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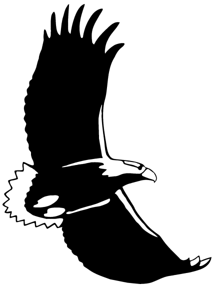

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Spring migration phenology of Eurasian Woodcocks tagged with GPS-Argos transmitters in Central Europe

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Eurasian Woodcock (*Scolopax rusticola*) plays a special role in the cultural heritage of most nations in Europe. In the last decade, ringing revealed the main migratory patterns of some well studied and intensively harvested Woodcock populations wintering in Western and Southern Europe. The same study sites and populations were in focus when the recently revolutionized satellite tracking technologies allowed the study of individual migrations. In contribution to these efforts, we present here the pre-nuptial migration data of Woodcocks captured and tagged with GPS-Argos transmitters in Central Europe, in 2020. Woodcocks migrated from the tagging site in Hungary to Ukraine, European Russia and Central Siberia by an average of 2,678 km (range 677–5,002 km). The duration of the migration ranged between 1–52 days, the overall migration speed was 382 km/day, the absolute maximum distance covered in a day was 866 km. The individual number of stopovers varied during the migration from 0 to 5. The average time spent at each stopover site was 5.6 days. Within the stopover sites, the daily displacements ranged between 11–3,329 m. The Carpathian Basin may be more important in the wintering of Woodcocks than previously assumed, as tagged birds stayed significantly longer compared to any later en route migratory stopover. In accordance with the results of previous DNA analysis, identified breeding grounds of tagged individuals represented a large part of the distribution area.

1. Introduction

Bird migration is a diverse and complex phenomenon, with a plethora of yet undiscovered details. Understanding migratory processes is often necessary to ensure the effective conservation management of avian species. The study of bird migration was historically linked to ringing (Anderson & Green 2009). However, besides the many advantages of ringing, there are also factors influencing the limited use of the data resulting from it, which is why many processes are still unknown or have not yet been proven. Such factors include significant spatial and temporal differences in the likelihood of capture, marking, recapture, observation probability of different species, and also in human ringing and reporting activity (Robinson *et al.* 2009).

Today, individual-based satellite tracking technologies are widely used, and they have already revealed previously unknown patterns of movement and behaviour in many animal species. The sizes and weights of the tags are decreasing, while their efficiency and the accuracy of their sensors are improving (Hofman *et al.* 2019).

The technological development of individual tracking also plays an important role in the study of the migration of the Eurasian Woodcock (*Scolopax rusticola*), a species of high international concern due to cultural heritage and hunting traditions. For more than three decades the significant ringing activity and the development of capturing methods allowed researchers to collect large amounts of data on the migration of Woodcocks wintering in Western and South-Western Europe (Gossmann *et al.* 1988). However, first data from Woodcocks tagged with Platform Transmitter Terminals (PTT) drew attention to the fact that wintering birds may originate from remote areas where the likelihood of ring recovery is extremely low (Arizaga *et al.* 2015). The results of Woodcocks tagged in the wintering areas in Western Europe, proved that several individuals migrated to areas far East from the Ural Mountains in spring (Arizaga *et al.* 2015, Hoodless *et al.* 2020, Tedeschi *et al.* 2020). Thanks to these recent tracking studies, a big step was taken towards understanding the migration of Woodcocks wintering in Western and Southern Europe, and it was possible to get basic knowledge about the timing, direction, and patterns of their movement. During the spring migration, the average departure time falls in the second decade of March, and the main direction of the migration is North-East, East (Arizaga *et al.* 2015, Hoodless *et al.* 2020, Tedeschi *et al.* 2020). The distance between the wintering and the breeding sites can be as much as 10,000 km. During spring migration birds move to a distance of 500–5,000 km on average (Arizaga *et al.* 2015), and after taking an average of about 400 km distance flights, they usually spend several days at stopover sites (Hoodless *et al.* 2020). Due to the limitations of the applied PTT technology, there is less information on the behaviour of tagged Woodcocks at the stopover sites. Although the species may not select for particular habitats as stopovers at a meso-scale range (Crespo *et al.* 2016), the migration routes of the individuals tracked for several years still showed remarkable similarity (Hoodless & Heward 2019, Tedeschi *et al.* 2020). With the comparison of tracking and weather data, it was also found that high air temperature and northward wind increased the probability of migration of the birds, while trends to greater humidity had the opposite effect (Le Rest *et al.* 2019).

The Central European region, including the Carpathian Basin, is considered to be the southern boundary of the breeding area of the species (Ferrand & Gossmann 2009a, Sørensen 2020). In both spring and autumn, migrating birds wintering in Western Europe appear there in greater numbers (Szemethy *et al.* 2014), but there are also regular sporadic sightings during winter and summer. As a game species, a relatively large amount of ringing and recovery data are available on wintering sites of the Woodcocks occurring in the Central European region, but very little direct information is available on the presumed breeding sites (Schally 2019). Due to the timing of the hunting seasons in many countries, most of the ring-recoveries are concentrated in the winter period and in wintering grounds in Western Europe. Ringing and recovery data for the Carpathian Basin are completely missing from the period between May and August (Schally 2019), the habitats of Woodcock during the summer can therefore only be inferred from indirect information. Based on the migration routes of Woodcocks tagged in Southern and Western European wintering grounds, it can be assumed that birds in the Carpathian Basin migrate in similar directions and distances in spring, but they also might deviate from them in some respects.

This study intends to expand the knowledge gained from the previous ringing and PTT telemetry studies on the spring migration of the Eurasian Woodcock. Based on localization data from high-precision GPS telemetry tracking devices deployed on Woodcocks in the Carpathian Basin (Hungary), we characterized (1) the behaviour of the tracked birds in the study area; (2)

the direction and timing of their migration; (3) the distance, speed, and duration of their migration; (4) the dynamics of their migration, including the number of their stopovers and the time spent there; and (5) the location of the breeding areas and the distances between them.

2. Material and methods

2.1. Data collection

We used tracking data of 6 Eurasian Woodcocks (Table 1), tagged between 24th February and 18th March 2020 in Central Hungary, in an agricultural-forest mosaic in the periphery of Budapest. The birds were captured with night-lighting method (Gossmann *et al.* 1988) in the same open agricultural habitat extending ~0.25 km^2. The age of the birds (in their second calendar year (2Y) or older (2+)) was assessed according to the moulting stages of their wing feathers (Ferrand & Gossmann 2009b), and their sex was determined by examining the DNA samples extracted from the feathers. The age and sex attributes (2Y as juvenile (J); 2+ as adult (A), male (M), female (F)) and the capture sequence were used to create an ID for each individual (*e.g.*, JM1 or AF2), used later to communicate results. The average net bodyweight of the birds was 334.8 g (range 295–380 g).

PinPoint GPS Argos 240 transmitters (Lotek Wireless Inc.) (weight: 12 g) were used for tagging. We fixed the devices with a knotted leg-loop harness (Rappole & Tipton 1991) using a 1.5 mm diameter NBR rubber cord passed through a 3.5 mm diameter transparent and flexible PVC tube on each side. The tags were supplied in a matt brown coating to complement the birds' plumage, and the flat and rounded design of the devices makes them less disadvantageous during flight (Pennycuick *et al.* 2012). Due to the elastic material of the harness, it was easy and quick to attach. The entire operation took less than 15 minutes, minimizing the potential negative effects of the capture and tagging (Lameris *et al.* 2018). As the expected lifespan of the transmitters is only a few months, the harness material which might detach in the medium term can also be considered a preferable solution.

The transmitters were programmed to record one GPS location per day, which was timed a few minutes after midnight to maximize the probability of proper satellite data communication, assuming that the birds would be feeding in open fields at those times (Duriez *et al.* 2005a). According to factory default settings, the tags transmitted the localization data to a central database via the Argos satellite system after every third successful fix. The data were imported to the Movebank database (Kranstauber *et al.* 2011), and were processed with Quantum GIS (v3.12).

2.2. Data selection

During the data preparation, we filtered GPS locations of adequate quality ("G"–"Ok") based on the manufacturer's CRC (Cyclic Redundancy Check) quality control algorithm. Argos localizations were not used, because the GPS data for the same days were also available. The accuracy of the GPS localizations was pre-tested on all transmitters. Based on the tests, they proved to be suitable for high-precision, detailed analysis. The mean distance between localizations recorded at

Bird ID	Tag ID	Age	Sex	Period (MM.DD)	Number of points
AM1	199443	2+	male	03.04–05.31.	71
JF1	199444	2Y	female	03.04–05.27.	70
JM1	199445	2Y	male	02.26–05.31.	86
AF1	199446	2+	female	03.13–04.12.	29
AF2	199447	2+	female	03.20–05.31.	68
AF3	199449	2+	female	03.20–05.30.	67

Table 1. The main characteristics of the GPS tracked Woodcocks.

fixed points was 23.1 m (n=404; range: 1–331 m), and the mean DOP value of the measurements was 2.95 (n=66; range: 1–9.6). Localizations within 24 hours after marking were also excluded from the analysis due to the potential behavioural effect of handling.

According to the results of previous studies, we assumed that the Woodcocks would reach their breeding grounds by the end of May at the latest (Arizaga *et al.* 2015, Hoodless *et al.* 2020), therefore, the data were also filtered to not be later than May 31st. This assumption was also confirmed with the data from June, which were recorded at longer intervals (every 5th day only) because the tagged birds showed sedentary behaviour at the breeding ground. The final number of points selected for processing was 391 in total.

2.3. Data analysis

To characterize the behaviour of the birds, we analysed the distribution of distances between the localizations of consecutive days. The points were classified into "stopover" and "migrating" categories based on several criteria. We considered points as stopover locations, which fell close to each other in space while there was at least 24 hours between them. Based on the preliminary evaluation of the data, localizations with a maximum distance of 4 km were considered to be close to each other. This distance is remarkably shorter compared to the previously published thresholds exceeding 30 km (Arizaga *et al.* 2015, Crespo *et al.* 2016, Le Rest *et al.* 2019, Hoodless *et al.* 2020), although those were applicable for Argos PTT data, which can be considered less accurate in general. We deviated from the 4 km threshold only in one single case, because there were consecutive points within such a distance, but they formed clearly separate non-overlapping groups. The points between which some days were missed (5 days at maximum) but did not fall further than the above threshold, were also considered to belong to the same group. Daily movements were measured only between localizations that occurred on consecutive days. Although the 4 km threshold was used for detailed analyses, the departure from the tagging site was determined from the time at which the first significant displacement (>50 km) occurred, and the reaching of the breeding areas was determined at the time when only shorter displacements (<50 km) happened.

Presumably, due to a technical reason, the tag of the individual AF1 stopped transmitting signals after 12th April 2020, therefore the data of this bird were not used for the analyses related to the breeding areas.

We assessed the behaviour of the tagged birds in the tagging area and summarized the number of days elapsed between the time of tagging and the date of departure for each individual. During the first 3–4 days of the study period, in addition to the midnight ones, a second localization point was recorded each noon in the case of 4 individuals (AM1, JF1, AF2, AF3). To characterize the space use of the birds, we determined the distances between the central coordinates of their diurnal and nocturnal points.

The time of the onset of the migration and its directions were compared among the individuals. We examined how far the GPS tagged Woodcocks moved away from the tagging site, measured in a straight line, and summed the total distance they covered during the migration. All distance measurements were performed with ellipsoidal (WGS 84) calculation to take into account the curvature of Earth. We summed up the number of days spent in migration per individual, including the time spent at the stopover sites. We examined the strength of the relationship between the duration of the migration and the total distance covered. We examined the distances travelled by the Woodcocks during the migration between the localizations of two consecutive days, excluding the displacements registered at the stopover sites.

For the assessment of the distances between stopovers, we summarized the lengths of the straight lines that connect consecutive stopover sites. The tagging site and the breeding sites were included in the calculation, but we did not include the short-term movements that occurred after reaching the breeding sites. For the speed calculation, reaching the breeding site was also considered as the endpoint, and the total distance travelled was divided by the number of days spent in movement. We measured the length of daily movements and also distance matrixes were calculated among the individual localization points within the stopover sites. We also examined the number of stopovers along the migration route and the number of days spent at each stopover site. In all cases where mean values were calculated, we also reported SD values.

We measured the distances in kilometres between the breeding areas of the individuals that successfully completed the migration. The main habitat characteristics of the stopover sites and breeding sites were assessed by using freely available satellite images (ESRI World Imagery) and the location points were arranged in two categories (open fields or closed forests) according to the land cover types they fell into.

3. Results

3.1. Local movements at the location of tagging

The Woodcocks captured and tagged in open feeding areas remained near the capture site for an average of 23.3 ± 6.1 days (range 14–30 days). Only one individual (AF1) changed its position on the 4th day after tagging and settled after taking a distance of 17 km, and then stayed at that site for 17 days. All the other birds stayed for two to four weeks within the 4 km radius of the place where they were tagged (average 1.4 ± 1.15 km, n=106 points). All daytime points (n=14) fell on covered, bushy or forested areas for all individuals, while night points were recorded also in open habitats several times (6 / 14 points). The distances between the spatial means of the daytime points and the spatial means of the nocturnal points of the individuals ranged between 99.3–327.9 m (average 203.3 m ± 95.4 m). Three Woodcocks also spent a relatively long time in abandoned orchards: AF2 – 12 points of 14; AF3 – 19 points of 24; AM1 – 14 points of 29.

3.2. Timing and direction of the migration

The average time of departure from the tagging location was 2nd April ± 7.6 days. The first bird (JM1) left the tagging site on 21st March, and the last one (AF3) started to migrate on 13th April (Fig. 1). The direction of the first migratory flights was NE for each marked individual (Fig. 2).

The Woodcock JF1 moved 344.2 km NE between 21st–22nd March, but interrupted its migration and returned to the tagging location by 25th March. Following this backward movement, JF1 remained in the same area and finally left the study site again on 6th April in the same NE direction (Fig. 3).

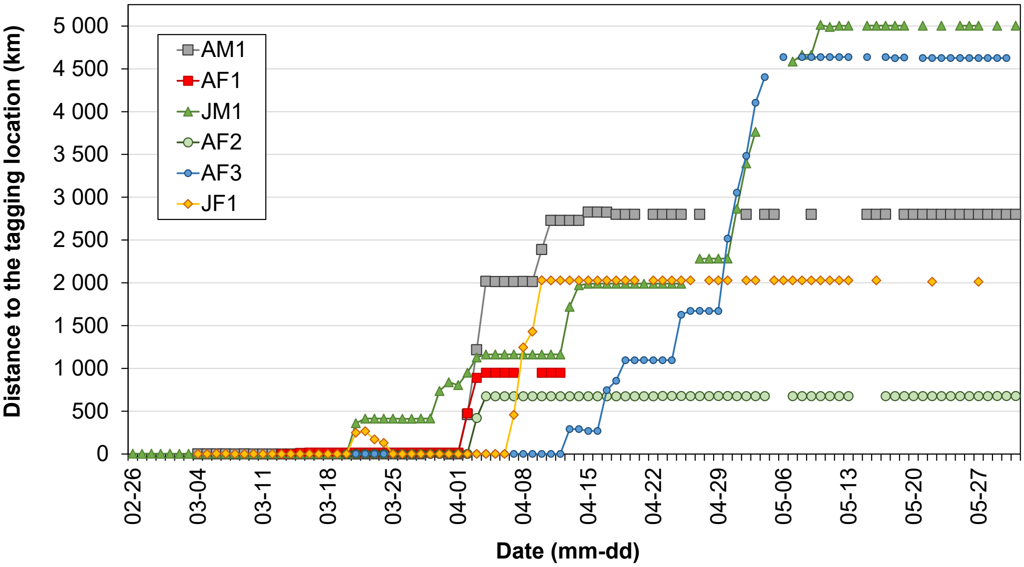

Fig. 1. Pre-nuptial migration dynamics of the tagged Woodcocks.

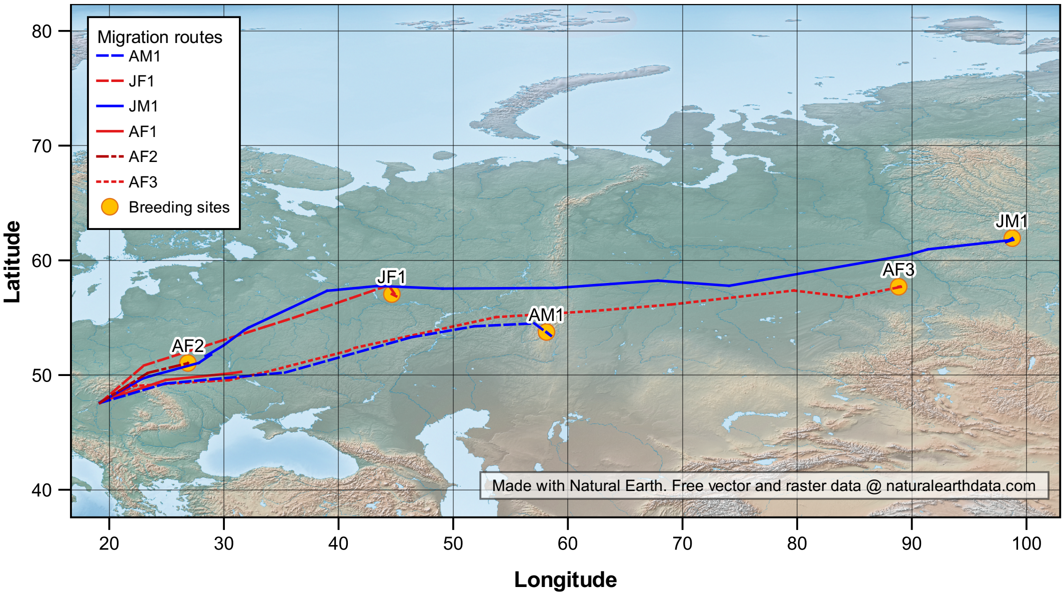

Fig. 2. Pre-nuptial migration routes and breeding areas of Woodcocks deployed with GPS transmitters in Hungary.

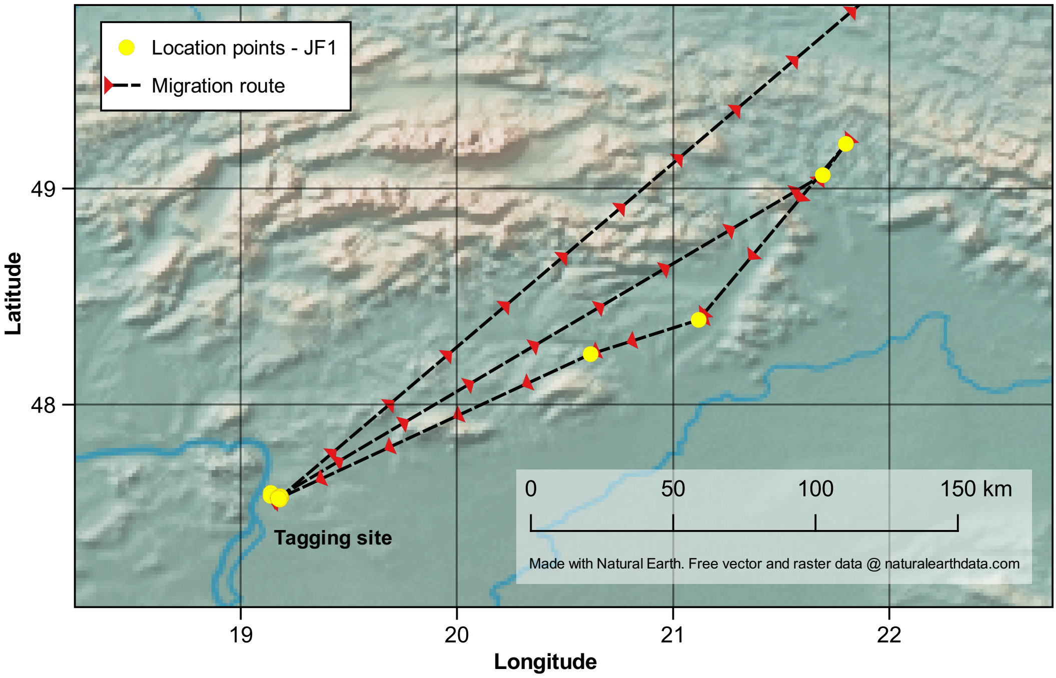

Fig. 3. Interrupted and return migration of the Woodcock JF1 to the tagging site.

Table 2. Main movement variables of the GPS tracked Woodcocks.

Bird ID	Migration distance (km)	Straight line distance (km)	Duration of migration (days)	Number of stopovers	Time spent at stopovers (days)	Distance/day (km)
AM1	2,966.3	2,799.5	13	2	10	487.3
JF1	2,738.5	2,014.0	4	0	0	432.8
JM1	5,456.6	5,002.4	52	5	34	272.8
AF1	958.3	950.0	NA	NA	NA	NA
AF2	687.2	677.3	1	0	0	342.3
AF3	4,883.4	4,626.8	23	4	14	373.3

3.3. Migration distance, speed, and duration

During their migration, the tracked Woodcocks moved away from the tagging site by an average of 2,678.3 ± 1,824.6 km (range 677.3–5,002.4 km). Although the routes of the birds deviated slightly from a straight line, no significant difference was found between the total distances travelled and the shortest (straight line) distances measured between the tagging and the breeding sites (Table 2). The number of days spent in migration (including time spent at stopover sites) ranged between 1–52 days (mean 18.6 days ± 20.5 days SD), and we have found a strong relationship between the total distance travelled and the duration excluding the time spent at stopovers (Pearson $r=0.88$; $p=0.05$). The bird migrating to the shortest distance (AF2) reached its breeding site on 4th April with a single, ~690 km overnight flight. The farthermost migrating bird (JM1) reached its breeding area on 12th May.

During the migration, the distances between the localizations of two consecutive days covered an average of 349.8 ± 239.8 km. The minimal distance was 10.7 km, but we also measured flight distances above 800 km/day by four individuals, while the absolute maximum distance was 865.8 km/day. By dividing the total distances with the total time spent in migration, the Woodcocks travelled with an average overall migration speed of 381.7 ± 82.5 km per day (range 272.8–487.3 km).

3.4. Migration dynamics and stopovers

The number of stopovers varied between 0–5 during the migration. Two birds reached their breeding grounds without any interruption longer than 24 h, with a route lasting one (AF2) and 4 days (JF1), respectively. Only birds which had moved at least to the Ural Mountains interrupted their migration for several days (AM1, JM1, AF3). The average of the stopover distances was 1,215.8 ± 972.2 km (range 151.5–3,095.5 km). The time spent at stopover sites was 5.6 ± 3.1 days (range 2–11 days) for these three Woodcock. Within the stopover sites, the daily displacements ranged between 11–3,329 m (mean 511.6 m ± 698.4 m SD, 205.3 m median), the distances between the individual points ranged between 0–4,304 m (mean 471 m ± 556 m SD, 299 m median), so they were clearly different from the values registered in the migration.

Within the stopover sites, the majority (61.5%) of the localization points recorded at night ($n=65$) were in forested, wooded vegetation, however, a significant proportion (38.5%) fell in open agricultural fields or grasslands. Woodcocks were often located in the immediate vicinity of settlements, but no other main habitat category could be attributed to migratory stopovers.

3.5. Location of the breeding sites

The breeding sites of the Woodcocks that successfully completed their migration ($n=5$) were located between 51.0–61.9°N and 26.8–98.7°E, typically in habitats with high forest cover.

Two Woodcocks settled in Siberia, Krasnoyarsk (JM1) and Tomsk region (AF3), one in the Zilairsky District on the south-eastern slopes of the Ural Mountains (AM1), one in the Nizhny Novgorod region in Russia (JF1) and one in the Rivne Oblast in Ukraine (AF2). Upon arrival at the breeding sites, we observed small-scale, but markedly different directional (southern and sometimes western) movements by the majority of the individuals (Fig. 4). The average distance between the breeding sites of tagged individuals was 2,354.3 ± 1,199.8 km (range 727.4–4,341.7 km).

4. Discussion

The collected localization data proved to be useful in the case of all tracked individuals to describe the variables that characterize their behaviour at the tagging site and also during migration. Regarding the species' cryptic behaviour and migration covering thousands of kilometres, this can be considered a good result in itself, because the rate of data loss is low compared to similar studies (Arizaga *et al.* 2015, Le Rest *et al.* 2019, Tedeschi *et al.* 2020). The real value of the present dataset is that, albeit with a small number of samples, we obtained daily and high-precision localization data even in closed-canopy forest habitats, which was not possible for this species due to the characteristics of solar PTT satellite transmitters.

Despite the small number of Woodcocks tagged, birds of both sexes and age classes were represented in the sample. Although the data obtained by tracking six individuals are not sufficient to draw general conclusions about the migratory behaviour of the species or even the population sampled, we present here novel information deriving from the individual tracking of Woodcocks captured in the Carpathian Basin.

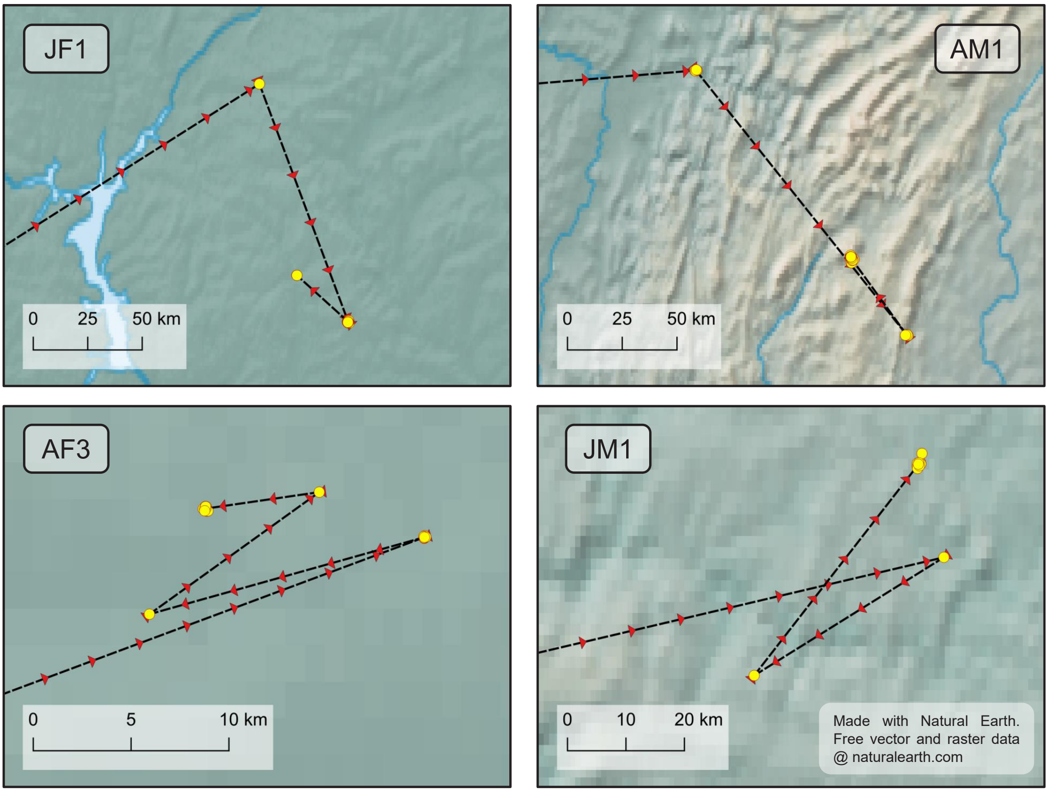

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Fig. 4. Examples of the patterns of arrival at the breeding sites by the tracked Woodcocks.

4.1. Local movements at the location of tagging

Overall, the Woodcocks spent significantly longer time at the tagging site than at the stopover sites on their way to their breeding sites. Moreover, the average time spent in the Carpathian Basin (23 days) was longer than the average periods (4–5 days) registered at stopover sites in other studies (Arizaga *et al.* 2015, Crespo *et al.* 2016, Hoodless *et al.* 2020). This may be explained by the optimization for favourable weather conditions (Le Rest *et al.* 2019, Tedeschi *et al.* 2020), or for the time needed for the sufficient degree of fat accumulation (Lindström & Piersma 1993, Bairlein 2002) in order to start the migration. Nevertheless, it may also be due to that the Carpathian basin is a border zone in terms of the range of the species, where Woodcock might occur also as a wintering and/or breeding species in favourable (*e.g.*, mild and rainy) weather conditions. Most likely, the tracked birds may have been such overwintering individuals. It is possible, that a slight delay in the departure occurred due to the tagging (Lameris *et al.* 2018), but it is not likely either, that staying for so long would be caused by such an effect.

The Woodcocks we tracked used closed-canopy, forested or bushy areas in all cases during daytime. Based on our data, apart from natural forested habitats, abandoned orchards can also be important diurnal resting locations for Woodcocks. We hypothesize that food-rich, untilled soils of orchards may provide appropriate food supply (earthworms) in this period.

