied (59%) contained more than 50% ponds. However, the sizes and habitat composition within the HRs were not the same across MB and MP wetlands and between individuals. Several factors can influence the HR size and shape (Rolando 2002). Species prospecting in environments that may change seasonally and contain variable food resources must adjust their distribution or space use according to resource availability to meet their energy requirement (Kirk *et al.* 2008, Kraan *et al.* 2009). In this study, no significant differences in HR sizes were observed between wetland complexes. However, the maximum total area used (Minimum Convex Polygon, MCP) was significantly larger in the MP than in the MB. Ponds and wet meadows are much more scattered in the MP than in the MB. Thus, the lower density of water areas (ponds and wet meadows) likely leads the birds to explore larger territory, possibly explaining the larger total area of the MCP in the MP. Furthermore, the lack of differences in the HR size between males and females was expected as Shovelers are considered to be ‘income’ breeders (Ganter & Cooke 1996, Gauthier *et al.* 2003). Accordingly, both males and females feed similarly on migratory stopovers to complete their trip to the breeding sites. This result is also supported by Arzel and Elmberg (2004), who found no sex differences in the foraging behaviour of Shovelers at the spring stopover sites (time spent feeding, day/night distribution, and feeding method). The use of sites during the stopover differed between individuals. Some individuals used up to ten different sites per day, whereas others used only two sites, although, only sites at which individuals spent more than 72 hours were kept for analysis. This variability may be due to different energy requirements and thus varied time allocated to feeding, differences in social status, or competition for access to food at some sites (Poisbleau 2005, Bengtsson *et al.* 2014). However, no interspecific competition related to food limitation has been demonstrated for the Mallard (*Anas platyrhynchos*), Eurasian Wigeon (*Mareca penelope*), Eurasian Teal (*Anas crecca*), and Shoveler (Arzel & Elmberg 2004).

4.2. Characterization of the feeding habitat during the prenuptial stopover

This study showed a distinction between the characteristics of the sites used during the day and those used during the night. During daytime, the birds were concentrated on open (unvegetated), relatively deep ponds and with a high density of freshwater invertebrates. These characteristics of the diurnal sites limit the risk of Shovelers predation during their diurnal activities, such as resting, grooming or feeding (Guillemain *et al.* 2007). Indeed, open water provides better visibility of predators (Legagneux 2007). When disturbance or predation is high at a site, birds increase their vigilance behaviour and decrease their feeding and resting times, with consequences on their energy stock (Le Corre 2009). The Marsh Harrier (*Circus aeruginosus*) is one of the main predators on dabbling ducks in these wetlands (Fritz *et al.* 2000). The nocturnal sites had significant emergent aquatic vegetation cover and a higher freshwater diversity than the diurnal sites. The characteristics of the nocturnal sites can be explained by the fact that Shovelers feed mainly at night (Guillemain *et al.* 2002, Poisbleau 2005). Wetlands with a high percentage of vegetation cover provide a more diverse habitat structure, consequently increasing the diversity, biomass, and density of freshwater invertebrates (Olson *et al.* 1995, Broyer & Curtet 2012). However, vegetation influences wetland use by birds (Fairbairn & Dinsmore 2001). Overly dense emergent vegetation can impact feeding activity and prey detection by ducks (De Leon & Smith 1999). Webb *et al.* (2010) demonstrated the importance of a 50% open water and 50% vegetation ratio for dabbling ducks during their prenuptial migration, which allows a greater diversity of food resources, plants, and freshwater invertebrates, especially for the waterfowl. Thus, this study demonstrates that during its prenuptial migration, Shovelers need suitable habitats for resting and feeding during a complete nychthemeral cycle.

4.3. Characterization of available food resources

A predominantly invertebrate-based diet of the Shoveler in spring appears to be consistent with the temporal dynamics of this food resource. For birds that need a diet of freshwater invertebrates, there is no synchronization between their peak migration and peak density of food resources at stopover areas (Arzel & Elmberg 2004). However, the behaviour of ducks in a site is linked to fluctuations in resource density (Arzel 2006). Nevertheless, we measured high densities of freshwater invertebrates in the MB and MP during migration of Shoveler. The 31 study sites revealed a mean density of 28,298 ± 24,342 individuals/m^3 per site. In a study carried out in several wetlands in West Virginia (USA), Balcombe *et al.* (2005) reported a mean of 14,800 ± 3,060 invertebrates/m^3 in emergent waters and 2,360 ± 1,130 invertebrates/m^3 in open waters. In Delta Marsh in south-central Manitoba, Kaminski and Prince (1981) measured aquatic invertebrate densities as a function of percent cover of emergent hydrophytes (8,381 individuals/m^3 for 30% cover, 9,938 individuals/m^3 for 50% cover, and 12,190 individuals/m^3 for 70% cover). According to the present study, the particularly high density of freshwater invertebrates could explain the attractiveness of the studied sites at MB and MP for Shovelers during their prenuptial migration.