The habitat change between day and night is a specific behaviour of the Woodcock. During those flights, individuals were recorded to cover only 0.25–1.5 km distances (Wilson 1982, Duriez *et al.* 2005b, Hoodless & Hirons 2007, Powell 2009). We observed the same behaviour of the tagged individuals in our study site, daytime resting locations fell on average only a few hundred meters from the nocturnal feeding areas. Woodcocks visited open, loose-soil and low-vegetation agricultural areas to feed at night, and often returned to the exact location of their capture.

4.2. Timing and direction of the migration

The large individual variance in departure dates of spring migration is not only the characteristic of Woodcocks (Verhoeven *et al.* 2019). On average, our tagged birds started their migration a few days later than for those marked in northern Spain (Arizaga *et al.* 2015), but departure dates coincided nearly with those marked in the United Kingdom (Hoodless *et al.* 2020) and in Italy (Tedeschi *et al.* 2020).

The large scale weather systems that influence the migration (Le Rest *et al.* 2019) originate mainly from the Mediterranean region, and thus their effect on the birds can be very similar in the case of birds wintering in Italy and Hungary. The Woodcocks, which can fly hundreds of kilometres in a night in favourable wind conditions (Hoodless & Heward 2019), also travel from Italy to the NE, some of them across the Carpathian Basin (Tedeschi *et al.* 2020), thus, the birds of the two areas can start their migration to the breeding grounds in the same period, with a difference of only a few days.

Although cases of backwards movement by Woodcocks during spring migration have previously been documented (Hoodless *et al.* 2020), the ~200 km backward migration of JF1 was still surprising. The bird returned and spent another 13 days at the original place of tagging, meanwhile other Woodcocks, including three other tagged birds, already departed. However, JF1 reached its breeding site by flying more than 2,000 km at a particularly effective movement (423 km/day) and arrived there relatively early (9th April). Such a backward movement along the migratory route is also surprising because, in the case of Woodcock, the Carpathians are not considered to be a barrier such as for example large water bodies (Bruderer & Liechti 1998). During that period, a cold air mass associated with strong northern surface winds reached the Carpathian Basin, creating conditions that prevented effective flying to the breeding areas (Le Rest *et al.* 2019) and bringing in cold weather for days, which might induce such behaviour (Richardson 1978). Additionally, arriving at the first stopover site, the bird may have faced unfavourable weather conditions and poor feeding opportunities, from which it decided to return to a well-known and safe place (Péron *et al.* 2011).

4.3. Migration distance, speed, and duration

The routes of the birds and the phenology of their migration also showed large individual differences. Some of the birds reached their European breeding grounds with a single major displacement, in a distance of 677–2,014 km in Ukraine and Russia, respectively. The birds of the other group migrated 2,800–5,000 km east of the Ural Mountains and included several stopovers along their routes. Previous ringing data from Hungary proved connection only with European breeding sites (Faragó 2009, Schally 2019), but our tracking data showed that Woodcocks migrating through Hungary may reach Siberia. Similar results have been published for other populations (Arizaga *et al.* 2015, Le Rest *et al.* 2019, Tedeschi *et al.* 2020), but since the Carpathian Basin lies closer to the main European breeding areas, it may be one of the wintering grounds from which the birds can reach those sites with a single night flight. Although the distances of migrations varied, all of them were within a relatively narrow latitudinal band (Fig. 2). Not only the broadly parallel migration routes were in accordance with the result of previous tracking studies, but also the breeding sites fell into their range (Arizaga *et al.* 2015, Hoodless & Heward 2019, Tedeschi *et al.* 2020). Especially the routes of Woodcocks tagged in Italy overlapped with the track of our birds.

The migration distance and the time spent on migration were closely related. The greatest distance between consecutive stopovers was measured for the farthest migrating individuals (3,034 and 3,095 km), but the average daily migratory rate of medium distance migrating individuals was the highest (432 and 487 km/day). The average distances measured between the localizations of two consecutive days and the maximum flight distances correspond to the parameters estimated for Woodcocks wintering in the United Kingdom (Hoodless *et al.* 2020). If flight speeds are calculated only for the night hours (~10 h), then they varied in the range of 1–80 km/h. The large variance is most likely caused by the combined effect of individual condition (nutrition, motivation) and weather factors (wind direction and speed). The values nevertheless correspond to those published in the international literature (Sánchez-García *et al.* 2018). Such performances are not considered extraordinary in similar species, *e.g.*, Great Snipes (*Gallinago media*) were able to cover distances of 4,300–6,800 km in 48–96 h during autumn trans-Sahara migration (Klaassen *et al.* 2011), or the Bar-tailed Godwit (*Limosa lapponica*) capable of crossing the whole Pacific Ocean (Gill *et al.* 2009). However, the average migration rate of all the birds we tracked exceeded the values published for the wintering populations in Spain and in Italy (Arizaga *et al.* 2015, Tedeschi *et al.* 2020). The Woodcocks – regardless of the locations of their wintering sites – seem to have incorporated hundreds of kilometres of “leaps” between their multi-day stopovers into the migration strategy.

4.4. Migration dynamics and the stopovers

Although there was a large variance in the phenology of the migration, individuals that started earlier and migrated farther were caught up and even temporarily overtaken by individuals that started later and eventually migrated closer, however the sample size didn’t enable the examination of the theory of leap-frog migration in Woodcock (Ferrand & Gossmann 2009a).

Following the last larger-scale, clearly migration-related displacement (>50 km), smaller-scale (2–40 km) but clearly distinctive habitat switches were observed in all individuals upon their arrival at their breeding sites. This phenomenon occurred in both males and females, and the displacements occurred mostly in a remarkably different direction from the main migration direction. That may have indicated the fine-scale breeding habitat choice: feeding, hiding, or even reproductive behaviour, but it is unlikely that these movements were forced by weather conditions that made the continuation of the migratory flight permanently impossible.

According to the calculation based on their registered bodyweight (Boos *et al.* 2005, Sánchez-García *et al.* 2018), the Woodcocks we tagged were predicted to be able to cover a distance of about 400–1,100 km in one flight without risking their survival. However, to use fat reserves and migrate quickly to be the first to arrive at the breeding ground is not necessarily the best strategy in stochastic environmental conditions in spring. The latest departing bird was a female (AF3 on 13th April) that reached its breeding site only nine days later (on 21st May) than the male that left the tagging site at the earliest (JM1 on 21st March). Both birds migrated more than 4,500 km, but it took the male more than twice as long as the female, thus their migration pattern differed markedly. These two extreme examples of possible strategies may indicate that, while in the case of females, the body condition on arrival and optimization to have reserves for the egg-laying may be important, while selection in the spring reproduction period may force males to optimize their time of arrival for the presence of conspecifics.

The Woodcock is a polygynous species, and it is possible that mate choice or even mating occurs during the spring migration. As roding males are known not maintaining exclusive territories (Hirons 1980), migrating males can also take part in mating for a few days by passing through potential breeding areas where females are present. Conspecifics acting as potential pairs or rivals may help to optimize migration and thus can play an important role in shaping the spring migration pattern of Woodcocks populations.

4.5. Location of the breeding sites

We found large distances between the breeding areas of the birds, which is in accordance with the high genetic diversity found in samples previously collected in the same region in spring (Schally *et al.* 2018). The migratory connectivity of Woodcock populations can be regarded as low, as the individuals tagged in the same areas migrated to very distant points of the known breeding range (Arizaga *et al.* 2015, Le Rest *et al.* 2019, Hoodless *et al.* 2020, Tedeschi *et al.* 2020).

The migration distance and phenology of birds tagged in the Carpathian Basin showed high similarity to Woodcocks tagged previously in Southern and Western European wintering grounds, except for the longer stopover time spent by them in the Central European region before their departure. Additionally, our daily GPS data revealed the small-scale local movements of birds within the stopover sites, and also refined the flight speed calculation of Woodcocks during spring migration. Due to the cryptic behaviour of the Eurasian Woodcock, the lack of data-based knowledge hinders the conservation of the species. Further individual tracking – combined with other monitoring methods – might refine the extent of the breeding and wintering range of the species and the timing of the migration. These parameters are crucial to evaluate the current management policy in the range states of the species. We are planning to continue our study to increase the sample size, which will allow us to better understand the migration of the species and thus draw up more detailed conservation implications in the future. Besides that, the latest fine-scale big data collection methodology, which is based on Wi-Fi technology, is also ready to be used (Wild *et al.* 2022), and it might further expand the possibilities of studying the behavioural background of Woodcock migration in the future.

Vårflyttningens fenologi hos centraleuropeiska Morkullor utrustade med GPS-Argos sändare

Morkullan (*Scolopax rusticola*) har en speciell roll i det kulturella arvet i manga Europeiska länder. Under det senaste årtiondet har ringmärkning kunnat identifiera morkullans huvudsakliga migrationsrutter hos några välstuderade Morkullepopulationer i Väst- och Sydeuropa. Den revolutionerande satllitspårningsteknologin har möjliggjort studier av dessa populationers migration på individnivå. Vi presenterar här migrationsdata från postjuvenila Morkullor som fångats och försetts med GPS-Argos sändare i Centraleuropa år 2020. Morkullorna migrerade från fångstplatsen till Ukraina, Europeiska delen av Ryssland och centrala Sibirien med en medeldistans på 2,678 km (mellan 677–5,002 km). Migrationens varaktighet varierade från 1–52 dagar med en medelhastighet på 382 km/dag. Den maximala distansen på en dag var 866 km. Antalet mellanlandningar under migrationen varierade mellan 0-5 stycken och de stannade i medeltal 5.6 dagar under mellanlandningarna. Under mellanlandningarna förflyttade de sig mellan 11–3,329 m. Den Pannoniska bassängen vid Karpaterna kan vara viktigare för övervintrande Morkullor än vad man tidigare trott, eftersom de sändarförsedda morkullorna stannade betydligt längre där än på andra mellanlandningsplatser. De identifierade häckningsområdena hos de sändarförsedda fåglarna representerade en stor del av utbredningen, i enlighet med tidigare studier baserade på DNA analyser.

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References

Anderson, G.Q.A. & Green, R.E. 2009: The value of ringing for bird conservation. — Ringing & Migration 24(3): 205–212. https://doi.org/10.1080/03078698.2009.9674393

Arizaga, J., Crespo, A., Telletxea, I., Ibáñez, R., Díez, F., Tobar, J.F., Minondo, M., Ibarrola, Z., Fuente, J.J. & Pérez, J.A. 2015: Solar/Argos PTTs contradict ring-recovery analyses: Woodcocks wintering in Spain are found to breed further east than previously stated. — Journal of Ornithology 156(2): 515–523. https://doi.org/10.1007/s10336-014-1152-7

Bairlein, F. 2002: How to get fat: Nutritional mechanisms of seasonal fat accumulation in migratory songbirds. — Naturwissenschaften 89(1): 1–10. https://doi.org/10.1007/s00114-001-0279-6

Boos, M., Boidot, J.-P. & Robin, J.-P. 2005: Body Condition in the Eurasian Woodcock Wintering in the West of France: Practical Study for Wildlife Management during Cold Spells. — Wildlife Biology in Practice 1(1): 15–23. https://doi.org/10.2461/wbp.2005.1.3

Bruderer, B. & Liechti, F. 1998: Flight Behaviour of Nocturnally Migrating Birds in Coastal Areas: Crossing or Coasting. — Journal of Avian Biology 29(4): 499–507. https://doi.org/10.2307/3677169

Crespo, A., Rodrigues, M., Telletxea, I., Ibáñez, R., Díez, F., Tobar, J.F. & Arizaga, J. 2016: No Habitat Selection during Spring Migration at a Meso-Scale Range across Mosaic Landscapes: A Case Study with the Woodcock (*Scolopax rusticola*). — PLOS ONE 11(3): e0149790. https://doi.org/10.1371/journal.pone.0149790

Duriez, O., Ferrand, Y., Binet, F., Corda, E., Gossmann, F. & Fritz, H. 2005a: Habitat selection of the Eurasian woodcock in winter in relation to earthworms availability. — Biological Conservation 122: 479–490. https://doi.org/10.1016/j.biocon.2004.08.011

Duriez, O., Fritz, H., Said, S. & Ferrand, Y. 2005b: Wintering behaviour and spatial ecology of Eurasian Woodcock *Scolopax rusticola* in western France. — Ibis 147: 519–532. https://doi.org/10.1111/j.1474-919x.2005.00423.x

Faragó, S. 2009: Erdei szalonka. — In Magyar Madárvonulási Atlasz (ed. Csörgő, T., Karcza, Zs., Halmos, G., Magyar, G., Gyurácz, J., Szép, T., Bankovics, A., Schmidt, A. & Schmidt, E.): 537–538. Kossuth Kiadó, Budapest. (In Hungarian with English summary)

Ferrand, Y. & Gossmann, F. 2009a: La bécasse des bois. — Effet de lisiére, Saint-Lucien. (In French)

Ferrand, Y. & Gossmann, F. 2009b: Ageing and sexing series 5: Ageing and sexing the Eurasian Woodcock *Scolopax rusticola*. — Wader Study Group Bulletin 116: 75–79.

Gill, R.E., Tibbitts, T.L., Douglas, D.C., Handel, C.M., Mulcahy, D.M., Gottschalck, J.C., Warnock, N., McCaffery, B.J., Battley, P.F. & Piersma, T. 2009: Extreme endurance flights by landbirds crossing the Pacific Ocean: Ecological corridor rather than barrier? — Proceedings of the Royal Society B: Biological Sciences 276(1656): 447–457. https://doi.org/10.1098/rspb.2008.1142

Gossmann, F., Ferrand, Y., Loidon, Y. & Sardet, G. 1988: Méthodes et Résultats de Baguages des Bécasses des Bois (*Scolopax rusticola*) en Bretagne. — In Third European Woodcock and Snipe Workshop (ed. Havet, P. & Hirons, G.J.M.): 34–41. Paris, France. ONC, IWRB, CIC.

Hirons, G. 1980: The Significance of Roding by Woodcock *Scolopax Rusticola*: An Alternative Explanation Based on Observations of Marked Birds. — Ibis 122(3): 350–354. https://doi.org/10.1111/j.1474-919X.1980.tb00888.x

Hofman, M.P.G., Hayward, M.W., Heim, M., M., Marchand, P., Rolandsen, C.M., Mattisson, J., Urbano, F., Heurich, M., Mysterud, A., Melzheimer, J., Morellet, N., Voigt, U., Allen, B.L., Gehr, B., Rouco, C., Ullmann, W., Holand, Ø., Jørgensen, N.H., Steinheim, G., Cagnacci, F., Kroeschel, M., Kaczensky, P., Buuveibaatar, B., Payne, J.C., Palmegiani, I., Jerina, K., Kjellander, P., Johansson, Ö., LaPoint, S., Bayrakcismith, R., Linnell, J.D.C., Zaccaroni, M., Jorge, M.L.S., Oshima, J.E.F., Songhurst, A., Fischer, C., McBride Jr, R.T., Thompson, J.J., Streif, S., Sandfort, R., Bonenfant, C., Drouilly, M., Klapproth, M., Zinner, D., Yarnell, R., Stronza, A., Wilmott, L., Meisingset, E., Thaker, M., Vanak, A.T., Nicoloso, S., Graeber, R., Said, S., Boudreau, M.R., Devlin, A., Hoogesteijn, R., May-Junior, J.A., Nifong, J.C., Odden, J., Quigley, H.B., Tortato, F., Parker, D.M., Caso, A., Perrine, J., Tellaeche, C., Zieba, F., Zwijacz-Kozica, T., Appel, C.L., Axsom, I., Bean, W.T., Cristescu, B., Périquet, S., Teichman, K.J., Karpanty, S., Licoppe, A., Menges, V., Black, K., Scheppers, T.L., Schai-Braun, S.C., Azevedo, F.C., Lemos, F.G., Payne, A., Swanepoel, L.H., Weckworth, B.V., Berger, A., Bertassoni, A., McCulloch, G., Šustr, P., Athreya, V., Bockmuhl, D., Casaer, J., Ekori, A., Melovski, D., Richard-Hansen, C., Vyver, D. van de, Reyna-Hurtado, R., Robardet, E., Selva, N., Sergiel, A., Farhadinia, M.S., Sunde, P., Portas, R., Ambarli, H., Berzins, R., Kappeler, P.M., Mann, G.K., Pyritz, L., Bissett, C., Grant, T., Steinmetz, R., Swedell, L., Welch, R.J., Armenteras, D., Bidder, O.R., González, T.M., Rosenblatt, A., Kachel, S & Balkenhol, N. 2019: Right on track? Performance of satellite telemetry in terrestrial wildlife research. — PLOS ONE 14(5): e0216223. https://doi.org/10.1371/journal.pone.0216223

Hoodless, A.N. & Hirons, G.J.M. 2007: Habitat selection and foraging behaviour of breeding Eurasian Woodcock *Scolopax rusticola*: A comparison between contrasting landscapes. — Ibis 149(Suppl. 2): 234–249. https://doi.org/10.1111/j.1474-919X.2007.00725.x

Hoodless, A.N. & Heward, C.J. 2019: Migration Timing, Routes, and Connectivity of Eurasian Woodcock Wintering in Britain and Ireland. — Proceedings of the Eleventh American Woodcock Symposium: 136–145. https://doi.org/10.24926/AWS.0120

Hoodless, A.N., Heward, C. & Williams, O. 2020: Migration and movements of Woodcocks wintering in Britain and Ireland. — British Birds 113: 256–278.

Klaassen, R.H.G., Alerstam, T., Carlsson, P., Fox, J.W. & Lindström, Å. 2011: Great flights by great snipes: Long and fast non-stop migration over benign habitats. — Biology Letters 7(6): 833–835. https://doi.org/10.1098/rsbl.2011.0343

Kranstauber, B., Cameron, A., Weinzerl, R., Fountain, T., Tilak, S., Wikelski, M. & Kays, R. 2011: The Movebank data model for animal tracking. — Environmental Modelling & Software 26(6): 834–835. https://doi.org/10.1016/j.envsoft.2010.12.005

Lameris, T.K., Müskens, G.J.D.M., Kölzsch, A., Dokter, A.M., Van der Jeugd, H.P. & Nolet, B.A. 2018: Effects of harness-attached tracking devices on survival, migration, and reproduction in three species of migratory waterfowl. — Animal Biotelemetry 6: 7. https://doi.org/10.1186/s40317-018-0153-3

Le Rest, K., Hoodless, A.N., Heward, C., Cazenave, J.-L. & Ferrand, Y. 2019: Effect of weather conditions on the spring migration of Eurasian Woodcock and consequences for breeding. — Ibis 161(3): 559–572. https://doi.org/10.1111/ibi.12657

Lindström, Å. & Piersma, T. 1993: Mass changes in migrating birds: The evidence for fat and protein storage re-examined. — Ibis 135(1): 70–78. https://doi.org/10.1111/j.1474-919X.1993.tb02811.x

Pennycuick, C.J., Fast, P.L.F., Ballerstädt, N. & Rattenborg, N. 2012: The effect of an external transmitter on the drag coefficient of a bird's body, and hence on migration range, and energy reserves after migration. — Journal of Ornithology 153(3): 633–644. https://doi.org/10.1007/s10336-011-0781-3

Péron, G., Ferrand, Y., Gossmann, F., Bastat, C., Guénézan, M. & Gimenez, O. 2011: Escape migration decisions in Eurasian Woodcocks: Insights from survival analyses using large-scale recovery data. — Behavioral Ecology and Sociobiology 65(10): 1949–1955. https://doi.org/10.1007/s00265-011-1204-4

Powell, A. 2009: Towards an understanding of the origins and ecology of Woodcock wintering in Britain and Ireland. — WI/IUCN-WSSG Newsletter 35: 26–30.

Rappole, J.H. & Tipton, A.R. 1991: New Harness Design for Attachment of Radio Transmitters to Small Passerines. — Journal of Field Ornithology 62(3): 335–337.

Richardson, W.J. 1978: Timing and Amount of Bird Migration in Relation to Weather: A Review. — Oikos 30(2): 224–272. https://doi.org/10.2307/3543482

Robinson, R.A., Grantham, M.J. & Clark, J.A. 2009: Declining rates of ring recovery in British birds. — Ringing & Migration 24(4): 266–272. https://doi.org/10.1080/03078698.2009.9674401

Sánchez-García, C., Williams, O. & Hoodless, A. 2018: Regulation of body reserves in a hunted wader: Implications for cold-weather shooting restrictions. — Journal of Applied Ecology 55(5): 2274–2284. https://doi.org/10.1111/1365-2664.13128

Schally, G. 2019: Assessment of the breeding and wintering sites of Eurasian Woodcock (*Scolopax rusticola*) occurring in Hungary based on ringing recovery data. — Ornis Hungarica 27(1): 110–116. https://doi.org/10.2478/orhu-2019-0007

Schally, G., Frank, K., Heltai, B., Fehér, P., Farkas, Á., Szemethy, L. & Stéger, V. 2018: High genetic diversity and weak population structuring in the Eurasian Woodcock in Hungary during spring. — Ornis Fennica, 95(2): 61–69.

Sørensen, I.H. 2020: Eurasian Woodcock. — In European Breeding Bird Atlas 2: Distribution, Abundance and Change (ed. Keller, V., Herrando, S., Voříšek, P., Franch, M., Kipson, M., Milanesi, P., Martí, D., Anton, M., Klvaňová, A., Kalyakin, M.V., Bauer, H.-G., Foppen, R.P.B.): 334–335. Lynx Edicions, Barcelona.

Szemethy, L., Schally, G., Bleier, N., Katona, K., Lehoczki, R., Nagypál, J. & Csányi, S. 2014: Results of Hungarian Woodcock Monitoring. — Review on Agriculture and Rural Development 3: 12–19.

Tedeschi, A., Sorrenti, M., Bottazzo, M., Spagnesi, M., Telletxea, I., Ibàñez, R., Tormen, N., De Pascalis, F., Guidolin, L. & Rubolini, D. 2020: Interindividual variation and consistency of migratory behavior in the Eurasian woodcock. — Current Zoology 66: 155–163. https://doi.org/10.1093/cz/zoz038

Verhoeven, M.A., Loonstra, A.H.J., Senner, N.R., McBride, A.D., Both, C. & Piersma, T. 2019: Variation From an Unknown Source: Large Inter-individual Differences in Migrating Black-Tailed Godwits. — Frontiers in Ecology and Evolution 7(31): 1–9. https://doi.org/10.3389/fevo.2019.00031

Wild, T.A., Wikelski, M., Tyndel, S., Alarcón-Nieto, G., Klump, B.C., Aplin, L.M., Meboldt, M., Williams, H.J. 2022: Internet on animals: Wi-Fi-enabled devices provide a solution for big data transmission in biologging. — Methods in Ecology and Evolution, 00: 1–16. https://doi.org/10.1111/2041-210X.13798

Wilson, H.J. 1982: Wintering site fidelity of Woodcock *Scolopax rusticola* in Ireland. — In XIVth International Congress of Game Biologists (ed. O'Gorman, F. & Rochford, J.): 219–231. Dublin, Ireland.

Ornis Fennica 99: 117–131. 2022

Age and sex ratios in the declining West Siberian/ North European population of Long-tailed Duck wintering in the Baltic Sea: Implications for conservation

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The West Siberian/North European population of Long-tailed Duck (*Clangula hyemalis*), which breeds in the Russian Arctic and northern Fennoscandia and winters in the Baltic Sea, has declined rapidly since the 1990s. To identify the causes of the decline and initiate effective conservation measures information on basic demographic parameters is needed. A photo survey method was used to estimate female age ratios and the proportion of males among adults in wintering Long-tailed Ducks at coastal and off-shore areas in the Baltic Sea. Female age ratios were defined as the number of first winter males, assumed equal to the number of first winter females, per adult female. Several thousand individuals were sampled each winter from 2008 to 2021. Female age ratios fluctuated between years and were consistently lower in the southern than in the central Baltic Sea. The proportion of males among wintering adults birds was male-biased, more so in the southern Baltic Sea than in other regions. A population model was used to analyse if low female age ratios between 2008 and 2021 has constrained population growth. Given that the estimated weighted mean female age ratio of 0.153 was representative at the population scale, an extremely high adult female mean annual survival rate of 0.872 would have been needed to maintain a stable population. Considering known sources of anthropogenic mortality in the Baltic Sea, and instead assuming a more realistic survival rate of *ca.* 0.80, a population decline of *ca.* 7.7% per year should have occurred during the study period.

1. Introduction

The Long-tailed Duck (*Clangula hyemalis*) is a sea duck species which breeds in Arctic tundra habitats and winters at sub-Arctic and temperate coastlines and at off-shore banks. Four larger populations are recognised: the West Siberian/ North European, the Iceland/Greenland, the North American, and the East Asian populations. At least the two largest populations, the West Siberian/North European and the North American populations have declined significantly in numbers since the 1990s and 1980s, respectively (Durinck *et al.* 1994, Skov *et al.*

2011, Bowman *et al.* 2015). Long-tailed Ducks belonging to the West Siberian/North European population breed in the Russian Arctic and in northern Fennoscandia and the vast majority of the birds winter in the Baltic Sea (Loshchagina *et al.* 2019, Karwinkel *et al.* 2020, Quillfeldt *et al.* 2021). Two Baltic wide surveys have shown that the number of wintering Long-tailed Ducks has decreased from approximately 4.3 million birds in 1992–1993 to approximately 1.5 million in 2007–2009 (Durinck *et al.* 1994, Skov *et al.* 2011). Winter surveys performed after 2009, which covered important parts of the Baltic Sea, have indicated a further decline (Nilsson 2012, 2016). Because of the rapid decline the species is globally classified as vulnerable on the IUCN Red List (Wetlands International 2021), and the West Siberian/North European population is classified as endangered on the HELCOM red list (HELCOM 2021). An International Single Species Action Plan for the conservation of the Long-tailed Duck has also been adopted by the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA) with the objective to significantly reduce direct anthropogenic mortality and understand the wider drivers of the population decline (Hearn *et al.* 2015).

To better understand the population dynamics and the causes of the decline more information on basic demographic parameters, *i.e.*, juvenile production, survival rates and sex ratios, is needed. Such data are difficult to obtain in the Arctic because Long-tailed Ducks nest at low densities over vast often inaccessible tundra regions. Previous field studies of the species breeding biology in the Arctic, and population modelling, have shown that the reproductive success varies greatly between years and that population growth rates are highly sensitive to changes in adult female survival rates and to duckling survival (Alison 1975, Pehrsson 1986, Schamber *et al.* 2009, Flint 2015, Koneff *et al.* 2017). However, the demographic studies hitherto performed, including analyses of survival rates, return rates of marked individuals to nesting sites, nest and hatching success and duckling survival have, by necessity, been local in scale and may not be representative at the population level.

A complimentary way to obtain population wide information on basic demographic parameters is to analyse age and sex ratios at wintering sites where large number of Long-tailed Ducks from several breeding areas are aggregated. One method is to determine the sex and age of birds shot by hunters (Hario *et al.* 2009, Koneff *et al.* 2017, Aarhus University 2021, Rintala *et al.* 2022). Other samples, for example of by-caught birds in fishery, or of oil damaged birds, where dead bodies or wings can be examined, have also provided information (Hearn *et al.* 2015). In other species of sea ducks, with delayed plumage maturation, direct field observations of wintering birds have also been used to determine age and sex ratios (Smith *et al.* 2001, Rodway *et al.* 2003, 2015, Iverson *et al.* 2004, Robertson 2008).

Also the methods used in winter to estimate demographic parameters have constraints and may be more or less biased. For example, analyses of hunting bags might be significantly biased because juvenile birds may be more vulnerable to hunting than adults (Koneff *et al.* 2017). The willingness or opportunities to shoot males and females, respectively, may also differ. Samples of by-caught birds in fish nets might be biased because less experienced juveniles might be caught more often than adults (Stempniewicz 1994). In addition, the age and sex ratios obtained from analyses of collected dead birds or from direct observations in the field at specific sites during the non-breeding season, might not be representative for the whole population unless age and sex specific migration and spatial segregation patterns are corrected for.

The aim of this study was to use a novel photo survey method to estimate age and sex ratios of wintering Long-tailed Ducks in the Baltic Sea. By the photo survey method very large number of birds belonging to the West Siberian/North European population of Long-tailed Duck could be sampled at several different coastal and off-shore sea areas each winter season (Larsson 2022). A specific aim was to analyse the broad scale winter distribution of 6–10 months old juveniles, henceforth called first winter birds, and analyse if a too low production of first winter birds during the 14-year study period between 2008 and 2021 has constrained population growth and the possibility to obtain a stable Long-tailed Duck population.

2. Material and methods

2.1. Photo surveys

Flocks of wintering Long-tailed Ducks were surveyed from various boats, fishing and research vessels at offshore and coastal wintering and spring stopover sites in the Baltic Sea between 2008 and 2021 (Fig. 1). Surveys in the central and southern Baltic Proper, *i.e.*, at the main wintering sites, were performed between January and mid-April. Surveys more north in the Åland archipelago and in the northwestern Gulf of Finland, where Long-tailed Ducks aggregate in spring before they leave the Baltic Sea and migrate to their Arctic breeding grounds, were performed between mid-April and beginning of May. Long-tailed Ducks usually return to the Baltic Sea from their Arctic breeding grounds in October. Various surveys indicate that adult males, on average, in autumn arrive at the Gulf of Finland and northern Baltic Proper slightly earlier than females and juveniles (Lehikoinen *et al.* 2006). To avoid possible biases related to sex segregated migration patterns in autumn only results from photo surveys performed from January and onwards are included in the further analyses.

When wintering flocks were detected swimming on the water, the boat or the vessel approached the flock, and when the birds flew off, usually against the wind, photos were taken from the side. Photos were also taken on flying birds which were passing nearby when the boat or vessel was engaged in line transect surveys. The flocks that were approached varied in size from a few individuals to several hundred, sometimes several thousand birds. During the photo surveys, the aim was to take photos on specific flocks or individuals only once. When large flocks flew off the water or were passing the boat, photos were taken sequentially on parts of the flock to reduce the risk of taking photos

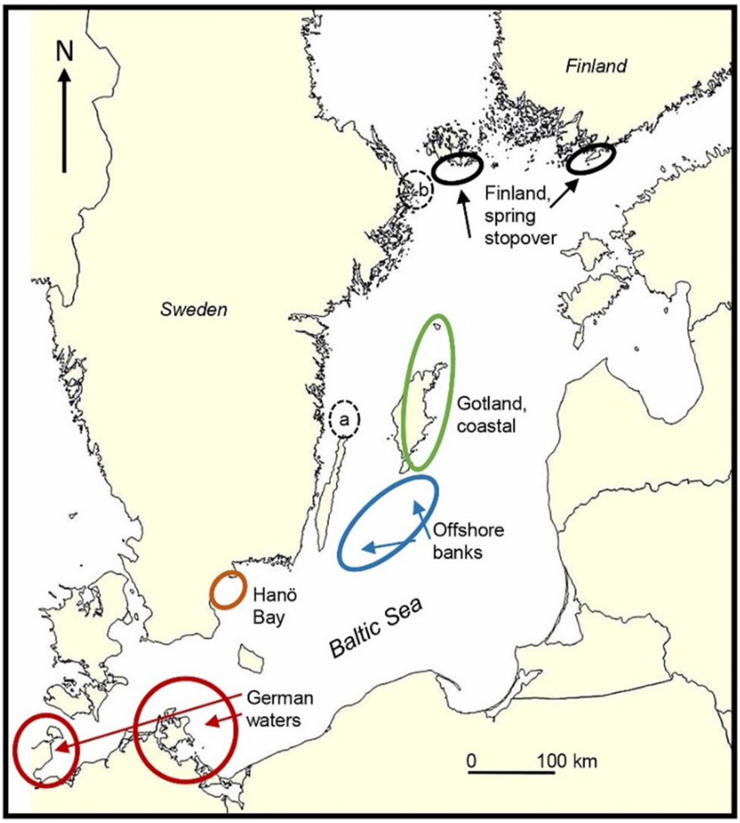

Fig 1. Map showing the five regions where photo surveys of wintering Long-tailed Ducks (*Clangula hyemalis*) were performed in the Baltic Sea between 2008 and 2021. Red, orange, blue and green circles show where photo surveys where performed in winter (January to mid-April). Black circles show where surveys were performed at spring stopover sites (mid-April to beginning of May). Dotted circles a, and b show where additional photo surveys were performed in winter 2017.

of the same birds more than once. Photos were taken with a high quality Nikon digital camera equipped with Nikon telephoto lenses between 200 and 500 mm. The photos, jpg image files, were viewed in Adobe Photoshop and analysed manually. All photos were taken and analysed by the author.

2.2. Plumage characteristics visible on photos of flying birds

In winter, between January and beginning of April, adult males have a complete black breast, well developed white scapulars, two fully elongated central tail feathers, a characteristic head feather pattern consisting of a large olive-grey patch from the bill base to around the eye and a large black oval patch on the lower cheeks. They also have a pink band on the bill. First winter males do not have a complete black breast and in most cases no elongated central tail feathers. Rarely, first winter males may have short central tail feathers, *i.e.*, visible but not fully elongated as in adult males. First winter males also have a pink band on the bill, although not always as bright as in adult males. The appearance of the white scapulars in first winter males varies from almost invisible to fully developed as in adult males. In first winter males the head patterns varies from female-like to fully adult male-like. Females appear brownish at a distance. Typically the sides of the head are whitish with a darker brownish cheek patch, crown and breast. The bill is dark grey and lack a distal pink band. Females lack elongated central tail feathers and white elongated scapulars. First winter females cannot be reliably distinguished from adult females on photos taken at a distance. Juvenile males can be distinguished from females by the presence of either a pale or pink distal band on the bill, white scapulars, an incomplete black breast band, or the typical male head feather pattern. In April the birds partly moult and the plumage becomes darker. The white scapulars in males are for example replaced by brown scapulars. A full description of plumage characteristics visible on photos of flying birds is presented in Larsson (2022).

2.3. Age and sex ratios

Individuals were classified from photos into three categories, that is, adult males, first winter males, and females, based on the plumage and bill characteristics. It was assumed that the overall sex ratio of first winter birds was equal during the time period when age ratio assessments were performed between January and mid-May. Hence, the sex ratio at hatching and the survival rate from hatching to first winter was assumed to be equal for males and females (Blums & Mednis 1996, Wood *et al.* 2021). By contrast, adult sex ratios were not assumed to be equal because mortality rates in ducks are often higher for adult females than for adult males during the breeding season.

The total numbers of adult males and first winter males observed on photos within a sampled area were counted directly. The total number of first winter females on photos within a sampled area was assumed to be equal to the total number of first winter males. The total number of adult females on photos within a sampled area was estimated as the total number of observed females minus the total number of observed first winter males. The total number of adults on photos was estimated as the sum of the observed total number of adult males and the estimated total number of adult females.

Female age ratios were estimated as the total number of observed first winter males, assumed equal to the number of first winter females, divided by the estimated total number of adult females. Female age ratios express the average number of first winter females, or first winter males, per adult female. Female age ratios are thus measures of the production of first winter birds in the population. The proportion of males among adults was estimated as the total number of adult males divided by the estimated total number of adults (see online only Supplementary Tables S1 and S2 for numerical calculations).

Lehikoinen *et al.* (2008) found in a study of Common Eiders (*Somateria mollissima*) that the sex ratio at hatching did not deviate from equal, but that female ducklings after hatching, but before fledging, had slightly higher mortality than male ducklings. They argued that sex differential mortality among hatchlings could be a cause for an observed male biased sex ratio among first-winter common eiders (~57% males) (Lehikoinen *et al.* 2008). If future studies will show that there is a biased sex ratio also among first winter Long-tailed Ducks the way to calculate female age ratios, as described above, should be adjusted. However, if existing, a slight deviation from unity in the sex ratio among first winter Long-tailed Ducks will not change the overall conclusions in the present study.

2.4. Surveyed regions

In total, 132 photo surveys were conducted between 2008 and 2021. The surveyed sites were grouped into five regions: (1) coastal waters east of the Swedish island of Gotland in the central Baltic Sea, (2) offshore banks in Swedish Exclusive Economic Zone in the central Baltic Sea, *i.e.*, Hoburgs Bank and Northern Midsjö Bank, (3) Hanö Bay, in Swedish waters in southern Baltic Sea, (4) German waters in the southern Baltic Sea at Fehmarn Belt and Pomeranian Bay including Adlerground, and (5) coastal Finnish spring stopover sites in the southern Åland archipelago and in the northwestern part of Gulf of Finland near Hanko (Fig. 1). Two previous Baltic wide surveys, in 1992–1993 and 2007–2009, respectively, and later surveys have shown that the surveyed regions 1 to 4 all are key wintering sites for Long-tailed Ducks in the Baltic Sea (Durinck *et al.* 1994, Skov *et al.* 2015, Nilsson 2016). Photo surveys in coastal waters east of Gotland were conducted between January and April, at offshore banks and at Hanö Bay in March and April and in German waters in the southern Baltic in January and February. In spring, wintering Long-tailed Ducks from the southern and central Baltic Sea move northward, mix and aggregate in the northern Baltic Proper, Åland archipelago, Gulf of Finland and Gulf of Riga before they leave the Baltic Sea for their Arctic breeding grounds. The photo surveys at the coastal Finnish spring stopover sites were therefore performed in the second half of April and beginning of May.

Several photo surveys were usually conducted at different sites and dates within the same region each season. In March 2017, surveys were also conducted at two additional Swedish sites outside the five defined regions, *i.e.*, (a) in coastal waters and offshore banks north of the island of Öland, and (b) in the Stockholm archipelago near Kapellskär in the northern Baltic Proper (Fig. 1).

Between 1,832 and 18,723 birds (mean = 8,857 birds) were photographed and analysed each winter season between 2009 and 2021. A smaller sample, photos of 471 birds, was obtained at spring stopover sites in the Åland archipelago in 2008. In 2020 and 2021, only the coastal waters east of the Swedish island of Gotland could be surveyed because of covid-19 travelling restrictions. The number of analysed photos from each region each year varied between 26 and 615 (mean = 269) (Supplementary Table S1).

The number of analysed photos and analysed birds varied between regions and years due to external factors such as weather conditions and the availability of ships and boats. The number of analysed birds were still very high at each region each year. The 95% confidence intervals of the estimated ratios and proportions of different bird categories were therefore generally low.

2.5. Standard errors of estimates

Since the aim of the study was to obtain broad scale Baltic wide estimates, female age ratios and the proportion of males among adults were estimated for each surveyed region and year from pooled samples. Possible age and sex specific segregation at smaller geographical and temporal scales were not considered. Standard errors and 95% confidence intervals of the estimated female age ratios and proportions of males were obtained by bootstrapping (Efron & Tibshirani 1994, Larsson 2022). The bootstrapping method is suitable to estimate standard errors when normality assumptions might not apply, for example when ratios are analysed. Photos taken in a region in specific years were resampled with replacement to produce one thousand resampled data sets. The number of photos in each resampled data set matched the number of photos in the original data set. The female age ratio and the proportion of males among adults were calculated for each of the resampled data sets to create sampling distributions of the two quantities. Standard errors were then estimated as the standard deviation of the sampling distributions of the female age ratio and the proportion of males among adults, respectively. For comparison, standard errors (SE) of the estimated proportions of males among adults were also calculated according to a general equation below (Eq. 1) applicable to proportions (Fowler *et al.* 1998),

$$\mathrm{SE} = \sqrt{\left(\frac{p(1-p)}{n-1}\right)} \qquad (1)$$

where p is the proportion of adult males, and n is the number of all adults in the sample (Supplementary Table S2).

2.6. Population model

To analyse if the production of first winter birds between 2008 and 2021 has constrained the population growth and the possibility to obtain a stable Long-tailed Duck population a simplified matrix-based population model developed by Robertson (2008) was used. This population model has been specifically developed to allow the fecundity component, *i.e.*, the juvenile/adult ratio, here the female age ratio, to be measured in mid- to late winter. The population model is especially suitable for analyses of fecundity data from long-tailed ducks and other sea ducks with recognizable sub-adult plumages in winter (Robertson 2008).

Survival rates of juveniles or adults have not yet been measured in studies of Long-tailed Ducks belonging to the West Siberian/North European population. Population specific data on survival rates can therefore not be used as input values to the population model. However, Koneff *et al.* (2017) compiled information on annual survival rates of sea ducks, in the absence of harvest, from mark-recapture studies in North America, expert judgements, and allometric relationships with body weight. In their analyses they used a median annual survival rate of 0.81 for adult Long-tailed Ducks and 0.71 for subadults, *i.e.*, for the 2nd year survival rate. The estimated survival rate of Long-tailed Duck based on allometric relationships with body weight was higher (0.86, SD=0.05) than the experts' estimates (Koneff *et al.* 2017). Here, in the further analyses annual survival rates between 0.75 and 0.87 are considered. Survival rates of first winter birds and older birds, *i.e.*, of all birds older than six month, are assumed equal.

To estimate the production of first winter birds needed to maintain a stable population equation (Eq. 2) was used, that is, equation 5 in Robertson (2008),

$$F = (1 - S\lambda^{-1}) \,/\, S^{4/3}\lambda^{-2} \qquad (2)$$

where F in this case, under the assumption that all two-year old and older females have equal reproductive success, is the female age ratio in winter. S is the adult female annual survival rate and λ is the deterministic population growth rate, where $\lambda=1$ indicates a stable population, $\lambda<1$ population decline and $\lambda>1$ population increase.

3. Results

3.1. Female age ratios and distribution of first winter birds

Female age ratios of wintering Long-tailed Ducks, and hence the production of first winter birds, clearly differed between years (Fig. 2). Furthermore, female age ratios differed between surveyed wintering regions, which show that the winter distributions of first winter birds and adults were not identical at the broad scale level (Fig. 2). For example, female age ratios were consistently lower in the German waters in the southern Baltic Sea than in coastal waters east of Gotland and at offshore banks in the central Baltic Sea. Also at Hanö Bay in the southern Baltic Sea the female age ratios were low in the three winters when the region was surveyed. The female age ratios were also generally lower at offshore banks in the central Baltic Sea than at coastal waters east of Gotland in the ten winters when both regions were surveyed (Fig. 2).

Because wintering Long-tailed Ducks from the southern and central Baltic Sea aggregate at Finnish stopover sites in late April and May, the time-series of female age ratios obtained at Finnish stopover sites can be expected to covary with time-series obtained at the more southern wintering sites. Indeed, the annual estimates

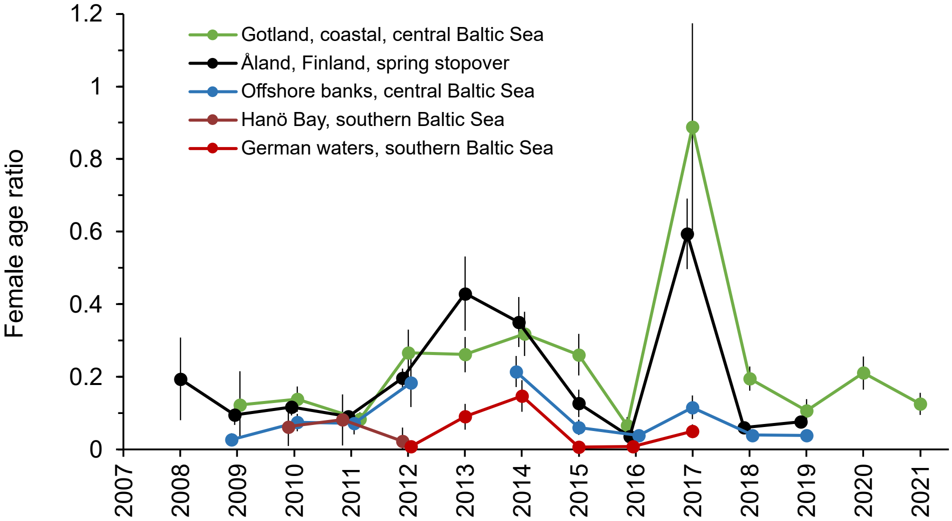

Fig. 2. Female age ratios of Long-tailed Ducks (*Clangula hyemalis*) in winter and spring, estimated as the number of first winter males, assumed equal to the number of first winter females, per adult female, in five different regions in the Baltic Sea between 2008 and 2021. Error bars indicate bootstrapped 95% confidence intervals. Sample sizes are given in Supplementary Tables S1 and S2. Non-overlapping 95% confidence intervals infer significant differences between specific estimates. In years when production of first winter birds was high, the winter distribution of first winter birds was to a large extent oriented towards coastal waters in the central and northern Baltic Proper. First winter birds observed between January and May hatched during the summer preceding the indicated calendar year.

of female age ratios at Finnish spring stopover sites correlated significantly with the estimates obtained at the coastal waters east of Gotland ($r=0.87$, $p<0.01$, $n=11$ years). Correlations between estimates of female age ratios at Finnish waters and offshore banks ($r=0.61$, $0.05<p<0.1$, $n=10$ years) and German waters ($r=0.56$, $p>0.05$, $n=6$ years), respectively, were also positive but not significantly so.

In years when female age ratios were low at the Finnish spring stopover sites, indicating low production of first winter birds, as observed in 2009, 2010, 2011, 2016, 2018 and 2019, the estimated female age ratios were low also in other regions that were surveyed earlier in the same winter (Fig. 2). However, in years when female age ratios were high at Finnish spring stopover sites and at coastal waters east of Gotland, indicating high production of first winter birds, as in 2013, 2014 and 2017, the female age ratios in German waters in southern Baltic Sea, and at offshore banks in the central Baltic proper, were considerably lower. In 2017, female age ratios at two additional coastal sites in the central and northern Baltic Proper were also found to be high (0.53 and 0.27 at sites a and b, respectively) (Fig. 1). Thus, in years when production of first winter birds was high, the winter distribution of first winter birds was to a large extent oriented towards coastal waters in the central and northern Baltic Proper.

3.2. Proportion males among adults

The proportion of males among adults was male biased (Fig. 3 and 4). The male bias was more pronounced in the southern Baltic Sea, that is, in German waters and at Hanö Bay, than in other regions. The proportion of males among adults was also slightly more male biased at offshore banks in the central Baltic Sea than at coastal waters east of Gotland and at Finnish spring stopover sites. Non-overlapping 95% confidence intervals can be used to identify significant differences between specific estimates (Fig. 3). No significant long-term trend of adult sex ratios was observed in any of the five surveyed regions over the study period (all $p>0.10$, linear regressions).

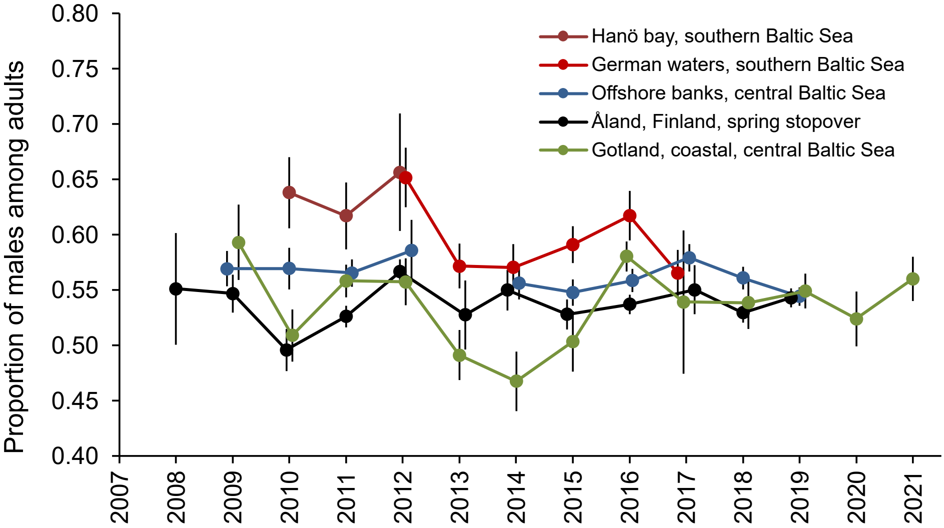

Fig. 3. Adult sex ratios of wintering Long-tailed Ducks (*Clangula hyemalis*), estimated as the total number of adult males divided by the total number of adults, differed between regions in the Baltic Sea. The overall adult sex ratio was male biased. The adult sex ratio in winter was more male biased in the southern parts of the Baltic Sea. Error bars indicate bootstrapped 95% confidence intervals. Non-overlapping 95% confidence intervals infer significant differences between specific estimates. Sample sizes are given in Supplementary Tables S1 and S2.

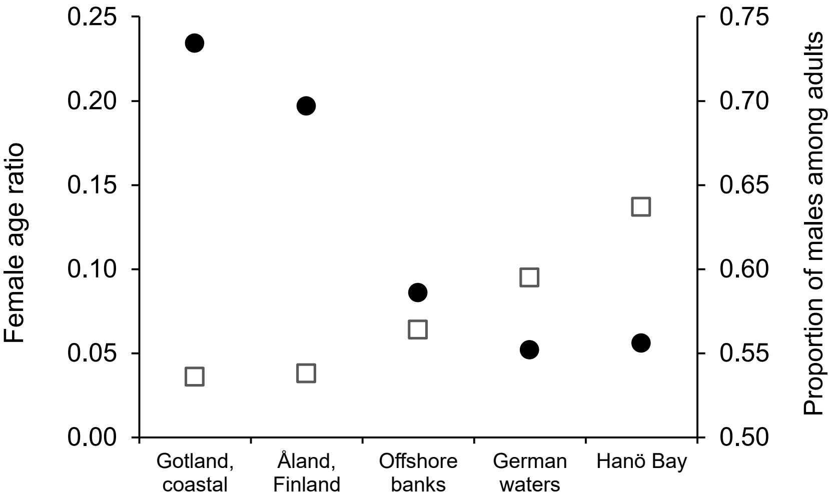

Fig. 4. Mean age and sex ratios of wintering Long-tailed Ducks (*Clangula hyemalis*) in five different regions in the Baltic Sea between 2008 and 2021. Black dots show means of yearly estimates of female age ratios. Open squares show means of yearly estimates of the proportion of males among adults. Sample sizes are given in Supplementary Table S2.

3.3. Population growth model

Relationships between female age ratios observed in winter, survival rates and population growth, based on a simplified deterministic matrix-based population model developed by Robertson (2008), are visualised in Fig. 5 and 6. Two alternative input values to the model for the fecundity component were chosen. As a first alternative, a weighted mean female age ratio, based on the mean female age ratios observed in winter in regions 1 to 4, was used to represent a population wide value (Supplementary Tabel S2). The weights given to the four mean female age ratios were chosen to approximately reflect the number of wintering individuals in different parts of the Baltic Sea, as presented in Skov *et al.* (2011). The mean female age ratio observed in German waters (0.052) was given a weight of 0.24 reflecting the proportion of the population estimated to winter in the southern Baltic Sea, that is, in Danish, German, and Polish waters. Similarly, the mean female age ratio observed at Hoburgs bank and Northern Midsjö banks (0.086) was given a weight of 0.24 reflecting the proportion of the population estimated to winter at these two offshore banks and at the closely situated Southern Midsjö bank. The mean female age ratio observed in coastal waters east of Gotland (0.234) was given a weight of 0.51 reflecting the proportion of the population estimated to winter along the coasts of the central Baltic Sea, that is, along the coasts of Lithuania, Latvia, Estonia, mainland Sweden north of Hanö Bay, and in other residual areas in the Baltic Sea (Skov *et al.* 2011). Lastly, the mean female age ratio observed at Hanö Bay (0.056) was given a weight of 0.01 reflecting the proportion estimated to winter at Hanö Bay and along the southernmost coast of Sweden. Thus, the weighted mean female age ratio used as input to the population model was (0.052*0.24) + (0.086*0.24) + (0.234*0.51) + (0.056*0.01) = 0.153.

As a second alternative, the mean female age ratio observed at Finnish spring stopover sites was used. The rationale for this choice was that previous surveys indicate that only a small

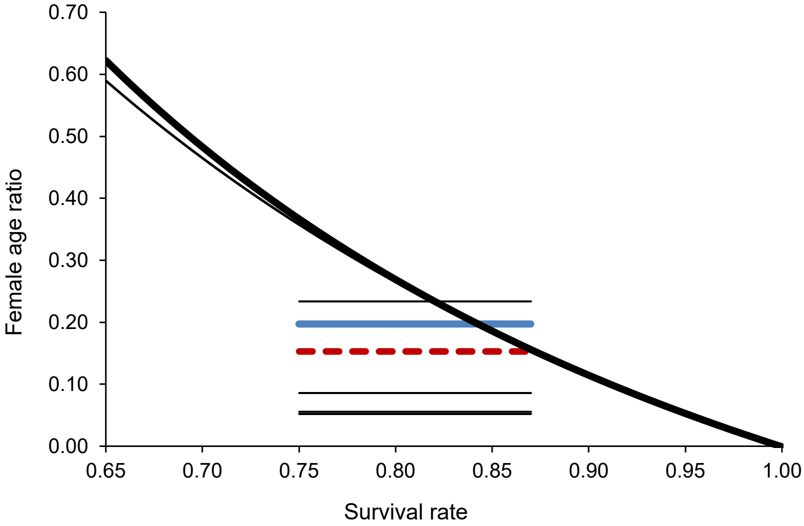

Fig. 5. Relationships between female age ratios observed in winter, adult female annual survival rates and population growth rates based on a deterministic matrix-based population model developed by Robertson (2008). The black thick curve shows the combinations of female age ratios and survival rates that will result in a stable population (λ=1), when age of first reproduction is two years. The black thin curve, only slightly deviating from the thick curve, shows the corresponding combinations when age of first reproduction is three years. Horizontal thin lines show the mean female age ratios observed in winter at four regions in the Baltic Sea. The thick blue horizontal line shows the female age ratio observed at spring stopover sites in Finland. The thick red dotted line shows the weighted mean female age ratio. The width of the horizontal lines represents possible adult female survival rates. Combinations of female age ratios and survival rates below the curved line will result in population declines.

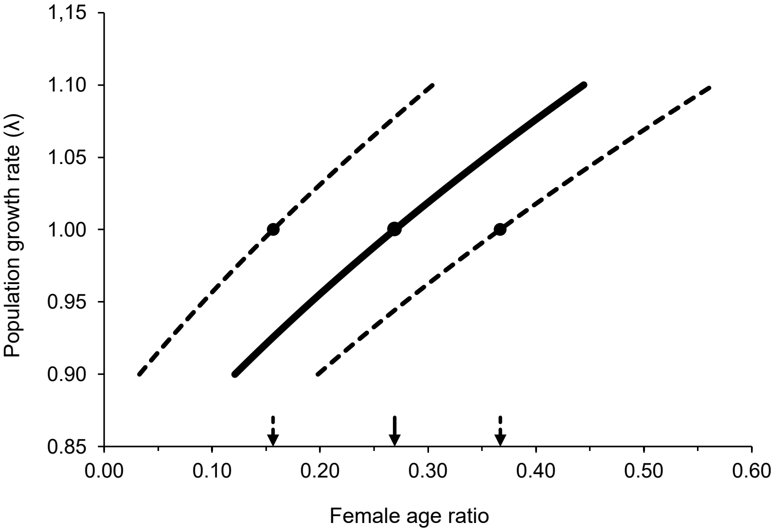

Fig. 6. Relationships between female age ratios observed in winter, adult female annual survival rates and population growth rates based on a deterministic matrix-based population model developed by Robertson (2008). The black thick curve shows the relationship between female age ratios and population growth rates (λ) when adult female annual survival rate is set to 0.80. The dotted curves above and below the solid curve show the corresponding relationships when adult female annual survival rate is set to 0.87 and 0.75, respectively. Arrows indicate the female age ratios, 0.156, 0.269 and 0.367, that are needed to obtain a stable population (λ=1) when survival rates is set 0.87, 0.80 and 0.75, respectively.

number of birds stay at the spring stopover sites in mid-winter, partly because of ice cover, and, hence, that the vast majority of the birds observed in the Finnish waters in late spring must consist of a mixture of birds from several wintering regions further south. The observed yearly female age ratios at the Finnish stopover sites between 2008 and 2019 varied from 0.036 to 0.594 and the overall mean female age ratio was 0.197 (n=12 years) (Fig. 5 and Supplementary Table S2).

Given that the weighted mean female age ratio of 0.153 was representative for the whole wintering population in the Baltic Sea, an extremely high adult female mean survival rate of 0.872 would have been needed to maintain a stable population (Fig. 5 and 6). If one instead assume that a female survival rate of approximately 0.80 is more realistic, and combine that value with the weighted mean female age ratio of 0.153, a population decline of approximately 7.7% per year (λ=0.923) should have occurred during the study period.

If the slightly higher mean female age ratio of 0.197 observed at spring stopover sites in Finland better represent the population wide value, an adult female mean survival rate of 0.843 would have been needed to maintain a stable population. Again, given a more realistic female survival rate of approximately 0.80, and the observed female age ratio of 0.197, a population decline should have occurred during the study period, in this case, of approximately 4.6% per year (λ=0.954) (Fig. 5 and 6).

4. Discussion

To better understand the dynamics of the West Siberian/North European population of Long-tailed Duck, and by conservation measures to stop and reverse the recent rapid population decline, accurate and non-biased data on basic demographic parameters are needed. Because Long-tailed Ducks breed at low densities over large tundra areas, studies of the reproductive output and survival rates at the Arctic Russian and northern Fennoscandian nesting grounds will for logistic reasons be local in scale and the data obtained might not be representative on a broad population scale. A complementary way to obtain demographic information is to conduct broad scale studies of a selected set of demographic parameters at wintering sites. In this 14-year study a novel photo survey method was successfully used at some of the most important coastal and offshore wintering and spring stopover sites for Long-tailed Ducks in the Baltic Sea. By the photo survey method it was possible to annually survey very large number of birds and estimate the yearly variation in female age ratios, *i.e.*, the variation in the production of first winter birds, as well as the proportion of males among adults and the spatial segregation of sex and age groups of wintering Long-tailed Ducks.