This study highlighted that at the diurnal and nocturnal sites, the individuals appeared to use sites abundant in Copepoda and Cladocera. These two taxa had similar abundance across diurnal and nocturnal sites. Copepoda and Cladocera do not always have a habitat preference between vegetated habitats and open water (Romare *et al.* 2003); they have a high energy value, averaging 5,767 cal/g at dry weight and 5,056 cal/g at dry weight, respectively (Moreau *et al.* 2021); and they are small, averaging 1.69 mm and 1.06 mm, respectively (Moreau *et al.* 2021). As discussed earlier, due to its spoon-shaped bill with high-density, closely spaced lamellae, the Shovelers are particularly adapted for feeding on small prey (Nudds & Bowlby 1984). Their diet is thus composed mainly of Copepoda and Cladocera during several stages of the migratory cycle (pre and postnuptial migration, reproduction) (DuBowy 1985, Eldridge 1990, Euliss *et al.* 1997). This is consistent with the expectations of the energy requirements related to migration (Batt *et al.* 1992). Thus, ducks appear to use sites where the food resources allow maximum energy intake while considering the safety of the site. The nocturnal sites were more diversified (in terms of taxa) than the diurnal sites. During the day, the individuals used poorly vegetated sites. Consequently, the diurnal sites had a low diversity, with a dominant presence of Copepoda and Cladocera. At night, the individuals moved to sites with a high density of microcrustaceans (Copepoda, Cladocera, and Ostracoda) as well as Coleoptera, Decapoda, Diptera, and Ephemeroptera. This higher diversity at nocturnal sites allows the Shoveler to find its preferred diet prey but also potentially more energetic prey. Indeed, one potential food source for the Shoveler is Chironomidae larvae. These organisms are predominantly benthic. Although Chironomidae densities are lower than those of microcrustaceans, their biomass is high. Chironomidae are larger organisms, *i.e.* around 2.6 to 15 mm (Moreau *et al.* 2021), and their dry weight is much higher than for microcrustaceans, *i.e.* 0.31 mg on average for Chironomidae (Moreau *et al.* 2021) versus 0.02 mg for Copepoda and Cladocera (Boreham 1994). Moreover, Chironomidae larvae are rich in protein (56%) (Baldassarre & Bolen 2006).

5. Conclusion

Regardless of wetlands, age classes or sexes and according to this study, an appropriate HR for the Shoveler at spring stopover is 8.49 ± 5.95 km² (mean ± standard error). Within its home range, the Shoveler mainly uses two habitat types with high freshwater invertebrate density: ponds (with or without vegetation) and wet meadows. Preserving deep and muddy ponds, which are used by Shovelers during the day and shallow and vegetated ponds or wet meadows, which are used during the night along the migration routes remains critical to fostering the relationship between freshwater invertebrates and the Shoveler during their prenuptial migration. Telemetric monitoring of migrating Shovelers and analysis of freshwater invertebrates in the wetlands of Vendée confirmed the processes related to this relationship during the prenuptial migration.

Lapasorsan (*Spatula clypeata*) kotialueen koko ja vuorokautinen elinympäristön käyttö kevätmuuton pysähdyspaikoilla Vendéen kosteikoilla, Länsi-Ranskassa

Ranskan Atlantin rannikolla sijaitsevat Marais Bretonin (MB) ja Marais Poitevinin (MP) alueiden kosteikot ovat tärkeitä useille sorsalajeille, erityisesti kevätmuuton aikaisina levähdyspaikkoina. Anatidae-heimon lintujen ekologisten vaatimusten ymmärtäminen näillä pysähdyspaikoilla on tärkeää, jotta voidaan määritellä hoitotoimenpiteitä, jotka voivat vaikuttaa niiden myöhempään lisääntymismenestykseen. Tämä tutkimus keskittyy lapasorsaan (*Spatula clypeata*), joka pysähtyy säännöllisesti näillä kahdella kosteikolla kevät- ja syysmuuttojen aikana ja on riippuvainen kosteikkoalueiden makean veden selkärangattomista ravintona. Viisitoista lapasorsaa varustettiin GPS/GSM-lähettimillä, ja niiden liikkeitä seurattiin näillä alueilla vuosina 2020 ja 2021. Tutkimuksen tavoitteena oli selvittää elinympäristöjen käyttöä pysähdyspaikoilla ja yhdistää kotialueen koko (*home range*, HR) ravintoympäristöjen ominaisuuksiin, kuten makean veden selkärangattomien tiheyteen ja monimuotoisuuteen.

Marais Bretonissa lapasorsien kotialueet koostuivat pääosin lammista (83 %), kun taas Marais Poitevinissa ne keskittyivät kosteille niityille (71 %). Lähettimillä varustetut linnut viettivät yli 72 tuntia yhteensä 31 eri kosteikolla, joita ne käyttivät sekä päivisin että öisin. Päivisin linnut suosivat syviä, vähäkasvustoisia lampia, joissa oli runsaasti mikroäyriäisiä, kun taas öisin ne hakeutuivat kosteille niityille tai lammille, joissa oli runsaasti vesikasveja ja selkärangattomia. Kaikki tutkitut kosteikot olivat makean veden selkärangattomien suhteen rikkaita, eikä selkärangattomien tiheyksissä havaittu merkittäviä eroja päivä- ja yöalueiden välillä. Kotialueiden koot olivat hyvin yhtenäisiä kahden tutkimusalueen, sukupuolten ja ikäluokkien välillä. Tutkimuksen mukaan lapasorsien optimaalinen kotialue keväisillä pysähdyspaikoilla on keskimäärin 8,49 ± 5,95 km^2.

Declaration of interest statement. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Online supplementary material

Supplementary material available in the online version of the article (https://doi.org/10.51812/of.142037) includes Figures S1–S4 and Tables S1–S3.