4.1. Spatial segregation patterns

Female age ratios differed between regions within the Baltic Sea (Fig. 2). Female age ratios were consistently lower in the German waters in the southern Baltic Sea than at offshore banks and coastal waters in the central and northern Baltic Proper. Hence, the winter distributions of first winter birds and adults were not identical at the broad Baltic wide level. The partial segregation of age groups, with a higher proportion of first winter birds wintering more north, was also more pronounced in years with high production of first winter birds.

The proportion of males among adults also differed between the studied regions (Fig. 3 and 4). The observed overall broad scale pattern was a male biased adult sex ratio. This result is consistent with observations from several other sea duck populations, and with the finding that the mortality rate of adult female sea ducks during the breeding season usually is higher than that of adult males (Flint 2015). In this study, the proportion of males among adults in winter was clearly more male biased in the German waters and at Hanö Bay in the southern Baltic Sea than in other regions. The proportion of males among adults was also slightly more male biased at the offshore banks than in coastal waters east of Gotland and at Finnish spring stopover sites. Similar spatial and temporal segregation between adult males and adult females at wintering and stop-over sites has previously also been reported in several other sea ducks (Petersen & Savard 2015). No significant long-term trend of adult sex ratios was observed over the study period.

There is a possibility that different age and sex ratios at different wintering regions to some extent could be an effect of that birds from different parts of the breeding range, and which experience different conditions in summer, have different centres of distribution in the Baltic Sea. However, the studies that exist on migration movements do not support such a segregation pattern. For example, Quillfeldt *et al.* (2021) found that Long-tailed Ducks marked with implanted satellite transmitters at breeding sites on Kolguev Island in northwestern Russia spent the winter in different parts of the Baltic Sea, including in the regions surveyed in the present study. Furthermore, by studying marked Long-tailed Ducks breeding in Alaska, Petersen *et al.* (2003) concluded that wintering populations would be expected to contain a mix of birds from different breeding areas, and breeding populations would include birds from different wintering areas. It should be noted that here, in the present study, segregation patters of age and sex groups of Long-tailed Ducks were analysed on a large Baltic wide scale. Additional small scale spatial and temporal segregation patterns, related to habitat use and environmental variables, cannot be excluded and warrants further studies. Irrespective of the causes for segregation patters in winter, knowledge about the patterns is necessary to interpret result from any type of surveys monitoring age and sex ratios or population size.

4.2. Population trajectories

Baltic wide surveys have shown that the West Siberian/North European population of Long-tailed Ducks declined by approximately 65% between 1992–1993 and 2007–2009 (Durinck *et al.* 1994, Skov *et al.* 2011) and regional surveys in parts of the Baltic Sea performed after 2009 have indicated further declines (Nilsson 2016). It is therefore of interest to analyse if the decline has been caused by low reproductive success, or low survival rates, for example because of additional anthropogenic mortality.

In this study it was found that the production of first winter birds, measured as the female age ratios in winter, clearly fluctuated between years. Furthermore, positive correlations between time-series also showed that female age ratios observed in different wintering regions fluctuated in a similar way. This indicates that monitoring efforts with the photo survey method, at a relatively few key wintering and spring stopover sites, can capture large scale population processes and provide reliable demographic information to further analyses.

The overall mean female age ratio was low during the study period between 2008 and 2021. Regardless of whether the weighted mean female age ratio of 0.153, or the slightly higher mean female age ratio of 0.197 observed at the Finnish stopover sites, was closest to the true population value, very high mean female survival rates of 0.872 and 0.843, respectively, would have been needed to balance the low female age ratios and maintain a stable population.

Results from this study as well as from other more elaborated sea duck population models all show that even very small changes in female adult survival rates will have large effects on predicted population trajectories (Flint 2015). No field studies have hitherto produced any estimates of the natural adult survival rates of birds from the West Siberian/North European Long-tailed Duck population. However, it is known that anthropogenic mortality of wintering Long-tailed Ducks can be considerable in the Baltic Sea region, because of recurrent spills of oil and chemicals from ships at important wintering sites (Larsson & Tydén 2005, Larsson 2016), by-catches in fishery (Bellebaum *et al.* 2012, Žydelis *et al.* 2009) and hunting (Hearn *et al.* 2015). In the International Single Species Action Plan for the Conservation of the Long-tailed Duck, Hearn *et al.* (2015) emphasised the difficulties to obtain good background statistics to quantify anthropogenic mortality rates for the West Siberian/North European population. However, they estimated that anthropogenic mortality from oil spills, by-catch and hunting accounted for an additional mortality of approximately 2–5% per year. Furthermore, Koneff *et al.* (2017), in their evaluation of risk of overharvest of sea ducks in North America, used a median adult survival rate in the absence of harvest of 0.81 for adult Long-tailed Ducks and 0.71 for subadults. It is therefore reasonable to assume that the true survival rate of 6 months old and older Long-tailed Ducks wintering in the Baltic Sea, when natural and anthropogenic mortality rates have been added, was 0.80 or lower during the study period. If so, then the total Baltic wintering population should have declined by an alarming rate of about 4% to 8% per year from 2008 to 2021.

4.3. Causes for fluctuating juvenile production

In this study, and in many other studies of arctic breeding sea ducks, geese and waders, the juvenile production has been observed to fluctuate markedly between years (Fig. 2) (Pehrsson 1986, Schamber *et al.* 2009, Nolet *et al.* 2013, Aharon-Rotman *et al.* 2015, Flint 2015). Breeding propensity, nest and hatching success and duckling survival at the Arctic breeding grounds may vary due to varying predation pressures and to varying climatic factors affecting the condition of breeding birds and their offspring. Arctic voles and lemmings are known to exhibit population cycles with peaks every 3–5 years. Generalist predators like the Arctic fox, and several species of avian predators, feed to a large extent on voles and lemmings but may shift to alternative prey, for example, eggs and chicks of waterfowl and waders, in years when rodents are scarce (Summers & Underhill 1987, Aharon-Rotman *et al.* 2015). In a recent study Rintala *et al.* (2022) argued that the reproductive success of Long-tailed ducks was related to lemming abundances in the previous year but also to direct and indirect effects of temperature and precipitation. Similarly, in a study of Dark-bellied Brent Geese (*Branta bernicla bernicla*) which breeds on coastal arctic tundra at the Taimyr Peninsula in northern Russia, Nolet *et al.* (2013) found that breeding success was dependent on lemming abundance, temperature at the breeding sites, *i.e.*, onset of spring, and population size. They also concluded that low juvenile production and the levelling off of the brent goose population from the 1990s and onwards was mainly the result of faltering lemming cycles (Ims *et al.* 2008, Nolet *et al.* 2013). Thus, although it seems very likely that the fluctuating reproductive success of Long-tailed Ducks, in general terms, to a large extent is affected by Arctic generalist predators switching between prey species in different years, additional important interactions related to weather and climate change at the breeding and wintering sites remains to be elucidated. For example, it cannot be excluded that carry-over effects are present, *i.e.*, that varying environmental conditions at the wintering and spring stopover sites affects the condition of spring migrating Long-tailed Ducks and their subsequent reproductive success in the Arctic (Waldeck & Larsson 2013, Larsson *et al.* 2014, Rintala *et al.* 2022). The variable production of first winter birds observed in the present study does not follow a strict 3–5 year cycle which indicates that also other factors than vole and lemming abundances are affecting juvenile production (Fig 2). Further analyses of temporal and spatial predation patterns as well as analyses of effects of climate change and other environmental factors at the breeding and wintering grounds are therefore needed.

5. Conclusions

The photo survey method used in this study is an effective method to obtain yearly values of basic demographic parameters of wintering Long-tailed Ducks. Compared to other methods, for example analyses of hunting bags, the photo survey has the great advantage that it does not suffer from the problem with small sample sizes and differential vulnerability of different sex and age groups. The results from this and previous studies clearly indicate that a combination of a too low average production of juveniles, and a too high anthropogenic mortality rate, has caused, and is still causing, a rapid decline of the West Siberian/North European Long-tailed Duck population. To be able to halt and reverse the ongoing population decline one urgently need management actions that reduce the direct anthropogenic mortality at the most important wintering sites in the Baltic Sea, as well as ensure the availability of high quality feeding conditions in networks of marine protected areas. It will be more feasible in the short term to affect the further population trajectory by implementing management actions that reduce anthropogenic mortality at the wintering sites than management actions that intend to increase the overall reproductive output in the Arctic.

Ålders- och könskvoter i den minskande Västsibiriska/Nordeuropeiska populationen av alfågel som övervintrar i Östersjön: konsekvenser för bevarandet

Den västsibiriska/nordeuropeiska populationen av alfågel (*Clangula hyemalis*) som häckar i arktiska Ryssland och norra Fennoscandia och övervintrar i Östersjön, har minskat snabbt i antal sedan 1990-talet. För att identifiera orsakerna till minskningen och initiera effektiva bevarande-åtgärder behövs information om grundläggande demografiska parametrar. En fotoinventeringsmetod användes för att skatta ungproduktion och adult könskvot hos övervintrande alfåglar i kustområden och på utsjöbankar i Östersjön. Flera tusen individer analyserades varje vinter från 2008 till 2021. Antalet unga honor, dvs. 6–10 månader gamla individer, antogs vara lika som antalet ungar hanar. En honlig ålderskvot beräknades som antalet unga honor per vuxen hona. Denna ålderskvot varierade mellan år men var konsekvent lägre bland övervintrande individer i södra än i centrala Östersjön. Könskvoten hos övervintrande adulta individer var skev, med ett överskott av adulta hanar. Överskottet av adulta hanar var större i södra Östersjön än i andra regioner. En populationsmodell användes för att analysera om en låg produktion av 6-10 månader gamla ungfåglar mellan 2008 och 2021 har begränsat populationstillväxten. Givet att den skattade genomsnittliga vägda honliga ålderskvoten på 0.153 var representativ på populationsnivå, så skulle en extremt hög adult årlig överlevnadsgrad för honor om 0.872 ha behövts för att upprätthålla en stabil population. Med hänsyn till kända mänskliga faktorer som påverkar alfåglars överlevnad, bland annat utsläpp av olja och kemikalier från fartyg, bifångst vid nätfiske och jakt, är det mer rimligt att anta en årlig överlevnadsgrad på ca 0,80 och därmed att den i Östersjön övervintrande alfågelpopulationen minskade i en alarmerande takt om cirka 7.7% per år mellan 2008 och 2021.

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References

Aarhus University 2021: Danish Wing Survey. — Available at https://fauna.au.dk/en/hunting-and-game-management/wing-survey (accessed 16.10.2022).

Aharon-Rotman, Y., Soloviev, M., Minton, C., Tomkovich, P., Hassell, C. & Klaasen, M. 2015: Loss of periodicity in breeding success of waders links to changes in lemming cycles in Arctic ecosystems. — Oikos 124: 861–870. https://doi.org/10.1111/oik.01730

Alison, R. M. 1975: Breeding biology and behaviour of the oldsquaw (*Clangula hyemalis* L.). — Ornithological Monographs 18: i–52.

Bellebaum, J., Schirmeister, B., Sonntag, N. & Garthe, S. 2012: Decreasing but still high: bycatch of seabirds in gillnet fisheries along the German Baltic coast. — Aquatic Conservation Marine and Freshwater Ecosystems 23: 210–221

Blums, P. & Mednis, A. 1996: Secondary sex ratio in Anatinae. — Auk 113: 505–511.

Bowman, T.D, Silverman, E.D., Gilliland, S.G., & Leirness, J.B. 2015: Status and trends of North American sea ducks: Reinforcing the need for better monitoring. — In Ecology and Conservation of North American sea ducks. Studies in Avian Biology (no. 46) (eds. Savard, J.-P.L., Derksen, D.V., Esler, D. & Eadie, J.M.): 1–28. CRC Press, Boca Raton, FL.

Durinck, J., Skov, H., Jensen, F. P. & Pihl, S. 1994: Important marine areas for wintering birds in the Baltic Sea. — EU DG XI Research Contract no. 2242/90-09-01. Ornis Consult Report.

Efron, B. & Tibshirani, R.J. 1994: An Introduction to the Bootstrap. — Chapman and Hall/CRC.

Flint, P.L. 2015: Population dynamics of sea ducks: Using models to understand the causes, consequences, evolution, and management of variation in life history characteristics. — In Ecology and Conservation of North American sea ducks. Studies in Avian Biology (no. 46) (eds. Savard, J.-P.L., Derksen, D.V., Esler, D. & Eadie, J.M.): 63–96. CRC Press, Boca Raton, FL.

Fowler, J., Cohen, L. & Jarvis, P. 1998: Practical Statistics for Field Biology, second edition. — Wiley, Chichester.

Hario, M., Rintala, J. & Nordenswan, G. 2009: Dynamics of wintering Long-tailed Ducks in the Baltic Sea – the connection with lemming cycles, oil disasters, and hunting. — Suomen Riista 55: 83–96. (In Finnish, with English summary).

Hearn, R.D., Harrison, A.L. & Cranswick, P.A. 2015: International Single Species Action Plan for the Conservation of the Long-tailed Duck *Clangula hyemalis*, 2016–2025. — AEWA Technical Series. No. 57. Bonn, Germany

HELCOM 2021: HELCOM Red List of Birds – *Clangula hyemalis*. — Available at https://helcom.fi/baltic-sea-trends/biodiversity/red-list-of-baltic-species/red-list-of-birds/ (accessed 16.10.2022).

Ims, R.A., Henden, J.-A. & Killengreen, S.T. 2008: Collapsing population cycles. — Trends in Ecology and Evolution 23: 79–86. https://doi.org/10.1016/j.tree.2007.10.010

Iverson, S.A., Smith, B.D. & Cooke, F. 2004: Age and sex distributions of wintering surf scoters: implications for the use of age ratios as an index of recruitment. — Condor 106: 252–262.

Karwinkel, T., Pollet, I.L., Vardeh, S., Kruckenberg, H., Glazov, P., Loshchagina, J., Kondratyev, A., Merkel, B., Bellebaum, J. & Quillfeldt, P. 2020: Year-round spatiotemporal distribution pattern of a threatened sea duck species breeding on Kolguev Island, south-eastern Barents Sea. — BMC Ecology 20:31. https://doi.org/10.1186/s12898-020-00299-2

Koneff, M.D., Zimmerman, G.S., Dwyer, C.P., Fleming, K.K., Padding, P.I., Devers, P.K., Johnson, F.A., Runge, M.C. & Roberts, A.J. 2017: Evaluation of harvest and information needs for North American sea ducks. — PLoS ONE 12(4): e0175411. https://doi.org/10.1371/journal.pone.0175411

Larsson, K. 2016: Sjöfart och naturvärden vid utsjöbankar i centrala Östersjön – Havsplanering kan reducera konflikter. — Havs- och vattenmyndighetens rapport 2016: 24. (In Swedish).

Larsson, K. 2022: Age and sex ratios of wintering Long-tailed Ducks can be determined by analysis of photos of flying flocks at sea: A method description. — Ornis Svecica 32, 00–00 (in press).

Larsson, K. & Tydén, L. 2005: Effects of oil spills on wintering Long-tailed Ducks *Clangula hyemalis* at Hoburgs bank in central Baltic Sea between 1996/97 and 2003/04. — Ornis Svecica 15: 161–171.

Larsson, K., Hajdu, S., Kilpi, M., Larsson, R., Leito, A. & Lyngs, P. 2014: Effects of an extensive *Prymnesium polylepis* bloom on breeding eiders in the Baltic Sea. — Journal of Sea Research 88: 21–28. https://doi.org/10.1016/j.seares.2013.12.017

Lehikoinen, A, Kondratyev, A.V., Asanti, T., Gustafsson, E., Lamminsalo, O., Lapshin, N.V., Pessa, J & Rusanen, P. 2006: Survey of arctic bird migration and staging areas at the White Sea, in the autumns of 1999 and 2004. —The Finnish Environment 25. Finnish Environment Institute.

Helsinki. http://hdl.handle.net/10138/38722

Lehikoinen, A., Öst, M., Hollmén, T. & Kilpi, M. 2008: Does sex-specific duckling mortality contribute to male bias in adult common eiders? — Condor 110: 574–578. http://dx.doi.org/10.1525/cond.2008.8574

Loshchagina, J., Vardeh, S., Glazov, P., Pollet, I.L. & Quillfeldt, P. 2019: Long-tailed Duck (*Clangula hyemalis*) ecology: insights from the Russian literature. Part 2: European part of the Russian breeding range. — Polar Biology 42: 2277–2297. https://doi.org/10.1007/s00300-019-02595-0

Nilsson, L. 2012: Distribution and numbers of wintering sea ducks in Swedish offshore waters. — Ornis Svecica 22: 39–60.

Nilsson, L. 2016: Changes in numbers and distribution of wintering Long-tailed Ducks *Clangula hyemalis* in Swedish waters during the last fifty years. — Ornis Svecica 26: 162–176. https://doi.org/10.34080/os.v26.21855

Nolet, B.A., Bauer, S., Feige, N., Kokorev, Y.I., Popov, I.Y. & Ebbinge, B.S. 2013: Faltering lemming cycles reduce productivity and population size of a migratory Arctic goose species. — Journal of Animal Ecology 82: 804–813. https://doi.org/10.1111/1365-2656.12060

Pehrsson, O. 1986: Duckling production of the Oldsquaw in relation to spring weather and small-rodent fluctuations. — Canadian Journal of Zoology 64: 1835–1841.

Petersen, M.R., McCaffery, B.J. & Flint, P.L. 2003: Post-breeding distribution of Long-tailed Ducks *Clangula hyemalis* from the Yukon-Kuskokwim Delta. — Wildfowl 54: 129–139.

Petersen, M.R. & Savard J.-P.L. 2015: Variation in migration strategies of North American sea ducks. — In Ecology and Conservation of North American sea ducks. Studies in Avian Biology (no. 46) (eds. Savard, J.-P.L., Derksen, D.V., Esler, D. & Eadie, J.M.): 267–304. CRC Press, Boca Raton, FL.

Quillfeldt, P., Morkūnas, J., Kruckenberg, H., Kondratyev, A., Loshchagina, J., Aarvak, T., Øien, I.J., Bellebaum, J. & Glazov, P. 2021: Year-round movements of Long-tailed Ducks *Clangula hyemalis* from Kolguev Island, Barents Sea. — Polar Biology 45: 71–87. https://doi.org/10.1007/s00300-021-02973-7

Rintala, J., Hario, M., Laursen, K. & Møller, A.P. 2022: Large-scale changes in marine and terrestrial environments drive the population dynamics of long-tailed ducks breeding in Siberia. — Scientifc Reports 12:12355. https://doi.org/10.1038/s41598-022-16166-7

Robertson, G.J. 2008: Using winter juvenile/adult ratios as indices of recruitment in population models. — Waterbirds 31: 152–158.

Rodway, M.S., Regehr, H.M., Boyd, W.S. & Iverson S.A. 2015: Age and sex ratios of sea ducks wintering in the Strait of Georgia, British Columbia: Implications for monitoring. — Marine Ornithology 43: 141–150.

Rodway, M.S., Regehr, H.M. & Cooke, F. 2003: Sex and age differences in distribution, abundance, and habitat preferences of wintering Harlequin Ducks – implications for conservation and estimating recruitment rates. — Canadian Journal of Zoology 81: 492–503.

Schamber, J.L., Flint, P.L., Grand, J.B., Wilson, H.M. & Morse, J.A. 2009: Population Dynamics of Long-tailed Ducks Breeding on the Yukon-Kuskokwim Delta, Alaska. — Arctic 62: 190–200.

Skov, H., Heinänen, S., Žydelis, R., Bellebaum, J., Bzoma, S., Dagys, M, Durinck, J., Garthe, S., Grishanov, G., Hario, M., Kieckbusch, J.J., Kube, J., Kuresoo, A., Larsson, K., Luigujoe, L., Meissner, W., Nehls, H.W., Nilsson, L., Krag Petersen, I., Mikkola Roos, M., Pihl, S., Sonntag, N., Stock, A. & Stipniece, A. 2011: Waterbird Populations and Pressures in the Baltic Sea. — TemaNord 2011:550. Nordic Council of Ministers, Copenhagen 2011.

Smith, C.M., Goudie, R.I. & Cooke, F. 2001: Winter age ratios and the assessment of recruitment of Harlequin Ducks. — Waterbirds 24: 39–44.

Stempniewicz, L. 1994: Marine birds drowning in fishing nets in the Gulf of Gdansk (southern Baltic): numbers, species composition, age and sex structure. — Ornis Svecica 4: 123–132.

Summers, R.W. & Underhill, L.G. 1987: Factors related to breeding production of Brent Geese *Branta b. bernicla* and waders (*Charadrii*) on the Taymyr Peninsula. — Bird Study 34: 161–171.

Waldeck, P., & Larsson, K. 2013: Effects of winter water temperature on mass loss in Baltic blue mussels: implications for foraging sea ducks. — Journal of Experimental Marine Biology and Ecology 444: 24–30.

Wetlands International 2021: Waterbirds Populations Portal. — Available at https://wpp.wetlands.org/ (accessed 16.10.2022).

Wood, K.A., Brides, K., Durham, M.E. & Hearn, R.D. 2021: Adults have more male-biased sex ratios than first-winter juveniles in wintering duck populations. — Avian Research 12: 51. https://doi.org/10.1186/s40657-021-00286-1

Žydelis, R., Bellebaum, J. Österblom, H. Vetemaa, M., Schirmeister, B., Stipniece, A., Dagys, M., van Eerden, M. & Garthe, S. 2009: Bycatch in gillnet fisheries – An overlooked threat to waterbird populations. — Biological Conservation 142: 1269–1281.

Online supplementary material

Supplementary material available in the online version includes Tables S1 and S2.

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Influence of habitat quality and diversity on two populations of Eurasian Curlew (*Numenius arquata*) with contrasting dynamics in Western France

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Like most shorebirds in Europe, breeding populations of Eurasian Curlew (*Numenius arquata*) are suffering from habitat loss and degradation mainly caused by changes in agricultural practices. In Deux-Sèvres (France), the number of pairs has gradually declined since the early 2000s in the main, historical breeding site, while a new breeding site has appeared recently 80 kilometres further north with increasing number of pairs through the survey period. Many wheat fields and rare dry grasslands are found in the north, whereas the landscape in the south is mainly composed of tillage plots, hay meadows, and pastures. This study aims to highlight differences in food availability and quality between the two areas. Sample series of ground-dwelling and vegetation-dwelling invertebrates were carried out during three key stages of the species breeding cycle with pitfall traps and sweep nets. Dry grasslands in the north were found to be the most favourable habitat in terms of prey availability for adults and for chicks during the brood-rearing period. Moreover, hay meadows and pastures in the south seemed to be resource-abundant feeding habitats. Therefore, the habitats of the northern site seem to offer a greater abundance of invertebrates and thus a potentially larger food resource than the southern one. It follows that the northern site likely offers better breeding conditions, especially for the growth of chicks. An increase in the area of dry grasslands in the north and the establishment of adapted agricultural management in the south would be favourable for the conservation of local curlew populations.

1. Introduction

Shorebird populations have been declining markedly worldwide for several decades (Stroud *et al*. 2006), particularly in Europe, where half of the species are classified as 'threatened' on the IUCN Red List (Butchart *et al*. 2010, Pearce-Higgins *et al*. 2017). Among the major threats involved in these declines are the loss and degradation of wintering and stopover habitats (van Roomen *et al*. 2012, Studds *et al*. 2017). However, many authors agree that falling productivity is the primary factor responsible for current population dynamics (Gregory *et al*. 2004, Macdonald & Bolton 2008, Roodbergen *et al*. 2012). Increasing predation on eggs and chicks has been evaluated as one of the main threats (Macdonald & Bolton 2008, Roodbergen *et al*. 2012, Bertholdt *et al*. 2017). It is also assumed that the modification of agricultural landscapes in recent decades has favoured access to broods by terrestrial predators such as the red fox, *Vulpes vulpes* (Bellebaum & Bock 2009, Niemczynowicz *et al*. 2017).

However, the loss and degradation of nesting habitats also explains the collapse of populations (Eglinton 2008, Zedler & Kercher 2005). Indeed, the transformation of agricultural practices in recent decades has led to the increasing scarcity and fragmentation of both wetlands, due to drainage, and grasslands, due to their conversion to arable land (Eglington 2008, Zedler & Kercher 2005). This agricultural revolution has been accompanied by a mechanisation and intensification of production methods. The frequency of mowing and density of herds have both increased and thereby led to the mechanical destruction or trampling of nests and chicks (Kruk *et al*. 1997, Kleijn *et al*. 2010).

In addition, another consequence of these modern agriculture techniques is a reduction in the availability of food resources for birds. On the one hand, the use of phytosanitary products has reduced the abundance of invertebrates, a primary food resource for insectivores such as shorebirds (Chamberlain *et al*. 2000, Clere & Bretagnolle 2001, Benton *et al*. 2002, Wilson *et al*. 2005). On the other hand, formerly favourable meadows that were characterized by a great floristic diversity and a heterogeneous vegetation structure have gradually been converted into a monospecific, fertilized sward, which is sometimes too dense to allow birds to feed in (Butler & Gillings 2004, Devereux *et al*. 2004, McCracken & Tallowin 2004, Eglington 2008). In addition, the homogenization of the vegetation structure and the simplification of plant communities have contributed to rarefaction in arthropods as well as to a reduction in their overall size (Kajak 1978, Green & Cadbury 1987, Siepel 1990, Blake *et al*. 1994, Vickery *et al*. 2001, McKeever 2003). In this context, smaller prey have become less profitable (in terms of energy gained per arthropod consumed) and therefore have increased the difficulty for adults and chicks to meet their energy needs.

The depletion of trophic resources could have major consequences on population dynamics, as reported by Kentie *et al*. (2013) for the black-tailed godwit, *Limosa limosa*, in areas of intensive agricultural areas in the Netherlands. This study reveals that chick survival was 2.5 times higher in traditionally managed grasslands (which featured late mowing, high floristic diversity, and maintenance of favourable water levels) than in intensive grasslands. These results suggest that the shift from historical management methods to intensive practices has exposed chicks to significant risk of dietary deficiency, thus decreasing their growth and potential for survival.

The Eurasian Curlew (*Numenius arquata*) is among the most threatened shorebird species in Europe, with strongly declining populations in several countries such as the UK or Ireland (48% in the UK between 1995 and 2015) (Harris *et al*. 2016). The species is now classified as vulnerable on the European IUCN Red List and benefits from an international action plan aimed at restoring its conservation status (Brown 2015). In France, the breeding population is declining moderately (Patrelle *et al*. 2017).

The French département of "Deux-Sèvres" hosts two populations of curlews with contrasted dynamics. Twenty years ago, all the breeding pairs were restricted to the southern sector, the plain of "La Mothe Saint-Heray-Lezay" (PLMSHL), an area characterized by a mixed agricultural landscape with meadows and pastures as well as a relatively well-preserved network of hedgerows. Since the early 2000s, a decrease of breeding pairs has been observed at this site. Around the same time, an increasing number of pairs have colonised two territories located 80 kilometres further north, the plain of "Oiron-Thenezay" (OITH) and the plains of Mireballais-Neuvillois (MINE) (Poirel 2017). Within these new breeding sites, the agricultural landscape is largely dominated by crops and tillage plots with only a few patches of dry grasslands.

The objective of this study is to find out whether differences in terms of habitat use and food availability between the PLMSHL and OITH sites could perhaps explain the opposing dynamics observed in the two core populations. For this purpose, a series of invertebrate samples were taken from several habitat types to determine which environments presented the most food resources for curlews. Breeding pairs were also monitored in parallel to find out which habitats the species was exploiting within both sites. We hypothesise that: (1) curlews select grasslands to feed, because (2) grassland habitats provide more important food resources than crops, and because (3) prey are more numerous and profitable in OITH than in PLMSHL considering the opposite dynamics of both populations.

2. Materials and methods

2.1. Study area

The study was carried out in a 'Zone de Protection Spéciale' or special protection area (SPA) on the plain of Oiron-Thénezay (OITH), located to the north-east of the Deux-Sèvres, as well as in a SPA on the plain of La Mothe-Saint-Héray-Lezay (PLMSHL), located to the south-east of the département (Fig.1). These sites are different in terms of landscape structure, habitat diversity, and agricultural practices (Berthomé & Turpaud-Fizzala 2012).

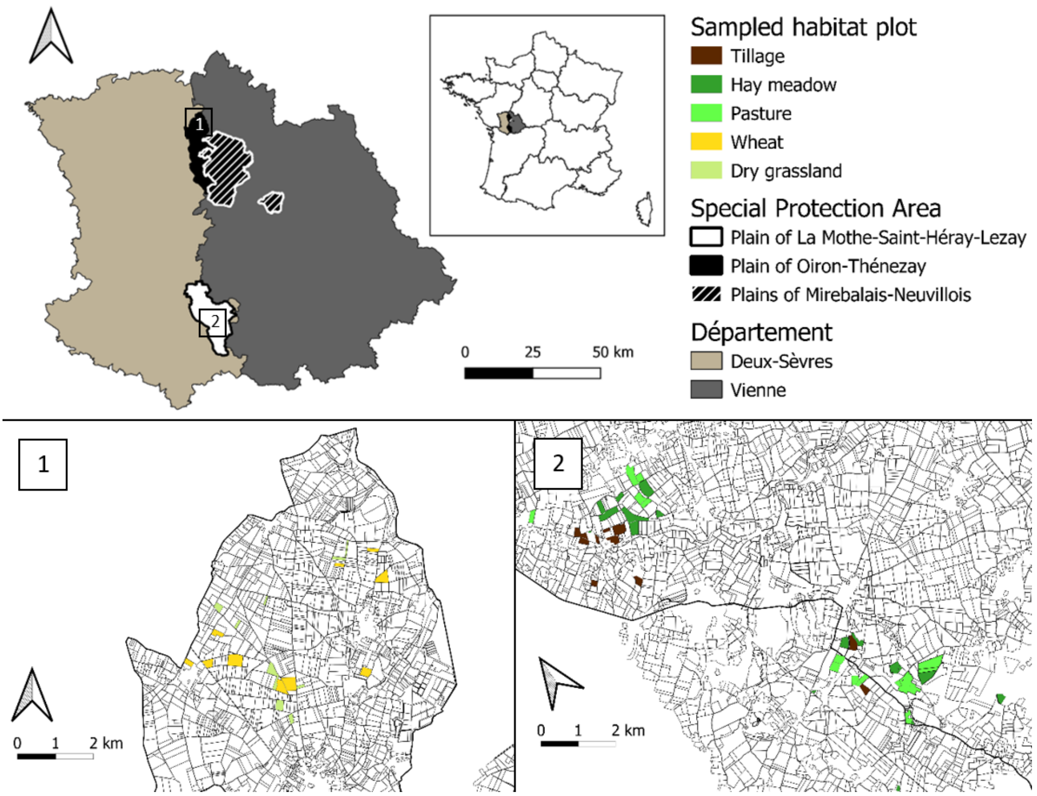

Fig. 1. Map of the Special Protection Areas of Oiron-Thénezay (OITH) in the north-east of Deux-Sèvres (black), of the Plain of La Mothe-Saint-Héray-Lezay (PLMSHL) in the south-east (white) and of the Plains of Mirebalais-Neuvillois (MINE) in the north-west of Vienne (hatched black). The plots sampled are represented in color in the two boxes at the bottom.

OITH (N 46°51'24", W 0°03'38") covers 15,580 ha. This intensive cereal-growing plain is marked by a shortage of hedgerows and by a continuous decrease of meadows since the late 1980s (Berthomé 2011). According to the latest estimates, meadows now account for only 10% of the utilised agricultural area (UAA), of which only about 3% are permanent dry grasslands. Agri-environmental management is applied to 4% of the total grassland area and allows for favourable habitats to be preserved for the breeding of the Little Bustard (*Tetrax tetrax*). This plan has been implemented since the 2000s in the département and encourages the transformation of agricultural plots into sown meadows, which favour the presence of invertebrates for improving the feeding and nesting conditions for little bustards. Benefits include delaying the mowing date from 15 May to 31 July (Bretagnolle *et al*. 2011). It should be noted that another SPA, on the plains of "Mirebalais-Neuvillois" (MINE), located in the neighbouring Vienne département, also hosts breeding pairs (Dubois 2011) (Fig. 1). MINE is adjacent to OITH (Fig. 1) and has the same types of habitats (Poirel., 2017). This is why breeding curlews in these two territories are considered to be part of the same core population. However, the study was not carried out in MINE because it is monitored by a different program. Nonetheless, data on breeding curlew numbers were provided to us to estimate the size of this core population straddling two territories.

PLMSHL (N 46°17'17", E 0°02'26"), the second study site, covers 24,451 ha. In this area, hedgerows are preserved, and grassland covers 29% of the UAA, of which 13% are permanent meadows, including rare wet meadows and some mesophilous grasslands (Berthomé & Turpaud-Fizzala 2012). Goat and cattle farming are among the reasons for the maintenance of hay meadows and pastures locally. This site is also a breeding ground for the little bustard, with 6% of the UAA of PLMSHL benefiting from agri-environmental measures (AEMs), as in OITH.

2.2. Long-term monitoring

In order to know about the temporal dynamics of the two population cores and variations in the distribution of breeding pairs within the two study sites, a compilation of historical data was carried out for 1981 to 2020 for OITH and PLMSHL. These data come from a digital naturalist database and from articles published in a local ornithological journal. A distribution map of breeding pairs was carried out for the years 2002, 2011, and 2019 by the Groupe Ornithologique des Deux-Sèvres (Gilet *et al*. 2002, Turpaud-Fizzala 2012, Lartigau 2018). It should be noted that the numbers of curlews present in MINE, the adjacent territory of OITH, were also analysed to assess the temporal dynamics of the OITH-MINE population core as a whole.

2.3. Breeding pair distribution

The monitoring of breeding pairs started from late February. To characterise breeding phenology and habitat use by birds, the territories of the pairs were surveyed from late March to early June 2019, after which the curlews were no longer expected to lay replacement eggs (Turpaud-Fizzala 2012). At both sites, observers were looking for breeding territories and tried to locate precisely the nest at least twice a week. The search areas were targeted on historical breeding areas. After every bird observation, the georeferenced location was noted. To estimate feeding habitat preferences, each individual observation was supplemented with a behaviour note as well as the habitat type on which it was observed. Behaviours such as foraging, resting, parading, mating, defending territory, and brooding were recorded. All foraging data were then compiled and the proportion of foraging curlews in each habitat type was compared to habitat availability in OITH and PLMSHL to highlight any potential habitat selection. Due to the difficulties encountered by some observers in differentiating certain types of grasslands or crops, all the observations of curlews were gathered in the following categories: 'Grasslands', 'Cereal crops', 'Tillage', and 'Other culture types'. The same gathering of habitat types was made to calculate their area in OITH and PLMSHL. The data of habitats areas were obtained from the Land Parcel Identification System (LPIS) (European Commission 2009) and calculations were made on Qgis (v3.4.2, QGIS Development Team 2017).

2.4. Invertebrate availability

Sampling of invertebrates living on the ground and in the vegetation strata was carried out at both study sites. The sampling was carried out in habitats known by local observers to be those most used by curlews in OITH and PLMSHL. It should be added that the grassland habitats were clearly different at both OITH and PLMSHL sites and therefore sampling could not be carried out on same habitats. In OITH, wheat and dry grasslands were the two habitats selected for the study (Fig. 3). Dry grasslands are calcicolous meadows with short plant formations, composed mainly of perennial herbaceous plants. In PLMSHL, tillage plots (sunflower and maize), pasture meadows, and hay meadows were sampled (Fig. 3).

In addition, two criteria had to be met for selecting a plot. First, the farmer must have given his authorization to access the land. Second, at least one sighting of curlews must have been made there in previous years.

Three series of sampling were carried out to study the availability of invertebrates throughout the breeding cycle of the species. Samples were collected from 25 April to 14 May (Session 1), from 28 May to 6 June (Session 2), and from 28 June to 8 July (Session 3). These periods correspond respectively to the peak of egg-laying, hatching, and fledgling of chicks (Turpaud-Fizzala 2012) (Fig. 2).

Ground-dwelling invertebrates living on the soil were sampled via pitfall trapping (Woodcock 2005). The traps were pots of 9 cm in diameter at their upper end and were filled with a saltwater solution (350 g of salt for 1 L of water) and a few drops of odourless washing-up liquid. They were set for 10 days. In addition, a plastic cover was suspended over each trap to prevent the pots from filling up in case of heavy rain or to protect them from excessive exposure to the sun (Woodcock 2005). The invertebrates were preserved in 70% alcohol. Each habitat was sampled in at least 10 plots with one trap each. To avoid an edge effect, the traps were placed in the plot as far as possible from adjacent plots (Clough *et al*. 2007). Each laying, mowing, or grazing event on the sampled meadows was noted.

Vegetation-dwelling invertebrates as a stratum were sampled via sweep netting (Doxon *et al*. 2011) with a net of 38 cm in diameter. For this purpose, 25 sweep movements were carried out by walking in a straight line in a predefined direction to stay as far away as possible from adjacent plots and thus limiting the possible edge effect (Puech 2014). Once trapped, the invertebrates were collected using a mouth aspirator and preserved in 70% alcohol.

All the organisms were identified to the order taxa using the identification key of Mignon *et al*. (2016), and the number of individuals was counted by order. All individuals less than 3 mm in length were excluded from the analysis as they were considered as not being able to be consumed by the curlew, according to Berg (1993) and Robson (1998). Each individual was measured

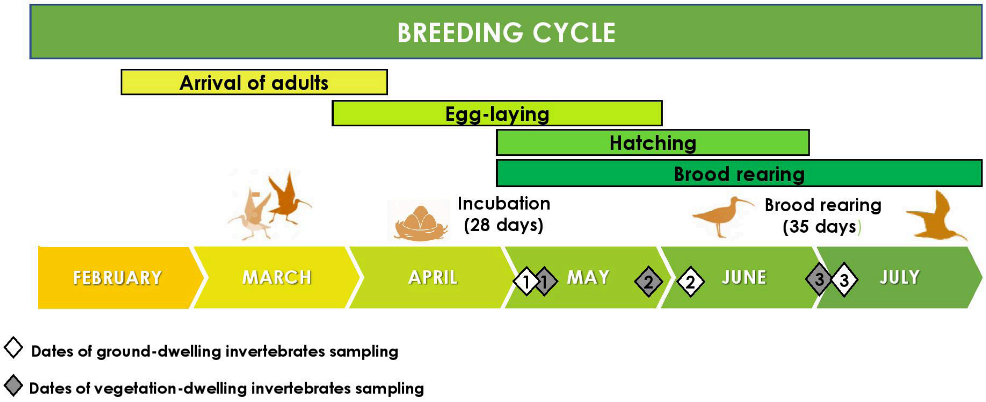

Fig. 2. Dates of ground and vegetation-dwelling invertebrates sampling according to the breeding cycle of the Eurasian Curlew in Deux-Sèvres.

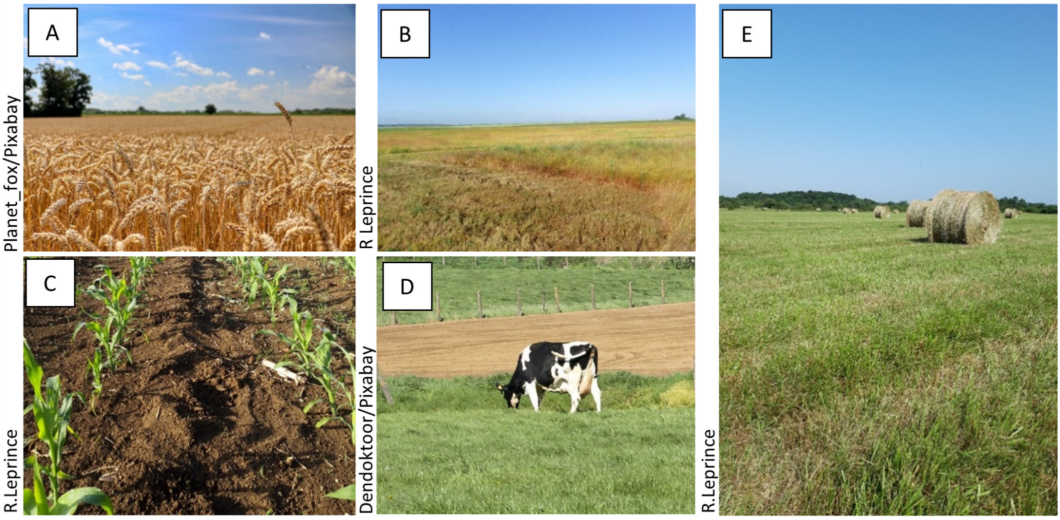

Fig. 3. Illustration of sampled habitats: A: Wheat (OITH), B: Dry grassland (OITH), C: Tillage (PLMSHL), D: Pasture (PLMSHL), E: Hay meadow (PLMSHL).

to an accuracy of 5 mm for length. Once the individuals were identified, they were collectively oven-dried at 65°C for 48 h per sample (Sabo *et al*. 2002). Dry mass (DM) was obtained using a balance with an accuracy of 0.001 g.

2.5. Statistical analyses

Habitat selection by curlew was assessed by comparing the habitat used while foraging (determined during monitoring survey) to availability (proportion of habitat present in study sites) using a χ^2 goodness-of-fit test (Zar 1999), while Bonferroni confidence intervals (Neu *et al*. 1974, Byers *et al*. 1984) were calculated to determine preference or avoidance of certain habitat types. Then, to determine the effect of the habitat type (wheat/dry grassland in OITH and tillage/hay meadow/pasture in PLMSHL) for each sampling session (1, 2, 3) on invertebrate abundance, we used likelihood ratio tests. Moreover, a type II ANOVA (Fisher 1925) was used to test the effect of that same independent variable on DM and length. When model assumptions could not be validated, non-parametric Kruskal–Wallis tests (Kruskal & Wallis 1952) were made. We used post hoc Tukey tests (Tukey 1949) for parametric methods and Dunn tests (Dunn 1964) for non-parametric methods to determine potential differences between the habitats. Furthermore, to test the effect of the sampling session in each habitat type on invertebrate abundance, DM, and length, Wald tests (Wald 1943) were used by adding the 'plot number' as a random factor. When model assumptions could not be validated, Friedman tests (Friedman 1939) and Wilcoxon tests for paired data (Wilcoxon 1945) were used. All the statistical tests were performed using R software (R Core Team 2019).

3. Results

3.1. Dynamic of breeding populations

The curlew population of PLMSHL has declined slightly over the past 20 years (Fig. 4). Between 24 and 28 breeding pairs were counted at this site between 2000 and 2002, while the breeding population fell to 14 to 21 pairs between 2017 and 2019 (Fig. 4). In OITH, the number of pairs has increased significantly since the recording of the first breeding pair in 2006, to reach 15 to 17 pairs between 2017 and 2019 (Fig. 4). Moreover, the emergence of breeding pairs on the plains of Mirebalais-Neuvillois (MINE) occurred at the same period as the increase at OITH. Despite some variations, the number of pairs in MINE has seemed to be stable since 2013 and varies between

4 and 8 pairs. The spatial distribution of breeding pairs slightly changed between 2002 and 2019 in PLMSHL, with the current population in 2019 more scattered than it was in 2002 (Fig. 5). In OITH, the population has clearly increased from the initial core areas that existed in 2011, except for the settlement of one pair in the southernmost part of the area. In addition, the density has increased notably (Fig. 5).

3.2. Feeding habitat selection

Regarding the availability of the different types of habitats on each study site, cereal crops represent 68.9% of the UAA in OITH and 43.7% in PLMSHL, while grasslands occupy only 10.3% in OITH and 29.7% in PLMSHL (Table 1, Supplementary Material Fig. S3). The proportions of curlews feeding in each habitat type

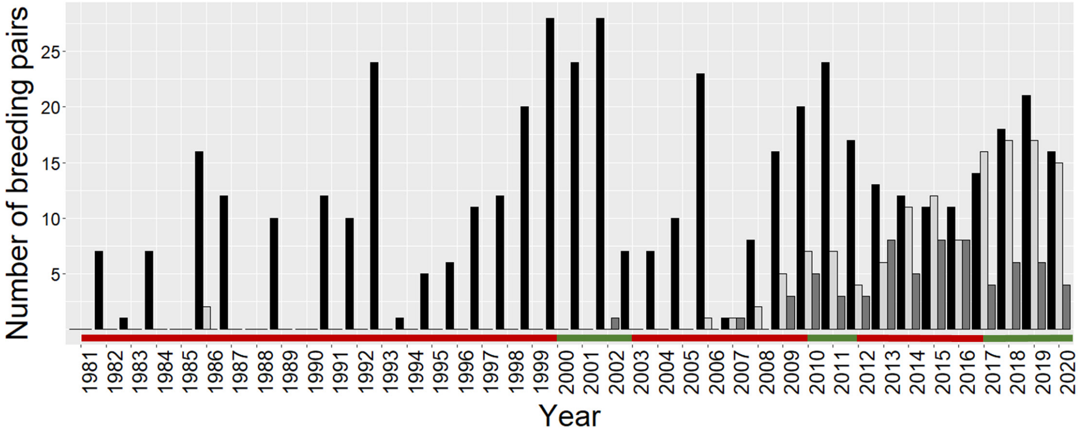

Fig. 4. Variation of the number of curlew pairs in PLMSHL in black, in OITH in light grey and in MINE in dark grey between 1981 and 2020. The periods benefiting from monitoring protocols are represented with a horizontal green bar and those not benefiting from it with a horizontal red bar.

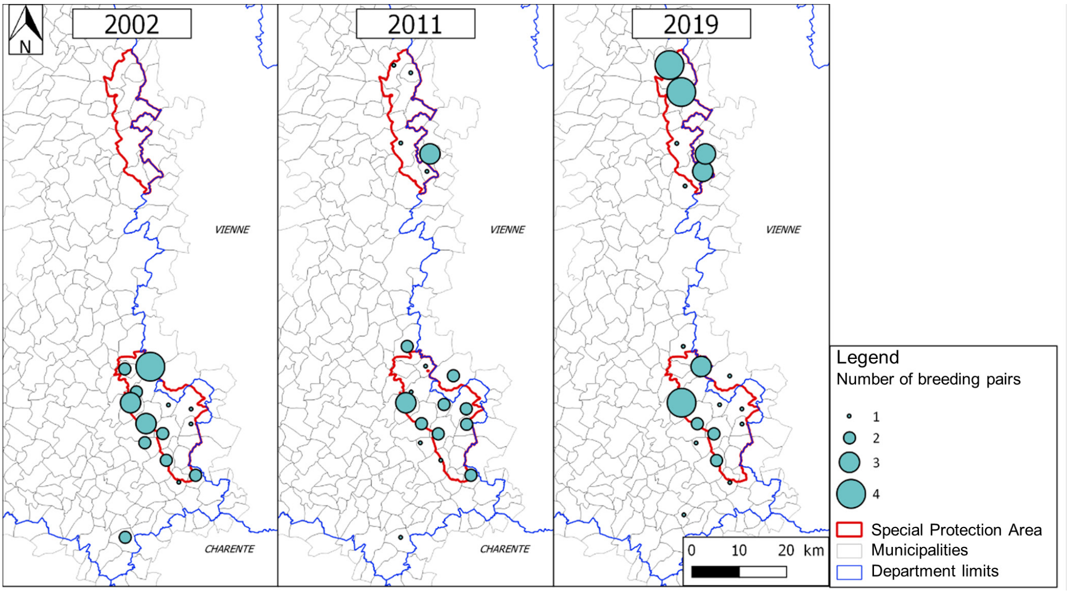

Fig. 5. Spatial dynamics of the Eurasian Curlew over PLMSHL in the south-east and OITH in the north-east of Deux-Sèvres for the years 2002, 2011 and 2019.

were found to be significantly different from the proportions expected in OITH (χ^2=1183.4, df=3, p<0.001) and in PLMSHL (χ^2=257.1, df=3, p<0.001) (Table 1). Indeed, Bonferroni confidence intervals (Table 1) showed that the curlews used the grasslands more than expected in OITH (63%, CI95=44.9-80.8%, n=374) and in PLMSHL (85%, CI95=65.6-104.8%, n=169), if we rely on their availability at the two study sites (Table 1). Conversely, cereal plots were less used in OITH (12.0%, IC95=−12.1–24.1%, n=374) and in PLMSHL (1.2%, IC95=−4.8%–7.2%, n=169) by curlews while foraging compared with their availability in the environment. On the other hand, no difference was found for tillage plots and other culture types (Table 1).

3.3. Invertebrate abundance

A total of 17 orders of Arthropoda were identified in all the samples. The two other main taxa were Gastropoda and Lumbricidae. All larvae from all orders were gathered under the category 'Larva'. Isopods (woodlice) (35.9%), beetles (35.0%), spiders (25.4%), and hemipters (24.7%) were the taxa most represented in all the samples from the two types of traps (total n=12.505 individuals; see Supplementary Material Tables S1–S2 for taxa abundance). However, a majority of isopods (35.9%) and spiders (17.1%) were found at the ground surface (Supplementary Material Table S1) and a majority of hemipters (23.5%) and beetles (20.8%) in the vegetation stratum (Supplementary Material Table S2).

During the 'laying' sampling session (S1: early May), no significant differences between habitats were observed concerning the ground-living invertebrates (χ^2=8.07, df=4, p=0.089, Fig. 6a, Table 2). However, in the vegetation stratum, wheat fields (OITH) had a lower abundance of arthropods than in the dry grasslands (OITH) (Tukey post hoc test: p<0.001, Fig. 7a, Table 2) or hay meadows (PLMSHL) (Tukey post hoc test: p=0.01, Fig. 7a, Table 2). It should also be noted that the absence of vegetation in tillage plots (PLMSHL) during that session prevented any sweep netting.

During the 'hatching' session (S2: early June), the abundance of invertebrates increased

Table 1. Results of the comparison between the proportion of foraging curlew in each habitat (use) and the proportion of habitat areas (availability) in OITH and PLMSHL. Values obtained are shown in the chi-squared test and the Bonferroni confidence intervals. NS = no significant difference between availability and use; > = habitat used more than availability; < = habitat used less than availability.

Habitat	Chi-squared test	Proportion of foraging curlew observed	Expected proportion of use (*e.g.* proportion of habitats area)	Observation number	Bonferoni confidence intervals	Conclusion
OITH						
Grasslands	χ^2=1183.4 df=3 p<0.001	62.8%	10.3%	235	44.9–80.8%	>
Cereal crops		12.0%	68.9%	45	–12.1–24.1%	<
Tillage		15.5%	10.4%	58	2.1–29.0%	NS
Other culture types		9.63%	10.4%	36	–1.3–20.6%	NS
PLMSHL						
Grasslands	χ^2=257.1 df=3 p<0.001	85.2%	29.7%	144	65.6–104.8%	>
Cereal crops		1.2%	43.7%	2	–4.8–7.2%	<
Tillage		13.0%	23.5%	22	–5.6–31.6%	NS
Other culture types		0.6%	3.1%	1	–3.6–4.8%	NS

significantly compared with the ‘laying’ session in wheat fields (OITH), both in vegetation (Tukey post hoc test: p<0.001, Fig. 7a, Table 2) and on the ground (Tukey post hoc test: p<0.001, Fig. 6a, Table 2), while dry grasslands (OITH) became richer only in the vegetation stratum (Tukey post hoc test: p<0.001, Fig. 7a, Table 2). Moreover, vegetation-dwelling invertebrates were significantly less numerous in tillage plots (PLMSHL) than in other habitats (Tukey post hoc tests: wheat: p<0.001; dry grassland: p<0.001; hay meadow: p<0.001; pasture: p<0.001, Fig. 7a, Table 2), while ground-dwelling invertebrates were more abundant in dry grasslands (OITH) than in pastures, tillage plots (PLMSHL), and hay meadows (PLMSHL) (Tukey post hoc

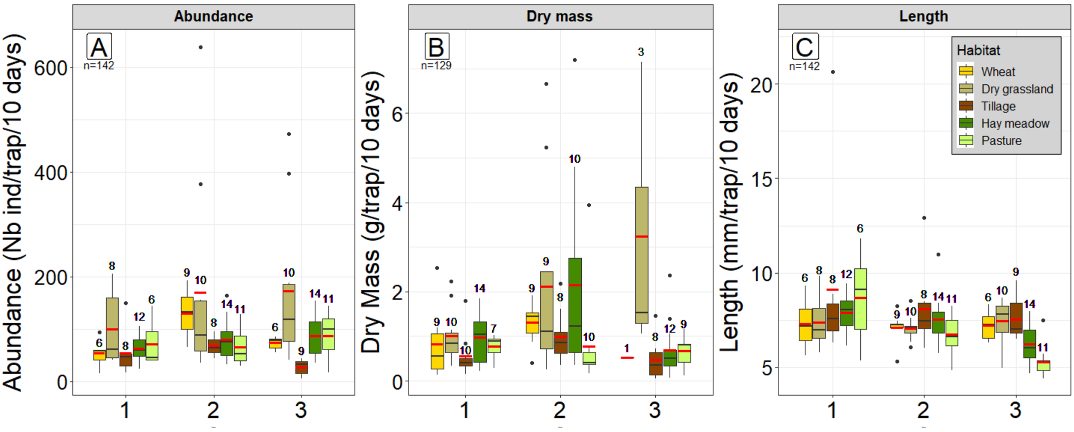

Fig. 6. Abundance of ground-dwelling invertebrates per trap (mean ± sd) (A), Dry mass of ground-dwelling invertebrates per trap (B), length of ground-dwelling invertebrates per trap (C) in the different habitats sampled for the three sampling sessions (S1: early May – laying session, S2: early June – hatching session, S3: early July-rearing session). Wheat (yellow), Dry Grassland (persimmon), Tillage (brown), Hay meadow (dark green), Pasture (light green). Means are represented by the horizontal red line. The number of samples per habitat is indicated above each box.

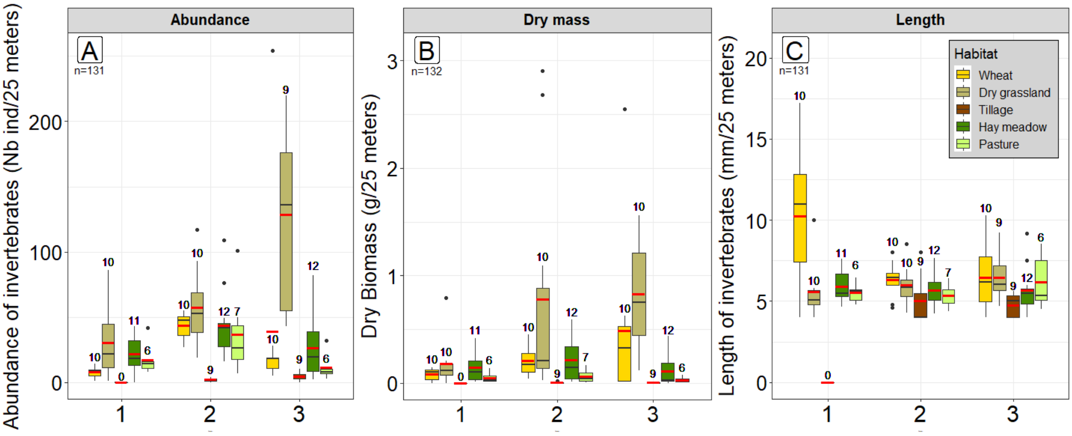

Fig. 7. Abundance of vegetation-dwelling invertebrates per 25 meters (mean ± sd) (A), Dry mass of vegetation-dwelling invertebrates per 25 meters (B), length of vegetation-dwelling invertebrates per 25 meters (C) in the different habitats sampled for the three sampling sessions (S1: early May – laying session, S2: early June – hatching session, S3: early July-rearing session). Wheat (yellow), Dry Grassland (persimmon), Tillage (brown), Hay meadow (dark green), Pasture (light green). Means are represented by the horizontal red line. The number of samples per habitat is indicated above each box.

Table 2. Average (±SE) invertebrate abundance (nb ind) and dry mass(g) per pitfall trap and per sweep-netting transect in the different habitat types sampled during the three sampling sessions. For each session, the coefficients of variation of abundance and dry mass within each habitat are given and are bold when the value is very high.

S	Study site	Habitats	Parameters	Pitfall trap		Sweep-net	
				Means	Coefficients of variation	Means	Coefficients of variation
1	OITH	Wheat	Abundance	53.8 ± 10.7	48.9%	7.9 ± 1.2	47.8%
			Dry mass	0.82 ± 0.25	90.2%	0.08 ± 0.02	75.0%
	OITH	Dry grassland	Abundance	100.4 ± 24.8	69.9%	30.0 ± 8.2	86.5%
			Dry mass	1.0 ± 0.19	61.0%	0.17 ± 0.07	**127.8%**
	PLMSHL	Tillage	Abundance	53.5 ± 14.6	77.0%	–	–
			Dry mass	0.55 ± 0.15	87.2%	–	–
	PLMSHL	Hay meadow	Abundance	62.1 ± 6.8	38.1%	21.5 ± 4.2	64.6%
			Dry mass	0.97 ± 0.14	55.7%	0.14 ± 0.04	**100.0%**
	PLMSHL	Pasture	Abundance	71.3 ± 18.3	62.8%	17.3 ± 5.1	72.3%
			Dry mass	0.77 ± 0.10	33.7%	0.05 ± 0.02	**100.0%**
2	OITH	Wheat	Abundance	129.3 ± 14.3	33.2%	43.3 ± 3.2	23.1%
			Dry mass	1.31 ± 0.16	35.8%	0.21 ± 0.05	69.9%
	OITH	Dry grassland	Abundance	169.2 ± 61.1	**114.2%**	57.5 ± 9.6	52.7%
			Dry mass	2.12 ± 0.76	**107.5%**	0.78 ± 0.35	**141.4%**
	PLMSHL	Tillage	Abundance	68.3 ± 6.8	28.3%	1.8 ± 0.5	78.9%
			Dry mass	0.99 ± 0.22	61.6%	0.06 ± 0.02	**250.0%**
	PLMSHL	Hay meadow	Abundance	79.2 ± 9.7	45.8%	43.5 ± 7.6	60.7%
			Dry mass	2.14 ± 0.71	**105.6%**	0.22 ± 0.06	99.3%
	PLMSHL	Pasture	Abundance	65.4 ± 10.1	51.1%	36.6 ± 12.1	87.4%
			Dry mass	0.78 ± 0.36	**107.5%**	0.06 ± 0.02	**96.7%**
3	OITH	Wheat	Abundance	73.5 ± 5.2	17.3%	38.8 ± 24.02	**196.1%**
			Dry mass	0.52	–	0.24 ± 0.07	89.5%
	OITH	Dry grassland	Abundance	172.7 ± 46.7	85.6%	128.6 ± 23.2	54.2%
			Dry mass	3.24 ± 1.96	104.3%	0.48 ± 0.12	73.4%
	PLMSHL	Tillage	Abundance	27.1 ± 4.8	53.1%	4.6 ± 1.2	80.0%
			Dry mass	0.48 ± 0.17	97.9%	0.01± 0.01	97.1%
	PLMSHL	Hay meadow	Abundance	86.5 ± 10.2	43.8%	26.5 ± 6.8	89.4%
			Dry mass	0.69 ± 0.18	**194.4%**	0.12 ± 0.04	**127.2%**
	PLMSHL	Pasture	Abundance	87.5 ± 13.0	49.3%	11.3 ± 4.3	92.9%
			Dry mass	0.67 ± 0.12	55.2%	0.03 ± 0.01	91.4%

tests: $p<0.001$; tillage: $p=0.003$; hay meadow: $p=0.006$, Fig. 6a, Table 2).

During the ‘rearing’ session (S3: early July), invertebrate abundance decreased at the ground level in wheat (OITH) and tillage plots (PLMSHL) compared with the “hatching” session (Tukey post hoc tests: wheat: $p=0.004$; tillage: $p=0.003$, Fig. 6a, Table 2). On the contrary, an increase was noticed in the vegetation stratum of dry grasslands (OITH) (Tukey post hoc test:

$p<0.001$, Fig. 7a, Table 2). During this period, dry grasslands (OITH) offered more invertebrates than other habitats both on the ground (Tukey post hoc tests: wheat: $p=0.02$; tillage: $p<0.001$; hay meadow: $p=0.01$; pasture: $p=0.03$, Fig. 6a, Table 2) and in the vegetation (Tukey post hoc tests: wheat: $p=0.02$; tillage: $p<0.001$; hay meadow: $p<0.001$; pasture: $p<0.001$, Fig. 7a, Table 2). Moreover, hay meadows (PLMSHL) and wheat fields (OITH) were richer than tillage plots (PLMSHL) (Tukey post hoc test: $p<0.001$, Fig. 7a, Table 2), and wheat fields (OITH) were richer than pastures (PLMSHL) in terms of vegetation, albeit not significantly (Tukey post hoc test: $p=0.06$, Fig. 7a, Table 2). On the ground, plots under tillage (PLMSHL) were poorer than the other four habitats (Tukey post hoc tests: wheat: $p=0.006$; dry grassland: $p<0.001$; pasture: $p=0.004$; hay meadow: $p<0.001$, Fig. 6a, Table 2). Every habitat showed strong variations in abundance between plots, particularly during the ‘hatching’ session and the ‘rearing’ session, especially in dry grasslands (OITH) (Fig. 6a and 7a, Table 2).

3.4. Invertebrate dry mass

Concerning the DM, no differences were observed between habitats for the ground-dwelling invertebrates (ANOVA, $F_{4.45}=1.66$, $p>0.05$, Fig. 6b, Table 2). However, a session effect was observed in wheat (OITH), where the DM per pitfall trap increased significantly between the ‘laying’ and ‘hatching’ sessions (Wilcoxon matched-pairs test: $p<0.05$, Fig. 6b, Table 2). Otherwise, none of the habitats presented differences between sessions (Friedman and Wilcoxon matched-pairs tests, $p>0.05$).

Concerning the vegetation-dwelling invertebrates, no differences were observed between the habitats during the ‘laying’ session (ANOVA, $F_{3.33}=1.28$, $p>0.05$, Fig. 7b, Table 2). Nonetheless, during the ‘hatching’ period, the DM per transect was significantly lower in tillage plots (PLMSHL) than in the four other habitats (Tukey post hoc tests: $p<0.001$, Fig. 7b, Table 2) and was higher in dry grasslands (OITH) than in pastures (PLMSHL) (Tukey post hoc test: $p=0.004$). Finally, during the ‘rearing’ session, dry grasslands presented a significantly higher DM per transect than hay meadows (PLMSHL), pastures (PLMSHL), and tillage plots (PLMSHL) (Tukey post hoc tests: $p<0.001$, Fig. 7b, Table 2) and displayed a higher, but not significant, tendency than wheat fields (Tukey post hoc test: $p=0.09$, Fig. 7b, Table 2). Moreover, wheat (OITH) presented a higher DM compared with tillage plots (PLMSHL) (Tukey post hoc test: $p<0.003$, Fig. 7b, Table 2) and displayed a higher, but not significant, tendency than pastures (PLMSHL) (Tukey post hoc test: $p=0.06$). A session effect was observed in dry grasslands (OITH), where the DM was higher in the ‘rearing’ period than in the ‘laying’ session (Wilcoxon matched-pairs test: $p=0.04$, Fig. 7b, Table 2). Finally, strong variations of DM between plots were observed, especially in dry grasslands (OITH), hay meadows (PLMSHL), and pastures (PLMSHL) during the ‘hatching’ session at the ground level and in wheat fields (OITH) during the ‘rearing’ session at the vegetation stratum (Fig. 6b and 7b).

3.5. Invertebrate size

The lengths of ground-dwelling invertebrates were similar across habitats during the “laying” and “hatching” sessions (ANOVA, $F_{4.35}=0.70$, $p>0.05$, Fig. 6c). However, during the ‘rearing’ session, they were longer in dry grasslands (OITH), tillage plots (PLMSHL), and wheat fields (OITH) than in pastures (PLMSHL) (Tukey post hoc tests: $p<0.004$, Fig. 6c). They were also longer in dry grasslands (OITH) and tillage plots (PLMSHL) than in hay meadows (PLMSHL) (Tukey post hoc test: $p\leq0.03$, Fig. 6c). Moreover, the length of ground-dwelling invertebrates decreased significantly between the ‘laying’ and ‘hatching’ sessions in pastures (PLMSHL) (Tukey post hoc test: $p=0.03$, Fig. 6c) and between the ‘hatching’ and ‘rearing’ sessions in pastures (PLMSHL) and hay meadows (PLMSHL) (Wilcoxon matched-pairs tests: $p=0.007$ and $p=0.009$, respectively). In vegetation, invertebrates were longer in wheat fields (OITH) than in dry grasslands (PLMSHL) (Wilcoxon matched-pairs test, $p=0.01$) and tended to be longer than in hay meadows (PLMSHL) and pastures (PLMSHL) (Wilcoxon matched-pairs test: $p=0.18$ and $p=0.17$, Fig. 7c) during the ‘laying’ session. The length then decreased significantly in wheat fields (OITH) in the ‘hatching’ session (Tukey post hoc test, p=0.02, Fig. 7c). No differences were observed between habitats until the ‘rearing’ session (ANOVA, hatching session: $F_{4.43}$=2.13, p>0.05; rearing session: $F_{4.40}$=1.91, p>0.05, Fig. 7c).

4. Discussion

The slow decline of the curlew core population observed in PLMSHL contrasts markedly with the steady increase of the core population of OITH and MINE since 2006. Various hypotheses can be proposed to explain these opposing trends. First of all, some individuals may have moved from PLMSHL to OITH and MINE. Turpaud-Fizzala (2012) estimated the number of fledglings per couple at 0.37 in PLMSHL. However, this rate was lower than the minimum productivity rate of 0.48 required to maintain populations as defined by Grant *et al.* (1999).

Consequently, it is unlikely that the adults or the few chicks produced at PLMSHL alone can explain the increase in numbers in OITH and MINE over the past 15 years. However, a few individuals of PLMSHL may have initiated colonization in OITH and MINE in the first years, with the numbers then increasing thanks to the arrival of adults or sub-adults from other populations in Europe which settled at the site during stopovers while migrating. In addition, it is possible that productivity in OITH and MINE is higher than in PLMSHL and that the chicks born there have returned to their birthplace.

Concerning the changes in distribution observed in PLMSHL, the conversion of meadows to cropland in some areas where the birds used to breed may be a cause of the movement of individuals within the area. Gilet *et al.* (2002) noted the disappearance of five out of six breeding pairs in the south of PLMSHL the year following the disappearance of large areas of grassland. Thus, the presence of grassland is probably a determining criterion for curlews to select their nesting area. Besides this factor, our study highlights the preference of the species for grassland for feeding at both study sites. Both Berg (1992) in Sweden and Valkama *et al.* (1998) in Finland have reported that curlews were concentrated mainly in grasslands in those countries, even when this habitat was poorly available in the environment. Its attractiveness can be explained by several factors, starting with the vegetation height. Indeed, depending on management practices, meadows offer a more heterogeneous vegetation structure than wheat fields and tillage plots, becoming maize or sunflower plots during the season, with ‘high sward’ plots, allowing curlews to escape from predators more easily, and ‘low sward’ plots, facilitating foraging (Pearce-Higgins & Grant 2006). In addition, in areas of intensive agriculture, grasslands constitute key feeding habitats where the food resource is more abundant and of better quality, as long as their management is not intensive (Hendrickx *et al*. 2007). Conversely, cereal fields seemed to be avoided by curlews, while no trend was observed in tillage areas. Ploughing and the repeated use of insecticides may explain the low attractiveness of these habitats due to their consequent lack of invertebrates (Chamberlain *et al.* 2000, Clere & Bretagnolle 2001). Also, once wheat has reached a certain level of development, the vegetation becomes too high and dense for birds to feed in.

The analysis of invertebrate availability and size confirms that dry grasslands often provide a better food resource in OITH, especially during the brood rearing period, although they were rarer at this site. Wheat fields also provide an important food resource, with numerous or large prey in the first half of the breeding season. In the PLMSHL, tillage plots may provide as much potential prey – or at least prey of the same size – as pastures and hay meadows at the ground level but remains a poor provider at the level of the vegetation stratum in all periods. Hay meadows and pastures seem to remain the most favourable habitats within PLMSHL, with a constant abundance of prey, although the quality declines during the breeding period due to a decrease in invertebrate size. Thus, food resources are generally higher in terms of availability and quality in the sampled habitats of OITH than those of PLMSHL, starting from the hatching period (early June), which suggests that conditions there may be more favourable for fledge growth and survival.

At the beginning of May (the laying period), parents need energy to defend their nests from predators (Turpaud-Fizzala 2012), especially since egg production during the pre-incubation period requires resources for females (Högstedt 1974, Berg 1992). In OITH, dry grasslands present more but smaller vegetation-dwelling invertebrates than wheat. Although less abundant, these prey types are therefore perhaps more profitably foraged in wheat fields because of their larger size. Moreover, hay meadows in PLMSHL offer more vegetation-dwelling invertebrates than the wheat fields of OITH while pastures display equivalent abundances of invertebrates to the dry grasslands and wheat fields of the site. Finally, tillage plots in PLMSHL seem to provide as much ground-dwelling invertebrates and of the same size as the other four habitats. Thus, both habitats sampled in OITH must be adequate for food supply, as well as in PLMSHL, hay meadows, pastures, tillage plots may be beneficial too.

From early June (the hatching period) onwards, an imbalance appears between OITH, where the quality and availability of potential prey in both sampled habitats increases, and PLMSHL, where tillage plots appears to be very poor in terms of vegetation-dwelling invertebrates and pastures host smaller ground-dwelling prey than during the laying period. Indeed, the dry grasslands and wheat fields of OITH became richer with vegetation-dwelling invertebrates than in the laying session, while ground-dwelling invertebrates became more numerous in the dry grasslands of OITH than in hay meadows, pastures, and tillage plots of PLMSHL. Dry grasslands and wheat fields are therefore two of the better-quality foraging habitats for adults and newly born chicks at this time. Hay meadows that have neither suffered a drop in abundance nor in the size of invertebrates also remain an interesting feeding habitat.

The decrease in the size of ground-dwelling invertebrates continues in early July (the rearing period), not only in pastures but also in hay meadows, where their length decreases as well. These results could be attributed to management practices employed in PLMSHL. Indeed, hay meadows are generally fertilised and mowed once or twice between May and June, while pastures begin to be grazed with a high density of livestock in the same period. Some studies have reported that intensive grazing, mowing, or fertilising may negatively affect the size of invertebrates (Blake *et al*. 1994, Birkhofer *et al*. 2015). Thus, management practices in PLMSHL might limit the availability of profitable prey for adults and chicks. In addition, early mowing is one of the main causes of reproductive failure: Turpaud-Fizzala (2012) indicated that in PLMSHL, mowing a plot close to that of the nest may be enough to cause the curlews to abandon it. Gilet *et al*. (2002) has also shown that pastures have the lowest reproductive success in Deux-Sèvres, and that this can be explained by the increased risk of eggs being trampled by cattle (Grant *et al*. 1999).

In addition, at this same period, the gap between dry grasslands in OITH and other habitats grows wider, with a greater abundance of vegetation-dwelling and ground-dwelling invertebrates than in the four other habitats and longer ground-dwelling invertebrates than in hay meadows and pastures. While prey in dry grasslands therefore become increasingly numerous and large in size in OITH through the breeding season, hay meadows and pastures decline in quality by losing their larger sized prey. It should be added that wheat fields sampled in OITH showed high abundances of invertebrates, especially in early June (hatching period). Although avoided by curlews, it seems that certain plots of wheat could provide a great abundance of invertebrates and perhaps enrich adjacent habitats with prey. It should also be noted that farmers who agreed to participate in the study were reluctant to use pesticides and herbicides. Therefore, the results of the study do not necessarily reflect the reality of all cereal fields. Collaboration with more conventional farmers would allow us to know if local wheat crops are in general as rich as those sampled in this study.

OITH seems to offer better feeding conditions during the rearing of chicks especially thanks to its dry grasslands. These results are similar to those of a local study that demonstrated that among the six special protection areas of the region, OITH was the site with the highest abundances of Orthoptera (Poirel pers. comm.). The peak of larval abundance for this order of insects being between June and July, the breeding area probably provides an important food resource for the chicks. Moreover, tillage plots (PLMSHL) was very poor for food species both on the ground and in the vegetation stratum, with very low abundance and DM from the beginning of June to July (hatching and rearing periods). Therefore, this habitat, very common within PLMSHL, seemed to limit the availability of potential prey in this territory, although curlews can benefit from higher visibility there, facilitating the detection of prey (Valkama *et al*. 1998), as well as access to endogenous fauna (such as earthworms and larvae), enabled by better penetrability of the soil (De Jong 2012).

The availability and size of potential prey are not the only parameters to be taken into account when judging the capacity of a habitat to provide a favourable food resource. Indeed, the nutritional quality of the invertebrates that a habitat offers seems to play a major role in its attractiveness to insectivorous birds (Kaspari & Joern 1993, McCarty & Winkler 1999). Razeng and Watson (2015) showed that prey with a greater energy gain for insectivorous birds contain a high proportion of crude fat and/or crude protein. An analysis of invertebrates by family would help to assess how much the habitats sampled for this study provide suitable prey for chicks. Moreover, juveniles of shorebirds do not appear to have the same requirements for prey selection. Their short bills do not yet allow them to probe the ground. For example, black-tailed godwit chicks appear to feed almost exclusively on flying insects, including several families of Diptera and Hymenoptera (Schekkerman & Beintema 2007). The abundance and size of prey within the vegetation is therefore probably a determining factor in ensuring good growth and survival conditions for young chicks.

Overall, this study encourages the implementation of new management measures. Currently, more than 1,500 ha of grassland are under AES contracts in PLMSHL and are therefore managed favourably for the conservation of lowland birds by imposing a grazing ban, mowing the grasslands between 20 May and 20 August, and applying fertilisers. However, these specifications are based on the phenology of the little bustard and therefore occur well after the first curlew eggs have been laid (Gilet *et al*. 2002, Turpaud-Fizzala 2012). Therefore, this study advises adapting these agri-environmental measures by bringing forward the date of non-intervention on the plots to improve the quality of habitats for curlew breeding and to avoid the destruction of broods (Pakanen *et al*. 2016, Sharps *et al*. 2016). In OITH, the sampled dry grasslands were all under AES contracts, but it should be noted that mowing activity is much lower in this area and that many grassland areas without AES contracts remain intact throughout the breeding season (Supplementary Material Figs. S1–S2). Therefore, practices in this sector may already be partially favourable.

In conclusion, dry grasslands have a great richness in prey for adults and the presence of suitable prey for chicks, especially during the rearing period of young curlews. This habitat, present only in OITH, may partly explain the increased attractiveness of this area for the species compared with PLMSHL. However, each habitat has considerable variability, largely related to management, probably through the use or non-use of certain pesticides, mowing intensity, or different grazing pressures. Appropriate management measures are therefore necessary to promote the availability of prey for curlews at sites where they are most likely to nest: that is, in the meadows. The increase of dry grassland areas via the introduction of new AESs would therefore be highly favourable to curlews in OITH. Moreover, introducing suitable management of the grasslands (both hay and pasture) of PLMSHL would likely favour the reproductive success of the breeding pairs and consequently maintain and increase the number of the breeding pairs. These AESs could, however, take greater account of the phenology of the species to maximise their efficiency.

Finally, given the fact that food resources appear to be more plentiful in OITH than in PLMSHL, we can hypothesise that breeding conditions for curlews are better in OITH because of the higher availability of potential prey. That said, one of the major factors in the decline of the Eurasian Curlew in Europe is predation on eggs and chicks, mainly by foxes and corvids (Roodbergen *et al*. 2012, Brown 2015). The vegetation structure (Laidlaw *et al*. 2015) or the proximity to woodlands (Douglas *et al*. 2014, Wilson *et al*. 2014) can influence the vulnerability of chicks and eggs to predators. It is therefore possible that the landscape features that oppose OITH and PLMSHL may have an influence on the predation rate and therefore on breeding success.

Pesimäympäristön laadun ja monimuotoisuuden vaikutus kuovipopulaatioihin Länsi-Ranskassa

Kuovin (*Numenius arquata*) populaatiot Euroopassa ovat pienentyneet elinympäristöjen pirstoutumisen ja laadun heikentymisen seurauksena. Syy tähän muutokseen on enimmäkseen maatalouden käytäntöjen muutokset. Ranskan Deux-Sèvresin alueella kuoviparien määrän on havaittu vähenneen vuodesta 2000 sen pääesiintymisalueella. Samaan aikaan noin 80 kilometriä pohjoiseen on ilmestynyt uusi pesimäalue, jossa parien määrä on kasvanut vastaavalla ajanjaksolla. Pohjoisella pesimäalueella on runsaasti vehnäpeltoja ja harvinaisempia kuivia ruohomaita, kun taas etelässä maatalousmaisema koostuu enimmäkseen kyntömaista, heinävaltaisista niityistä ja laitumista. Tässä tutkimuksessa pyrimme arvioimaan näiden kahden alueen eroja ravinnon saatavuuden ja laadun suhteen. Keräsimme tietoa maaperän ja kasvillisuuskerroksen selkärankaisista kuoppapyydyksillä ja haaveilla kuovien lisääntymisajanjaksolla kolmessa eri vaiheessa. Kuivien ruohomaisen havaittiin olevan ravinnon saatavuuden kannalta parhaimmat elinympäristöt pohjoisessa poikasten hoidon ajanjaksolla. Heinävaltaiset niityt ja laitumet olivat puolestaan parhaimpia elinympäristöjä eteläisellä pesimäalueella. Tulosten perusteella pohjoisen alueen elinympäristöt tarjoavat enemmän ravintoa kuoveille kuin etelän alueen elinympäristöt. Siksi pohjoisella alueella on todennäköisesti paremmat pesintäolosuhteet, erityisesti poikasten kasvun kannalta. Kuivien ruohomaiden pinta-alan lisääminen pohjoisella pesimäalueella ja toisaalta maatalouskäytäntöjen sopeuttaminen eteläisellä pesimäalueella suosisi kuovin paikallisia kantoja.

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References

Bellebaum, J. & Bock, C. 2009: Influence of ground predators and water levels on lapwing (*Vanellus vanellus*) breeding success in two continental wetlands. — Journal of Ornithology 150:221–230. http://dx.doi.org/10.1007/s10336-008-0341-7

Benton, T. G., Bryant, D. M., Cole L. & Crick, H. Q. P. 2002: Linking agricultural practice to insect and bird populations: A historical study over three decades. — Journal of Applied Ecology 39:673–687. https://doi.org/10.1046/j.1365-2664.2002.00745.x

Berg, A. 1992: Habitat selection by breeding curlews (*Nwnenius arquata*) on mosaic farmland. — Ibis 134:355–360.https://doi.org/10.1111/j.1474-919X.1992.tb08015.x

Berg, A. 1993: Food resources and foraging success of curlews (*Numenius arquata*) in different farmland habitats. — Ornis Fennica 70:22.

Bertholdt, N. P., Gill, J. A., Laidlaw, R. A. & Smart, J. 2017: Landscape effects on nest site selection and nest success of northern lapwing (*Vanellus vanellus*) in lowland wet grasslands. — Bird Study 64:30–36. https://doi.org/10.1080/00063657.2016.1262816

Berthomé, J. F. 2011: Document d'Objectifs du site Natura 2000 FR5412014 ZPS Plaine d'Oiron-Thénezay. GODS, Niort, 128 p. (In French)

Berthomé, J. F. & Turpaud-Fizzala V. 2012: Document d'objectifs du site FR5412022 ZPS Plaine de la Mothe-Saint Héray-Lezay. GODS, Niort, 178 p. (In French)

Birkhofer, K., Smith, H. G., Weisser, W. W., Wolters, V. & Gossner, M. M. 2015: Land-use effects on the functional distinctness of arthropod communities. — Ecography 38:889–900. https://doi.org/10.1111/ecog.01141

Blake, S., Foster, G. N., Eyre, M. D. & Luff, M. L. 1994: Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. — Pedobiologia 38:502–512.

Bretagnolle, V., Villers, A., Denonfoux, L., Cornulier, T., Inchausti, P. & Badenhausser, I. 2011: Rapid recovery of a depleted population of little bustards (*Tetrax tetrax*) following provision of alfalfa through an agri-environment scheme. — Ibis 153:4–13. https://doi.org/10.1111/j.1474-919X.2010.01092.x

Brown, D. J. 2015: International single species action plan for the conservation of the Eurasian curlew (*Numenius arquata arquata*, *N. a. orientalis*, and *N. a. suschkini*). — AEWA Technical Series 58.

Butchart, S. H. M., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C. & Bruno J. 2010: Global biodiversity: Indicators of recent declines. — Science 328:1164–1168. https://www.science.org/doi/10.1126/science.1187512

Butler, S. J. & Gillings, S. 2004: Quantifying the effects of habitat structure on prey detectability and accessibility to farmland birds. — Ibis 146:123–130. https://doi.

org/10.1111/j.1474-919X.2004.00352.x

Byers, C. R., Steinhorst, K. S. & Krausman, P. R. 1984: Clarification of a technique for analysis of utilization-availability data. — Journal of Wildlife Management 48:1050-1053. https://doi.org/10.2307/3801467

Chamberlain, D. E., Fuller, J., Bunce, G. H., Duckworth, J. C. & Shrubb, M., 2000: Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. — Journal of Applied Ecology 37:771–788. https://doi.org/10.1046/j.1365-2664.2000.00548.x

Clere, E. & Bretagnolle, V. 2001: Food availability for birds in farmland habitats: Biomass and diversity of arthropods by pitfall trapping technique. — Revue d'Ecologie.

Clough, Y., Holzschuh, A., Gabriel, D., Purtauf, T., Kleijn, D., Kruess, A., Dewenter, I. S. & Tscharntke, T., 2007: Alpha and beta diversity of arthropods and plants in organically and conventionally managed wheat fields. — Journal of Applied Ecology 44:804–812. https://doi.org/10.1111/j.1365-2664.2007.01294.x

De Jong, A. 2012: Seasonal shift of foraging habitat among farmland breeding Eurasian curlews (*Numenius arquata*). — Ornis Norvegica 35:23. https://doi.org/10.15845/on.v35i0.237

Devereux, C. L., Mckeever, C. U., Benton, T. G. & Whittingham, M. J. 2004: The effect of sward height and drainage on common starlings (*Sturnus vulgaris*) and northern lapwings (*Vanellus vanellus*) foraging in grassland habitats. — Ibis 146:115–122. https://doi.org/10.1111/j.1474-919X.2004.00355.x

Douglas, D. J. T., Bellamy, P. E., Stephen L. S., Pearce-Higgins J. W., Wilson J. D. & Grant M. C. 2014: Upland land use predicts population decline in a globally near-threatened wader. — Journal of Applied Ecology 51:194-203. https://doi.org/10.1111/1365-2664.12167

Doxon, E. D., Davis, C. A. & Fuhlendorf, S. D. 2011: Comparison of two methods for sampling invertebrates: Vacuum and sweep-net sampling. — Journal of Field Ornithology 82:60–67. https://doi.org/10.1111/j.1557-9263.2010.00308.x

Dubois, T. 2011: Document d'objectifs du site Natura 2000FR5412018 ZPS des plaines du Mirebalais et du Neuvillois. LPO Vienne, Poitiers, 122 p. (In French)

Dunn, O. J. 1964: Multiple comparisons using rank sums. — Technometrics 6:241–252. https://doi.org/10.1080/00401706.1964.10490181

Eglington, S. 2008: Managing water levels on wet grasslands for breeding waders: The use of shallow wet features. — PhD Thesis, University of East Anglia.

European Commission 2009: Commission Regulation (EC). No. 1122/2009

Fisher, R. A. 1925: Statistical methods for research workers. — 1st edition, Oliver and Boyd, Edinburgh.

Friedman, M. 1939: A correction: The use of ranks to avoid the assumption of normality implicit in the analysis of variance. — Journal of the American Statistical Association 34:109. https://doi.org/10.2307/2279169

Gilet, V., Dieuleveut, T., Bernard, R. & Corbin, J., 2002: Reproduction et protection rapprochée du Courlis cendré Numenius arquata en Pays Mellois en 2002. — Le Lirou 21:10–14. (In French)

Grant, M. C., Orsman, C., Easton, J., Lodge, C., Smith, M., Thompson, G., Rodwell, S. & Moore, N. 1999: Breeding success and causes of breeding failure of curlew (*Numenius arquata*) in Northern Ireland. — Journal of Applied Ecology 36:59–74. https://doi.org/10.1046/j.1365-2664.1999.00379.x

Green, R. E. & Cadbury, C. J. 1987: Breeding waders of lowland wet grasslands. — RSPB Conservation Review 1:10–13.

Gregory, R. D., Noble D. G. & Custance J. 2004: The state of play of farmland birds: Population trends and conservation status of lowland farmland birds in the United Kingdom. — Ibis 146:1–13. https://doi.org/10.1111/j.1474-919X.2004.00358.x

Harris, S. J., Massimino, D., Newson, S. E., Eaton, M. A., Balmer, D. E., Noble D. G., Musgrove A. J., Gillings, S., Procter, D. & Pearce-Higgins, J. W. 2016: The breeding bird survey 2015. — BTO Research Report 687.

Hendrickx, F., Maelfait, J.-P., Wingerden, W. V., Schweiger, O., Speelmans, M., Aviron, S., Augenstein, I., Billeter, R., Bailey, D. & Bukacek, R. 2007: How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. — Journal of Applied Ecology 44:340–351. https://doi.org/10.1111/j.1365-2664.2006.01270.x

Högstedt, G. 1974: Length of the pre-laying period in the lapwing (*Vanellus vanellus L.*) in relation to its food resources. — Ornis Scandinavica (Scandinavian Journal of Ornithology) 5:1–4. https://doi.org/10.2307/3675888

Kajak, A. 1978: The effect of fertilizers on numbers and biomass of spiders in a meadow. — Symposia of the Zoological Society of London 42:125–129.

Kaspari, M. & Joern, A. 1993: Prey choice by three insectivorous grassland birds: Reevaluating opportunism. — Oikos 68:414–430. https://doi.org/10.2307/3544909

Kentie, R, Hooijmeijer, J. C., Trimbos, K. B., Groen, N. M. & Piersma, T. 2013: Intensified agricultural use of grasslands reduces growth and survival of precocial shorebird chicks. — Journal of Applied Ecology 50:243–251. https://doi.org/10.1111/1365-2664.12028

Kleijn, D., Schekkerman, H., Dimmers, W. J., Van Kats, R. J. M., Melman, D. & Teunissen, W. A. 2010: Adverse effects of agricultural intensification and climate change on breeding habitat quality of black-tailed godwits (*Limosa limosa*) in the Netherlands. — Ibis 152:475–486. https://doi.org/10.1111/j.1474-919X.2010.01025.x

Kruk, M., Noordervliet, M. A. W. & Ter Keurs, W. J. 1997: Survival of black-tailed godwit chicks (*Limosa limosa*) in intensively exploited grassland areas in the Netherlands. — Biological Conservation 80:127–133. https://doi.org/10.1016/S0006-3207(96)00131-0

Kruskal, W. H. & Wallis, W. A. 1952: Use of ranks in one-criterion variance analysis. —Journal of the American Statistical Association 47:583–621. https://doi.org/10.1080/01621459.1952.10483441

Laidlaw, R. A., Smart, J., Smart, M. A. & Gill, J. A. 2015: The influence of landscape featureson nest predation rates of grassland breeding waders. — Ibis 157:700-712. https://doi.org/10.1111/ibi.12293

Lartigau, C. 2018: Protection des limicoles en milieu agricoles. — Lirou 37:9–13. (In French)

Macdonald, M. A. & Bolton, M. 2008: Predation on wader nests in Europe. — Ibis 150:54–73. https://doi.org/10.1111/j.1474-919x.2008.00869.x

McCarty, J. P. & Winkler, D. W. 1999: Foraging ecology and diet selectivity of tree swallows feeding nestlings. — The Condor 101:246–254. https://doi.org/10.2307/1369987

McCracken, D. I. & Tallowin, J. R. 2004: Swards and structure: The interactions between farming practices and bird food resources in lowland grasslands. — Ibis 146:108–114. https://doi.org/10.1111/j.1474-919x.2004.00360.x

McKeever, C. U. 2003: Linking grassland management, invertebrates and northern lapwing productivity. PhD Thesis, University of Stirling.

Mignon, J., Haubruge, E. & Frédéric, F. 2016: Clé d'identification des principales familles d'insectes d'Europe. Presses agronomiques de Gembloux. (In French)

Neu, C. W., Byers, C. R. & Peek, J. M. 1974: A technique for analysis of utilization-availability data. — Journal of Wildlife Management 38:541-545. https://doi.org/10.2307/3800887

Niemczynowicz, A., Świętochowski, P., Brzeziński, M. & Zalewski, A. 2017: Non-native predator control increases the nesting success of birds: American mink preying on wader nests. — Biological Conservation 212:86–95. https://doi.org/10.1016/j.biocon.2017.05.032

Pakanen, V.-M, Aikio, S., Luukkonen, A., & Koivula, K. 2016: Grazed wet meadows are sink habitats for the southern dunlin (*Calidris alpina schinzii*) due to nest trampling by cattle.— Ecology and Evolution 6:7176–7187. https://doi.org/10.1002/ece3.2369

Patrelle, C., Fouquet, M., Coquatrix, E. & Dumeige. B. 2017: Plan national de gestion (2015–2020). (In French)

Pearce-Higgins, J. W., Brown, D. J., Douglas, D. J. T., Alves, J. A., Bellio, M., Bocher, P., Buchanan, G. M., Clay, R. P., Conklin, J., Crockford. N., Dann, P., Elts, J., Friss, C., Fuller, R. A., Gill, J. A., Gosbell, K., Johnson, J. A., Marquez-Ferrando, R., Masero, J. A., Melville, D. S., Millington, S., Minton, C., Mundkur, T., Nol, E., Pehlak, H., Piersma, T., Robin, F., Rogers, D. I., Ruthrauff, D. R., Senner, N. R., Shah, J. N., Sheldon, R. D., Solloviev, S. A., Tomkovich, P. S. & Verkuil, Y. I. 2017: A global threats overview for Numeniini populations: Synthesising expert knowledge for a group of declining migratory birds. — Bird Conservation International 27:6–34. https://doi.org/10.1017/s0959270916000678

Pearce-Higgins, J. W. & Grant, M. C. 2006: Relationships between bird abundance and the composition and structure of moorland vegetation. — Bird Study 53:112–125. https://doi.org/10.1080/00063650609461424

Poirel, C. 2017: Changement de répartition, succès reproducteur, sélection d'habitat: la situation du Courlis cendré (*Numenius arquata*) dans la Vienne en 2015–2016. —L'Outarde 53:5–13. (In French)

Puech, C. 2014. Hétérogénéité des pratiques agricoles biologiques et conventionnelles dans les paysages bretons: Effets sur les communautés d'insectes auxiliaires à différentes échelles. PhD Thesis, Université de Rennes 1. (In French)

QGIS Development Team (2017). Quantum GIS. Open Source Geospatial Foundation Project.

R Core Team 2019: R version 3.6.0. — R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Razeng, E., & Watson, D. M. 2015: Nutritional composition of the preferred prey of insectivorous birds: Popularity reflects quality. — Journal of Avian Biology 46:89–96. https://doi.org/10.1111/jav.00475

Robson, G. 1998: The breeding ecology of curlew (*Numenius arquata*) on North Pennine moorland. PhD Thesis, University of Sunderland.

Roodbergen, M., van der Werf, B. & Hötker. H. 2012: Revealing the contributions of reproduction and survival to the Europe-wide decline in meadow birds: Review and meta-analysis. — Journal of Ornithology 153:53–74. https://doi.org/10.1007/s10336-011-0733-y

Sabo, J. L., Bastow, J. L. & Power, M. E. 2002: Length–mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. — Journal of the North American Benthological Society 21:336–343. https://doi.org/10.2307/1468420

Schekkerman, H. & Beintema, A. J. 2007: Abundance of invertebrates and foraging success of black-tailed godwit (*Limosa limosa*) chicks in relation to agricultural grassland management. — Ardea 95:39–54. https://doi.org/10.5253/078.095.0105

Sharps, E., Garbutt, A., Hiddink, J. G., Smart, J. & Skov, M. W. 2016: Light grazing of saltmarshes increases the availability of nest sites for common redshank (*Tringa totanus*) but reduces their quality. — Agriculture, Ecosystems & Environment 221:71–78. https://doi.org/10.1016/j.agee.2016.01.030

Siepel, H. 1990: The influence of management on food size in the menu of insectivofious animals. — Proceedings of the Section Experimental and Applied Entomology 1:69–74.

Stroud, D. A., Baker, A., Blanco, D. E., Davidson, N. C., Delany, S., Ganter, B., Gill, R., González, P., Haanstra, L., Morrison, R. I. G., Piersma, T., Scott, D. A., Thorup, O., West, R., Wilson, J., Zockler, C. 2006: The conservation and population status of the world's waders at the turn of the millennium. In: Boere, G. C., Galbraith, C. A., Stroud, D. A. (eds) Waterbirds around the world. The Stationery

Office, Edinburgh, pp. 643–648.

Studds, C. E., Kendall, B. E., Murray, N. J., Wilson, H. B., Rogers, D. I., Clemens, R. S., Gosbell, K., Hassell, C. J., Jessop, R. & Melville, D. S. 2017: Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. — Nature Communications 8:1–7. https://doi.org/10.1038/ncomms14895

Tukey, J. W. 1949: Comparing individual means in the analysis of variance. — Biometrics 99–114. https://doi.org/10.2307/3001913

Turpaud-Fizzala, V. 2012: Etude et protection du Courlis cendré en Deux-Sèvres - Bilan 2010–2011. — Le Lirou 31:17–31. (In French)

Valkama, J. P. R., Robsertson, P. & Currie, D. 1998: Habitat selection by breeding curlews (*Numenius arquata*) on farmland: The importance of grassland. — Annales Zoologici Fennici 35:141–148.

van Roomen, M., Laursen, K., van Turnhout, C., van Winden, E., Blew, J., Eskildsen, K., Günther, K., Hälterlein, B., Kleefstra, R. & Potel, P. 2012: Signals from the Wadden Sea: Population declines dominate among waterbirds depending on intertidal mudflats. — Ocean & Coastal Management 68:79–88. https://doi.org/10.1016/j.ocecoaman.2012.04.004

Vickery, J. A., Tallowin, J. R., Feber, R. E., Asteraki, E. J., Atkinson, P. W., Fuller, R. J. & Brown, V. K. 2001: The management of lowland neutral grasslands in Britain: Effects of agricultural practices on birds and their food resources. — Journal of Applied Ecology 38:647–64. https://doi.org/10.1046/j.1365-2664.2001.00626.x

Wald, A. 1943: Tests of statistical hypotheses concerning several parameters when the number of observations is large. — Transactions of the American Mathematical Society 54:426–82. https://doi.org/10.1090/s0002-9947-1943-0012401-3

Wilcoxon, F. 1945: Individual comparisons by ranking methods. — Biometrics Bulletin 1:80–83. https://doi.org/10.2307/3001968

Wilson, A. M., Vickery, J. A., Brown, A., Langston, R. H. W., Smallshire, D., Wotton, S. & Vanhinsbergh, D. 2005: Changes in the numbers of breeding waders on lowland wet grasslands in England and Wales between 1982 and 2002. — Bird Study 52:55–69. https://doi.org/10.1080/00063650509461374

Wilson, J. D., Anderson, R., Bailey, S., Chetcuti, J., Cowie, N. R., Hancock, M. H., Quine, C. P., Russel, N., Stephen, L. & Thompson D. B. A. 2014: Modelling edge effects of mature forest plantations on peatland waders informs landscape-scale conservation. — Journal of Applied Ecology 51:204-213. https://doi.org/10.1111/1365-2664.12173

Woodcock, B. A. 2005: Pitfall trapping in ecological studies. — Insect sampling in forest ecosystems 5:37–57. https://doi.org/10.1002/9780470750513.ch3

Zar, J. H. 1999: Biostatistical analysis. (Fourth edition). Prentice-Hall, New Jersey. 931p.

Zedler, J. B. & Kercher, S., 2005: Wetland resources: Status, trends, ecosystem services, and restorability. — Annual Review Environment and Resources 30:39–74. https://doi.org/10.1146/annurev.energy.30.050504.144248

Online supplementary material

Supplementary material available in the online version includes Figs. S1–S3 and Tables S1–S2.

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Spatial ecology of the Red Kite (*Milvus milvus*) during the breeding period in Spain

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Studies focusing on the spatial ecology of the Red Kite (*Milvus milvus*) during the breeding season are scarce, despite this season having major importance in its conservation. Spain has one of the largest breeding populations of this species, but it is very threatened in this country. Here, 28 Red Kites were tagged in Spain with GPS satellite transmitters to study the movements of breeding adults during the breeding season (March–June), evaluating the differences according to sex, and investigating the habitat selection. The area used by females was smaller than the used by males (95% KDE = 4.48 vs. 3.30 km^2). Females also traveled less distance per hour and remained closer to the nest. Thus, females had a higher frequency of locations at distances <250 m from the nest, while males had a higher frequency at distances >1 km. Distances recorded at >5 km were scarce for both sexes, and maximum distances reached were usually (61% of seasons) less than 15 km. Both sexes increased the frequency of movements between 1–3 km during the central hours of the day. Red Kites mainly used areas occupied by non-irrigated arable land, forests, scrubs, and herbaceous vegetation. The selection of certain types of crops highlights the importance of the agroforestry landscape for the conservation of the species. On the other hand, we documented for the first time how part of the Spanish breeding population is a short-distance migrant within the Iberian Peninsula while other part of the population makes post-breeding movements during summer.

1. Introduction

Understanding spatial ecology during the breeding season is fundamental for the conservation of birds, especially for threatened raptors, such as the Red Kite in Spain. The breeding strategies, which include incubation, chick-rearing, and fledging, result from a trade-off between current breeding success and parents' future condition (Trivers 1972, Nur 1988, Clutton-Brock 1991, Williams

2018). The knowledge about home range areas and movements performed by raptors during reproduction is essential for the delimitation of protected areas around the nests (Kays *et al.* 2015, López-López *et al.* 2016). Given that the Red Kite breeding population has decreased in Spain in recent years (Molina 2015), the study of its spatial ecology could help to design more effective conservation measures for the species in the Iberian Peninsula.

Despite the importance of this topic, studies concerning the spatial ecology of the Red Kite during the breeding season are scarce. Most of the previous studies on this topic were based on field observations or radio-tracking (Newton *et al.* 1989, Bustamante 1993, Newton *et al.* 1994, Mougeot *et al.* 2011), while the studies using GPS telemetry are uncommon (Mammen *et al.* 2014, Pfeiffer & Meyburg 2015). However, GPS telemetry could provide fundamental information about the behaviour of the species (López-López *et al*. 2010, Urios *et al*. 2015, López-López 2016). Studies based on this tracking technology, combined with direct observations to know the stage of development of chicks, are necessary to understand the breeding ecology of this species and other raptors.

The deeper the knowledge of its breeding ecology, the better conservation tools will be available to protect the species. In some countries, there has been a population increase in recent years (Aebischer 2010, Cereghettia *et al.* 2019, BirdLife International 2019), but the species is still listed as “endangered” in the Spanish List of Threatened Species because their breeding populations have clearly decreased in the last decades (Molina 2015). The main causes of this decline are human persecution (including poisoning and illegal hunting), collisions and electrocutions, car accidents, inter-specific competition, and habitat deterioration (Viñuela *et al.* 1999, Carter 2001, Sergio *et al.* 2005, Berny & Gaillet 2008, Knott *et al.* 2009, Mougeot *et al.* 2011, Mateo-Tomás *et al*. 2020, Viñuela *et al*. 2021).

Here we used 28 individuals tagged with GPS telemetry to study the spatial ecology of Red Kite during the breeding period (including laying, hatching, and fledging; from March to June) in Spain. Our goals were a) to estimate the home range, mean distance to nest, and hourly travelled distance during the reproductive season; b) to evaluate the differences in spatial ecology according to sex; c) to study the habitat selection during the breeding season; and d) to analyze the diversity of post-reproductive strategies (sedentarism, sedentarism with post-reproductive movements, or intra-peninsular migration) used by the Spanish breeding population of the Red Kites.

2. Materials and methods

2.1. Study species

The Red Kite (*Milvus milvus*) is a medium-sized opportunistic raptor from western Palearctic (Cramps & Simmons 1980, IUCN 2018). It is a facultative colonial bird that can form breeding aggregations when food is abundant (Ortlieb 1980, Villafuerte *et al.* 1998, Mougeot & Bretagnolle 2006). Red Kites usually start to breed at 2–4 years of age, but they can take up to 7 years to reach sexual maturity. Egg laying usually takes place in March–April, and the clutch size is typically 1–3, up to 5. Eggs are incubated for 31–32 days, and fledging takes place at the age of 50–60 days (Davies & Davies 1973, Bustamante 1993, Newton *et al.* 1989, Veiga & Hiraldo 1990, Newton *et al.* 1996, Evans *et al.* 1999, Sergio *et al.* 2005, Mougeot & Bretagnolle 2006). Most Red Kites in north-eastern Europe are migrants (García-Macía *et al.* 2021), and they move southward, mainly to the Iberian Peninsula and France, to spend the wintering season (Del Hoyo *et al.* 1994, Fabienne 2009, De la Puente & De la Torre 2015). However, there are also breeding populations in the southern distribution range as in Spain, which has the third largest population after Germany and France (BirdLife International, 2019). In the most recent census, the breeding pairs in Spain were estimated at 2,312–2,440 pairs (Molina 2015).

2.2. Tagging

From 2013 to 2017, 28 adult Red Kites (6 males and 22 females) were captured and tagged in different Spanish provinces (Supplementary Material Table S1). We used the data of 47 breeding events (Supplementary Material Table S2), and a total of 55,869 locations, with an average of 1,190 ± 432 locations per event. Adult birds were trapped using a dho-gaza net with an Eagle Owl (*Bubo bubo*) decoy (De la Puente & Cardiel 2009), while one individual was tagged as a chick in the nest. All individuals were weighed and ringed, and a blood sample was obtained for sex determination by DNA. Birds were tagged using a GPS/satellite transmitter that was affixed to the back using a Teflon harness, a non-abrasive material, fixed with several cotton thread stitching points to be safely released from the birds once they ceased to function after about five years (Garcelon 1985; García *et al.*, 2021). The weight of tags was below the recommended 3% of the birds' body mass (Kenward 2001; mean percentage ± SD = 2.30 ± 0.19%, range = 1.90–2.62%). Birds were released within 30 min after capture.

We used different transmitter models: 20–23-g SAKER GPS-GSM (Ecotone Telemetry; n=26), 22-g PTT-100 solar-powered Argos/GPS (Microwave Telemetry Inc.; n=2) or 30-g PTT solar Argos/GPS (Microwave Telemetry Inc.; n=1). Ecotone and 30-g Microwave tags were programmed to collect locations every hour from 06:00 to 19:00 h (local hour), and 30-g Microwave tag had the same duty cycle but until 20:00 h. 22-g Microwave transmitters recorded 1 location per hour from 06:00 to 18:00 h. Thus, all tags provided fixes at a 1-hour frequency.

2.3. Spatial parameters and analysis

We defined the "breeding period" as the time from 1 March to 30 June, since the first laying takes place between March and April and chicks leave the natal area 10–12 weeks after hatching (Bustamante 1993, Newton *et al.* 1996, Mougeot *et al.* 2011, Nachtigall & Herold 2013). Hence, our study covered the crucial stages of the breeding period (incubation and chick-rearing). It was verified by field observations that all individuals used in this study reproduced successfully, and incubation and chick-rearing took place between March and June. We excluded the breeding events with less than 3 complete months of data from the analyses, due to individual deaths or transmitters failures.

We estimated the breeding home range for each breeding season with the 95%, 75%, and 50% fixed Kernel Density Estimation (KDE; Worton 1989) using the Animal Movement extension for ArcView 3.2 (Hooge & Eichenlaub 1997). We used the least squares cross-validation procedure to calculate the smoothing parameter S (Silverman 1986). We also calculated the 100% Minimum Convex Polygon (MCP) encompassing all the locations for each breeding season. The different polygons were transformed into an Equal-Area Cylindrical projection. We calculated the distance to the nest position (the nest used during the respective year) of every recorded location of all Red Kites and the distance covered (km) in 1 h using only consecutive locations (Mellone *et al.* 2012, García-Macía *et al*. 2021).

We analyzed sex differences in the home range sizes, distances to nest, and travelled distances. We used the different measurements of home range areas (MCP and KDEs), the average daily distances to the nest, and the average daily hourly travelled distances as response variables in six different linear mixed models (LMM). In all models, "sex" was included as fixed factor. "Year" was included as random effect in the models with the estimated areas (MCP and KDE; km^2) as response variables, while "individual" identity and "year" were included as random effects in the models with the distances to the nest and the hourly travelled distances as response variables. The requirements to perform the LMMs were verified, including the normality of residuals with the Shapiro-Wilk test. The response variables were log-transformed to fulfill that requirement (Mean ± SD after transformation: MCP = 4.45 ± 1.28; KDE95 = 0.37 ± 1.64; KDE75 = –0.60 ± 1.58; KDE50 = –1.30 ± 1.58; travelled distances = –1.167 ± 1.59; distance to nest = 0.96 ± 1.58).

Kruskal-Wallis test (data were non-normal) was used to determine if there were significant differences in the travelled distance between the different hours of the day. Games-Howell test (Zar 1999) was used to check if there was a peak of hourly activity throughout the day.

All statistical analyses were performed with IBM SPSS Statistics v. 22.0 (IBM Corp. 2020) and R Statistics v. 4.0.5 (R Core Team 2022). The significance level was established at $p<0.05$.

2.4. Habitat selection

To determine the habitat selection within the home ranges, we used the CORINE 2018 land cover map (raster resolution = 100 m) provided by the European Environment Agency (2018). We grouped the original land cover classes (“CLC”) into nine categories to facilitate the interpretation of the results (Fig. 1): artificial surfaces (CLC codes: 111–142), non-irrigated arable land (CLC code: 211), permanently irrigated land (CLC code: 212), permanent crops and pastures (CLC code: 221–231), heterogeneous agricultural areas (CLC codes: 241–244), forests (CLC codes: 311–313), scrub and/or herbaceous vegetation associations (CLC codes: 321–324), open spaces (bare rocks or sparsely vegetated areas; CLC code: 331–335) and wetlands and water bodies (CLC code: 411–523).

We performed a third-order habitat selection (Johnson 1980) analysis to evaluate whether Red Kites are found in certain habitats more frequently than expected by their availability, comparing the observed values against a set of random samples (Gotelli & Ellison 2004). First, we generated 2000 random points within each MCP of each breeding season, which represents the maximum potential area used by the individuals. Then, we assigned the corresponding habitat type to every random point and to every real location recorded during the breeding season. We used Monte Carlo simulations to determine habitat preferences, comparing the frequency of real tracking data with the generated random locations (Manly 1997, Soutullo *et al.* 2008, Limiñana *et al.* 2012, López-López *et al.* 2016, Vidal-Mateo *et al.* 2019). These expected frequencies were calculated by sampling the same number of real locations from the generated random points; this process was repeated 1,000 times using the “shuffle rows” option in Excel’s PopTools add-in (Hood 2010). The observed values (tracking data) were compared against 1,000 generated random locations with Monte Carlo analysis using Excel’s PopTools. Comparisons were two-tailed, and the significance level was established at $p<0.05$.

3. Results

The average home range area during the breeding season was 3.65 km^2 according to 95% KDE, 1.48 km^2 to 75% KDE, 0.78 km^2 to 50% KDE, and 169.15 km^2 to MCP (Table 1). Males had larger 95% KDEs than females (4.48 km^2 vs. 3.30 km^2). We did not find significant differences between sexes according to the rest of the home range sizes

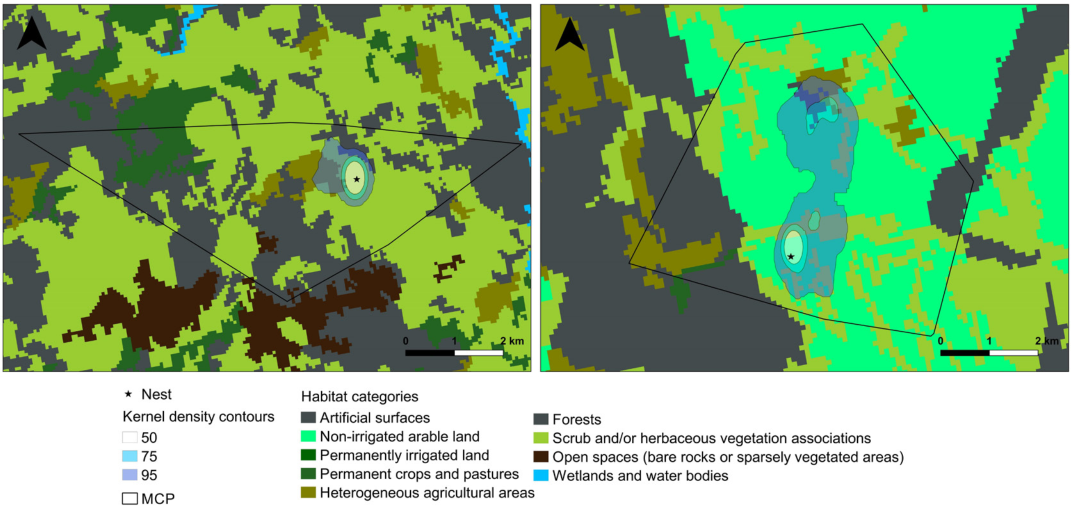

Fig. 1. Example of two home range areas of adult Red Kites tracked by GPS satellite telemetry during the breeding season. Polygons represent Kernel Density Estimations (KDE) and Minimum Convex Polygon (MCP). Left: male in Ávila; right: female in Madrid (Spain).

Table 1. Home range size (in km^2), mean distance to nest and hourly distances of 47 breeding seasons of Red Kites tracked by GPS satellite telemetry in Spain according to their sex and migratory or resident behaviour. Results are expressed as mean and standard deviation. Minimum and maximum values appear in parenthesis. MCP: Minimum Convex Polygon; KDE: Kernel Density Estimation.

	n	MCP (km^2)	95% KDE (km^2)	75% KDE (km^2)	50% KDE (km^2)	Mean distances to nest (km)	Mean hourly distances (km per h)
Overall	47	169.15 ± 187.43 (7.30–832.71)	3.65 ± 4.26 (0.06–17.94)	1.48 ± 2.23 (0.02–10.47)	0.78 ± 1.26 (0.01–5.95)	1.14 ± 0.75 (0.15–3.96)	0.94 ± 0.61 (0.16–3.36)
Males	14	181.01 ± 128.51 (23.85–404.81)	4.48 ± 2.62 (0.84–9.36)	1.13 ± 0.92 (0.29–3.22)	0.46 ± 0.41 (0.15–1.58)	1.41 ± 0.36 (1.05–2.38)	1.48 ± 0.30 (1.17–2.39)
Females	33	164.12 ± 209.06 (7.30–832.71)	3.30 ± 4.78 (0.06–17.94)	1.64 ± 2.60 (0.02–10.47)	0.91 ± 1.47 (0.01–5.95)	1.02 ± 0.85 (0.15–3.96)	0.71 ± 0.56 (0.16–3.36)

estimators (MCP, 75% KDE, and 50% KDE), but the estimates of the models indicated the same trend, and female home range tended to be smaller (Table 1, Fig. 2).

We also found significant differences between sexes in the distances to the nest and the hourly travelled distances. Females stayed closer to the nest than males (EMMs = –1.58 vs. 0.04) and performed shorter movements (EMMs = –1.34 vs. 0.17; Fig. 2, Table 2). Males stayed at 1.41 ± 0.36 km from the nest, while females stayed at 1.02 ± 0.85 (Table 1). Females had a higher frequency of locations (69.1%) at distances <250 m from the nest (Fig. 3), while males had a higher frequency than females at distances > 1 km from the nest (45.7% and 16.7%, respectively). The frequency of distances recorded at > 5 km from the nest was low for both sexes (Fig. 3). The maximum distances reached during the entire breeding season ranged between 2.89 and 47.61 km, but they were usually (61% of seasons) less than 15. (Supplementary Material Table S2). On the other hand, males travelled 1.48 ± 0.30 km per hour, while females travelled 0.71 ± 0.56 (Table 1). 67.5 % of movements for females had a length <250 m (Fig. 4), with differences in these frequencies comparing them to males ($\chi^2 = 9294.01$, df=6, $p<0.001$). Only 22.6% of movements for males were <250 m, whereas they had a higher frequency of longer distance movements (>1 km): 53.8% vs. 18% of females (Fig. 4).

The frequency of movements varied according to the hour of the day, in both sexes (males: $\chi^2=2220.67$, df=78, $p<0.001$; females: $\chi^2=1595.57$, df=78, $p<0.001$). Although we observed no prominent peak of activity in the analyses, the frequency of short movements were higher during the first and last hours of the day, whereas the frequency of long movements increased during the central hours of the day (10–16 h). This temporal pattern was shown by both males and females (Fig. 5). The Red Kites in our study mainly used areas occupied by scrub, herbaceous vegetation, and crops (Fig. 1, Table 3). Most locations occurred in scrub and/or herbaceous vegetation associations (34.83%) and non-irrigated arable land (23.05%), which were used more frequently than expected from their availability. Red Kites also showed a preference for permanent crops, pastures, and heterogeneous agricultural areas. In contrast, forests were used less than expected from their availability, although the number of locations recorded in this habitat was high (21.87%). Permanently irrigated lands and open spaces were also avoided.

From the 29 tagged Red Kites, 17 remained close to the breeding area during the whole year (58%), 4 individuals (14%) performed short distance migrations (range = 299–560 km) within the Iberian Peninsula, and 8 individuals (28%) made post-reproductive movements after the chicks had left the nest. These movements covered distances between 100 and 600 km and lasted between 2 and 8 weeks. In some cases, this was a consistent pattern in subsequent years, but not in others.

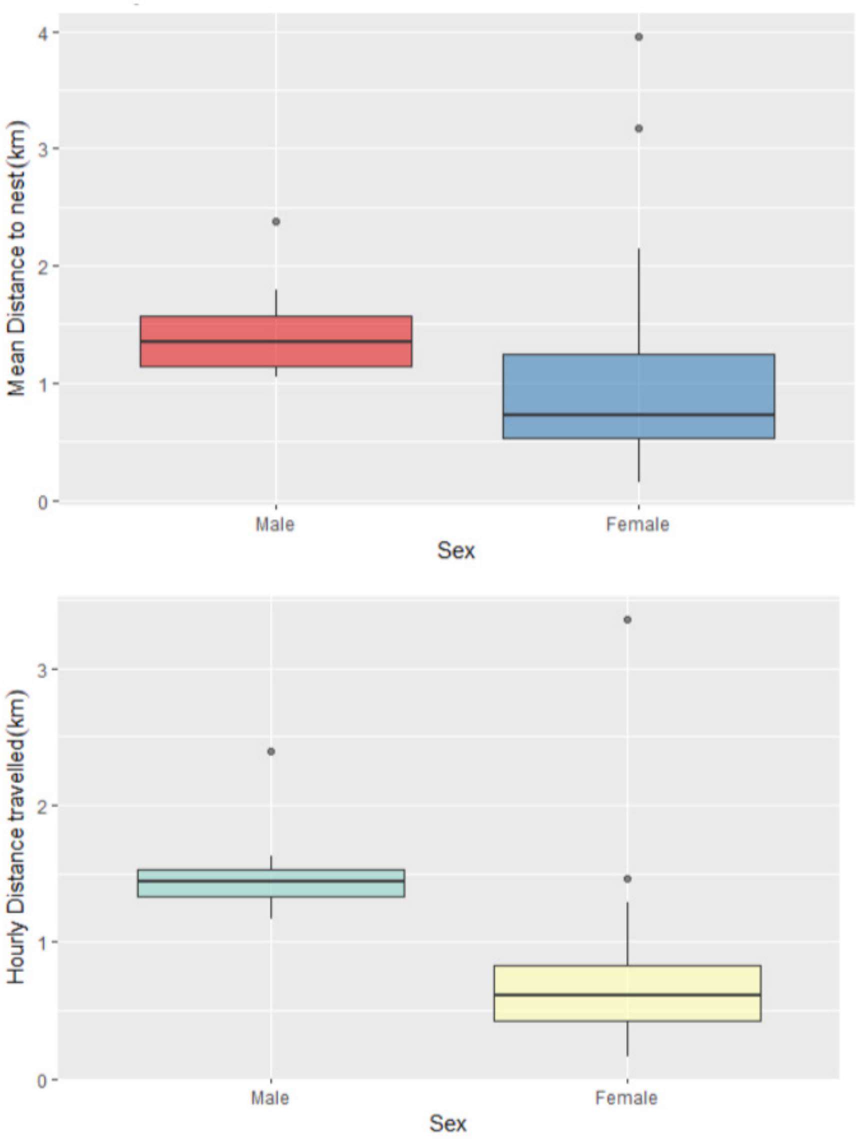

Fig. 2. Differences between sexes according to mean distances to nest and hourly travelled distances (raw data).

4. Discussion

Our study provides the first description, and comparison between sexes, of breeding home ranges and movement patterns of Red Kites breeding in Spain. We showed how female Red Kites had smaller breeding areas than males, stayed closer to the nest, and had lower mobility during the reproductive season. We also studied the habitat preferences of the species, highlighting the importance of the agroforestry landscapes for its conservation.

According to the Minimum Convex Polygon, the home range size was 169 km^2 on average, similar to other home MCP estimations for the Red Kite using both GPS tracking (Mammen *et al*. 2014, Pfeiffer & Meyburg 2015), and direct observations or VHF tracking (Porstendörfer 1994, Porstendörfer 1998, Walz 2001, Nachtigall *et al*. 2010, Nachtigall & Herold 2013, Mammen

Table 2. Results of the linear mixed models (LMM) of home range areas and distances. A) Comparison between sexes (fixed effect), B) Information about random effects of the model. Estimates, standard error (SE), standard deviation (SD), degrees of freedom (df), and p-value are shown. MCP: Minimum Convex Polygon; KDE = Kernel Density Estimation. Response variables were log-transformed to comply with the normality of residuals.

A) Fixed effect (Sex)

Variable	Fixed factor	Estimate	SE	df	p-value
KDE 95% (n=47)	Intercept	0.278	0.107	45	0.0130
	Sex (Male)	0.281	0.107	45	0.0115
KDE 75% (n=47)	Intercept	–0.206	0.109	45	0.065
	Sex (Male)	0.141	0.109	45	0.202
KDE 50% (n=47)	Intercept	–0.553	0.125	1.75	0.059
	Sex (Male)	0.083	0.109	43.99	0.453
MCP (n=47)	Intercept	1.946	0.127	2.23	0.003
	Sex (Male)	0.151	0.085	43.59	0.085
Distance to nest (daily average; n=5302)	Intercept	–0.234	0.120	6.50	0.0444
	Sex (Female)	–0.370	0.061	19.67	<0.001
Hourly distance (daily average; n=5302)	Intercept	–0.3215	0.133	7.43	0.0445
	Sex (Female)	–0.396	0.074	19.61	<0.001

B) Random effects

Variable	Random effects	SD
KDE 95% (n=47)	Year	0.0004
	Residuals	0.06
KDE 75% (n=47)	Year	0.002
	Residuals	0.681
KDE 50% (n=47)	Year	0.101
	Residuals	0.686
MCP (n=47)	Year	0.164
	Residuals	0.532
Distance to nest (n=5302)	Individual	0.2503
	Year	0.228
	Residuals	0.631
Hourly distance (n=5302)	Individual	0.305
	Year	0.246
	Residuals	0.671

et al. 2014). However, the smaller home range sizes estimated and the great frequency of distances close to the nest indicate the Red Kites concentrated their movements on smaller surfaces during breeding. Indeed, the 95% KDE (3.65 km^2) was fifty times smaller on average than MCP estimations, and more than 90% of the total locations were less than 5 km from the nest. The Kernel Density Estimations (or similar analyses to estimate home range sizes) based on GPS telemetry provide very useful information to understand the breeding and foraging behavior of raptors, because they exclude unrepresentative outliers and provide accurate estimations of the core territory of the species.

The variability found in the home range sizes estimators (*e.g.*, 95% KDE range = 0.06–17.94; Table 1) may be due to several factors. Better environmental conditions and food resources allow birds to reduce their home range (Hernández-Pliego *et al.* 2017, Tucker *et al.* 2019). On the other hand, the smaller number of fledglings per nest, the larger the adults' breeding area (Pfeiffer & Meyburg 2015). The period considered for the analyses may also affect the home range estimations. 95% KDE provided by Pfeiffer and Meyburg (2015) was thirty times larger than ours, probably because they included a few weeks more than we did, when individuals had greater mobility. The breeding season could be divided into several phases, characterized by different degrees of movements in the couple, being the chick-rearing and post-fledging the phases with higher mobility (López-López *et al.* 2021). Other factors, such as the nutritional stage of the chicks and GPS sampling frequency, might also explain the differences in the home range estimations between different studies or within the individuals in the same study. More studies with Red Kites' pairs, and considering the different phases of breeding, should be conducted in the future to have more specific knowledge about the spatial ecology of this species during breeding (Worton, 1989).

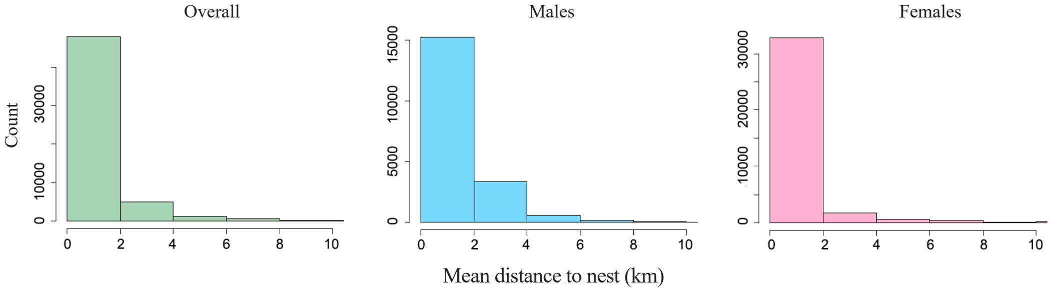

Fig. 3. Frequency of movements according to the distance to the nest categorized by sex.

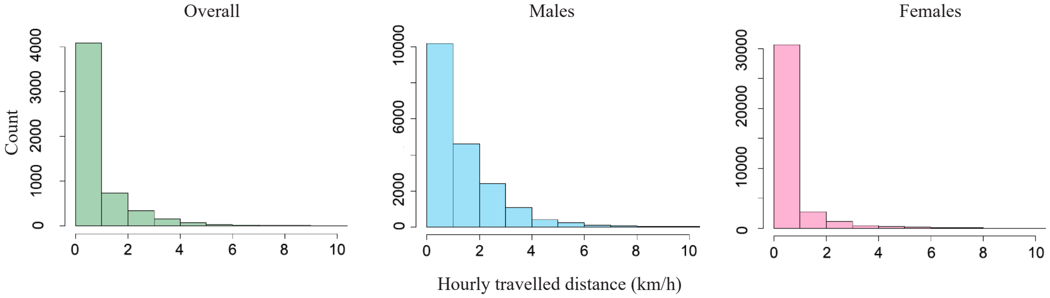

Fig. 4. Frequency of movements recorded at 1 h intervals categorized by sex.

Female Red Kites usually used smaller areas and had less mobility than males during the breeding season. Females showed smaller 95% KDEs, higher frequencies of locations very close to the nest, and shorter movements than males. Not all sex comparisons using the rest of the home range estimators (MCP, 75% KDE, and 50% KDE) were significant, but the slopes of the models were always positive for the males compared to the females, which indicates the same tendency. The absence of significance in some models may be due to the small sample size (n=47), or other environmental factors not considered in the models. In any case, the sex differences may be due to the different roles assumed by the members of the pair. On the one hand, females probably spent more time incubating the eggs, protecting the chicks, and providing food to the nest from its surroundings. On the other hand, males may travel to habitats with higher productivity for hunting, even if these were far from the nest. Thus, this role differentiation allows both the protection of the nest and the feeding of the chicks, improving breeding performance (Keeley & Bechard 2017, Martínez *et al.* 2020, López-López *et al*. 2021).

Red Kites showed a preference for lands occupied by scrub, herbaceous vegetation, and non-irrigated crops, which may influence the location of the nests in those habitats (Heuck *et al.* 2013). In fact, our results showed that Red Kites concentrated their movements around the nest. We suggest that the selection of open wooded lands (Del Hoyo *et al.* 1994, Bird Life International 2019) could be linked to the location of carrions and preys. Although this species has scavenging habits, visiting supplementary feeding stations or dumps, they can also hunt small mammals and birds, or even reptiles and amphibians (Cramp & Simmons 1980, Blanco *et al.* 1990, García *et al.* 1998, García & Viñuela 1999, Mougeot & Bretagnolle 2006). The selection of certain types of crops highlights the importance of conserving the agroforestry landscape and its heterogeneity. The Red Kite may be sensitive to changes in land use, including the substitution of traditional crops and the homogenization of landscapes (Viñuela *et al.* 1999, Knott *et al.* 2009).

The striking diversity of post-reproductive strategies performed by the Spanish breeding population of the Red Kite may be one of the keys for

Table 3. Habitat selection for Red Kite in Spain during the breeding season. The percentage of locations in each habitat type is indicated for the observed locations and for the expected values. P-value for the comparison between the observed locations and random points is indicated. (+), habitat is selected; (–), habitat is avoided.

Habitat type	Random points (%)	GPS locations (%)	p-value
Artificial surfaces	3.00	0.93	<0.001 (–)
Non-irrigated arable land	20.41	23.05	<0.001 (+)
Permanently irrigated land	1.83	0.45	<0.001 (–)
Permanent crops and pastures	5.41	6.66	<0.001 (+)
Heterogeneous agricultural areas	10.04	12.05	<0.001 (+)
Forests	24.57	21.87	<0.001 (–)
Scrub and/or herbaceous vegetation associations	32.39	34.83	<0.05 (+)
Open spaces (bare rocks or sparsely vegetated areas)	1.48	0.06	<0.001 (–)
Wetlands and water bodies	0.87	0.09	<0.001 (–)
Total number of locations	94000	55869	

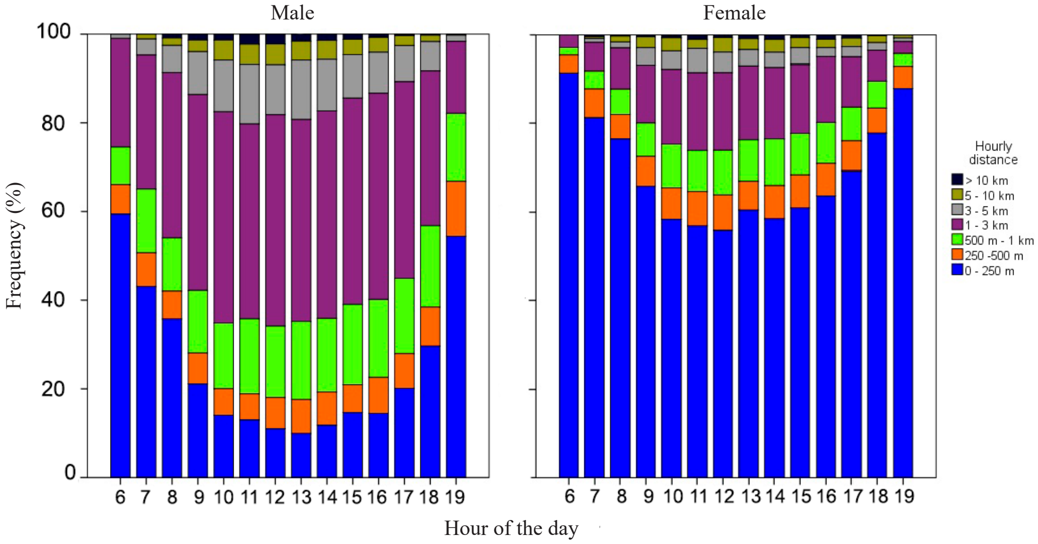

Fig. 5. Frequency of movements recorded at 1 h intervals categorized by different distance ranks per sex according to the time of day.

its conservation. Our tracking data revealed that part of the breeding population in Spain performs short-distance migratory movements, whereas other part engages in post-breeding movements across the Iberian Peninsula. This variability in the post-reproductive behaviour of the Spanish Red Kites may respond to several environmental factors, but we consider that availability of food and knowledge of the breeding area could be the most important ones (McIntyre & Schmidt 2012). Moreover, the short migration and post-reproductive movements in the Spanish breeding population are not constant among years for the same individuals. The Red Kites might change their post-breeding strategy depending on availability of resources (Joseph *et al.* 2003, Bildstein 2006, Losos & Ricklefs 2009, Gangoso *et al.* 2013). Further studies could relate the inconsistency of behaviour between consecutive years to the availability of resources or any other factor.

In conclusion, our study provides the first data about travelled distances and home range sizes of the Red Kites during the breeding season in Spain, proving the differences between sexes. This study allows a better knowledge of the reproductive spatial ecology of this species, which could be essential for the conservation of the threatened breeding Spanish population.

Isohaarahaukan lisääntymisajan spatiaalinen ekologia Espanjassa

Isohaarahaukan (*Milvus milvus*) lisääntymisen ajan spatiaalisesta ekologiasta tiedetään vähän, vaikka pesimisajan ekologian ymmärtämisellä on tärkeä merkitys lajin suojelun kannalta. Espanjasta löytyy Euroopan suurimpia pesiviä populaatioita, mutta kanta on pienemässä. Tässä tutkimuksessa asennettiin gps-lähettimiä 28 pesivään aikuiseen isohaarahaukkaan lisääntymisajanjaksolla (maalis–kesäkuu). Tavoitteena oli tutkia sukupuolten välisiä liikkumiseroja ja habitaatin valintaa. Havaitsimme naaraiden liikkumisalueiden olevan pienempiä kuin koiraiden. Naaraat myös liikkuivat hitaammin ja pysyivät lähempänä pesää. Naaraat olivat useammin alle 250 metrin päässä pesästä ja koiraat useammin yli kilometrin päässä pesästä. Yli viiden kilometrin etäisyydet pesästä olivat harvinaisia sekä naarailla että koirailla, ja kaukaisimmat havainnot olivat yleensä alle 15 kilomteriä pesästä. Lentäminen oli yleisintä 1–3 kilometrin etäisyydellä keskipäivällä molemmilla sukupuolilla. Isohaarahaukat suosivat enimmäkseen keinokastelemattomia peltoja, metsiä, pensaikkoja ja ruohomaita. Koska isohaarahaukat suosivat tiettyjä viljelyjä, maa- ja metsätalouden ympäristöillä on tärkeä merkitys lajin suojelussa. Tutkimuksessa dokumentoimme myös ensimmäistä kertaa, että osalla tutkimastamme espanjalaisesta populaatiosta muuttomatkat ovat lyhyitä (ts. ne pysyvät Iberian niemimaan alueella), kun taas toinen osa populaatiosta liikkuu kesäisin laajemmalla alueella, kun pesintä on ohi.

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References

Aebischer, A. 2010: Distribution and recent population changes of the Red Kite in the Western Palaearctic – results of a recent comprehensive inquiry. — Proceedings of the International Red Kite symposium 2009: 12–14.

Berny, P. & Gaillet, J. R. 2008: Acute poisoning of Red Kites (*Milvus milvus*) in France: dates of the SAGIR network. — Journal of Wildlife Diseases 44: 417–426. http://dx.doi.org/10.7589/0090-3558-44.2.417

BirdLife International 2019: Species factsheet: *Milvus milvus*. Downloaded from http://www.birdlife.org on 02/05/2019.

Bildstein, K.L. 2006: Migrating raptors of the world: their ecology & conservation. — Cornell University Press, New York, USA.

Blanco, J. C., Hiraldo F. & Heredia B. 1990: Variations in the diet and foraging behaviour of a wintering red kite (*Milvus milvus*) population in response to changes in food availability. — Ardeola 37: 267–278. https://www.ardeola.org/en/volumes/372/articles/267-278/?stc=ok

Bustamante, J. 1993: Postfledging dependence period and development of flight and hunting behavior in the red kite *Milvus milvus*. — Bird Study 40: 181–188. https://doi.org/10.1080/00063659309477181

Cardiel, I. 2006: El milano real en España. II Censo Nacional (2004). — SEO/BirdLife, Madrid. (In Spanish)

Carter, I. (ed.) 2001: The Red Kite. — Chelmsford, Arlequin Press, UK.

Cereghettia, E. Scherler, P., Fatteberta, J. & Grüeblera, M.U. 2019: Quantification of anthropogenic food subsidies to an avian facultative scavenger in urban and rural habitats. — Landscape and Urban Planning 190: 1–10. https://doi.org/10.1016/j.landurbplan.2019.103606

Clutton-Brock, T.H. 1991: The evolution of parental care. — Princeton University Press, USA.

Cramp, S. & Simmons, K. E. L. 1980: Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palaearctic Vol. 2. — Oxford University Press, Oxford.

Davies, P. W. & Davis, P. E. 1973: The ecology and conservation of the Red Kite in Wales. — British Birds 66: 183–224.

De la Puente, J. & Cardiel, I. 2009: Efectividad de las redes dho-gaza y búho real naturalizado para la captura de milanos reales (*Milvus milvus*) reproductores. — Revista de Anillamiento 24: 16–19. (In Spanish)

De la Puente, J. & De la Torre, V. 2015: Abstracts book of the II International Symposium on the Red Kite. Binaced (Huesca, Spain) 2015. — Grupo Ornitológico SEO-Monticola & Fondo de Amigos del Buitre, Madrid.

Del Hoyo, J., Elliott, A. & Sargatal, J. 1994: Handbook of the Birds of the World Vol. 2: New World Vultures to Guineafowl. — Lynx Edicions, Barcelona.

European Environment Agency. 2018: CLC 2018 - Copernicus Land Monitoring Service. Available at https://land.copernicus.eu/pan-european/corine-land-cover/clc2018 (Accessed 24/11/2022)

Evans, I. M., Summers, R. W., O'Toole, L., Orr-Ewing, D. C., Evans, R. D., Snell, N. & Smith, J. 1999: Evaluating the success of translocating Red Kites *Milvus milvus* to the UK. — Bird Study 46: 129–144. https://doi.org/10.1080/00063659909461125

Fabienne, D. 2009: Proceedings of the Red Kite international Symposium. — LPO, France.

Gangoso, L., López-López, P., Grande, J.M., Mellone, U., Limiñana, R., Urios, V. & Ferrer, M. 2013: Ecological Specialization to Fluctuating Resources Prevents Long-Distance Migratory Raptors from Becoming Sedentary on Islands. — PLoS ONE 8(4): e61615. https://doi.org/10.1371/journal.pone.0061615

Garcelon, D. K. 1985: Mounting backpack telemetry packages on bald eagles. — Institute for Wildlife Studies, Arcata (California).

García, J. T. & Viñuela, J. 1999: Importancia de los muladares para la conservación del Milano Real en España. — In El Milano Real en España. Censo, Distribución y Conservación (ed. Viñuela, J., Martí, R. & Ruiz, A.): 187–198. SEO/BirdLife, Madrid. (In Spanish)

García, J. T., Viñuela, J. & Sunyer C. 1998: Geographic variation of the winter diet of the Red Kite *Milvus milvus* in the Iberian Peninsula. — Ibis 140: 302–309. https://doi.org/10.1111/j.1474-919X.1998.tb04393.x

García, V., Iglesias, J.J. & Moreno-Opo, R. 2021: Null effects of Garcelon harnessing method and transmitter type on soaring raptors. — Ibis 163(3): 899–912. https://doi.org/10.1111/ibi.12942

García-Macía, J., Vidal-Mateo, J., De la Puente, J., Bermejo, A., Raab, R. & Urios, V. 2021: Seasonal differences in migration strategies of Red Kites (*Milvus milvus*) wintering in Spain. — Journal of Ornithology 163: 27–36. https://doi.org/10.1007/s10336-021-01918-5

Gotelli, N. J. & Ellison, A. M. 2004: A primer of ecological statistics. — Sinauer Associates, Sunderland.

Heuck, C., Brandl, R., Albrecht, J. & Gottshalk, T.K. 2013: The potential distribution of the Red Kite in Germany. —Journal of Ornithology 154: 911–921. https://doi.org/10.1007/s10336-013-0955-2

Hernández-Pliego, J., Rodríguez, C., Dell'Omo, G. & Bustamante, J. 2017: Combined use of tri-axial accelerometers and GPS reveals the flexible foraging strategy of a bird in relation to weather conditions. — PLoS ONE 12: e0177892. https://doi.org/10.1371/journal.pone.0177892

Hood, G. M. 2010: PopTools version 3.2.5. Accessed at http://www.poptools.org

IBM Corp. 2020: IBM SPSS Statistics for Windows, Version 27.0. IBM Corp, Armonk, NY.

Hooge, P. N. & Eichenlaub, B. 1997: Animal Movement Extension for ArcView. — Alaska Science Center, Biological Science Office, U. S. Geological Survey, Anchorage, AK.

IUCN 2018: The IUCN Red List of Threatened Species. Version 2018-1. Accessed at www.iucnredlist.org on 04/04/2019.

Johnson, D.H. 1980: The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. — Ecology 61(1): 65–71.

Joseph, L., Wilke, T. & Alpers, D. 2003: Independent evolution of migration on the South American landscape in a long-distance temperate-tropical migratory bird, Swainson's flycatcher (*Myiarchus swainsoni*). — Journal of Biogeography 30: 925–937. https://doi.org/10.1046/j.1365-2699.2003.00841.x

Kays, R., Crofoot, M, C., Jetz, W. & Wikelski, M. 2015: Terrestrial animal tracking as an eye on life and planet. — Science 348: aaa2478. https://doi.org/10.1126/science.aaa2478

Keeley, W.H. & Bechard, M.J. 2017: Nesting behavior, provisioning rates, and parental roles of Ferruginous Hawks in New Mexico. Journal of Raptor Research 51: 397–408. https://doi.org/10.3356/JRR-16-85.1

Kenward, R. E. 2001: A Manual for Wildlife Radio Tagging. — Academic Press, London.

Knott, J., Newbery, P. & Barov, B. 2009: Action plan for the red kite *Milvus milvus* in the European Union. — BirdLife International for the European Union.

Limiñana, R., Soutullo, A., Arroyo, B. & Urios, V. 2012: Protected areas do not fulfil the wintering habitat needs of the trans-Saharan migratory Montagu's harrier. — Biological Conservation 145: 62–9. https://doi.

org/10.1016/j.biocon.2011.10.009

López-López, P., De la Puente, J., Mellone, U., Bermejo, A. & Urios, V. 2016: Spatial ecology and habitat use of adult Booted Eagles (*Aquila pennata*) during the breeding season: implications for conservation. — Journal of Ornithology 157: 981–93. https://doi.org/10.1007/s10336-016-1357-z

López-López, P., Limiñana, R., Mellone, U. & Urios, V. 2010: From the Mediterranean Sea to Madagascar: Are there ecological barriers for the long-distance migrant Eleonora's falcon? — Landscape Ecology 25: 803–813 https://doi.org/10.1007/s10980-010-9460-7

López-López, P., Perona, A., Egea-Casas, O., Morant, J. & Urios, V. 2021: Tri-axial accelerometry shows differences in energy expenditure and parental effort throughout the breeding season in long-lived raptors. — Current Zoology 68(1): 57–67. https://doi.org/10.1093/cz/zoab010

Losos, J.B. & Ricklefs, R.E. 2009: Adaptation and diversification on islands. — Nature 457: 830–836. https://doi.org/10.1038/nature07893

Mammen, K., Mammen, U. & Resetaritz, A. 2014: Rotmilan. Greifvögel und Windkraftanlagen: Problemanalyse und Lösungsvorschläge. Schlussbericht für das Bundesministerium für Umwelt, Naturschutz und Reaktorsicherheit. — Michael-Otto-Institut im NABU. Leibniz-Institut für Zoound Wildtierforschung, BioConsult SH, Bergenhusen, Berlin, Husum. (In German)

Manly, B. F. J. 1997: Randomization, bootstrap and Monte Carlo methods in biology, 2nd ed. — Chapman & Hall, London.

Martínez, J.E., Zuberogoitia, I., Escarabajal, J.M., Cerezo, E., Calvo, J.F. & Margalida, A. 2020: Breeding behaviour and time-activity budgets of Bonelli's eagles Aquila fasciata: marked sexual differences in parental activities. — Bird Study 67: 35–44. https://doi.org/10.1080/00063657.2020.1733487

Mateo-Tomás, P., Olea, P.P., Mínguez, E., Mateo, R. & Viñuela, J. 2020: Direct evidence of poison-driven widespread population decline in a wild vertebrate. — Proceedings of the National Academy of Sciences 117 (28): 16418–16423. https://doi.org/10.1073/pnas.1922355117

McIntyre, C.L. & Schmidt, J.H. 2012: Ecological and environmental correlates of territory occupancy and breeding performance of migratory Golden Eagles *Aquila chrysaetos* in interior Alaska. — Ibis 154(1): 124–135 https://doi.org/10.1111/j.1474-919X.2011.01181.x

Mellone, U., Klaassen, R.H.G., Garcia-Ripolles, C., Limiñana, R., Lopez-Lopez, P., Pavon, D., Strandberg, R., Urios, V., Vardakis, M. & Alerstam, T. 2012: Interspecific comparison of the performance of soaring migrants in relation to morphology, meteorological conditions and migration strategies. — PLoS ONE 7(7): e39833. https://doi.org/10.1371/journal.pone.0039833

Molina, B. 2015: El milano real en España. III Censo Nacional. Población invernante y reproductora en 2014 y método de censo. — SEO/BirdLife, Madrid. (In Spanish)

Mougeot, F. & Bretagnolle, V. 2006: Breeding biology of the Red Kite *Milvus milvus* in Corsica. — Ibis 148: 436–448. https://doi.org/10.1111/j.1474-919X.2006.00558.x

Mougeot, F., Garcia, J. T. & Viñuela, J. 2011: Breeding biology, behaviour, diet and conservation of the Red Kite (*Milvus milvus*), with particular emphasis on Mediterranean populations. — In Ecology and conservation of European dwelling forest raptors and owls (ed. Zuberogoitia, I., Martínez, J.E.): 190–204. Editorial Diputación Foral de Vizcaya, Bilbao, Spain.

Nachtigall W. & Herold S. 2013: Der Rotmilan (*Milvus milvus*) in Sachsen und Südbrandenburg. Jahresber Monitoring Greifvögel Eulen Europas 5. — Sonderband: 1–104.

Nachtigall, W., Stubbe, M. & Herrmann, S. 2010: Aktionsraum und Habitatnutzung des Rotmilans (*Milvus milvus*) während der Brutzeit–eine telemetrische Studie im Nordharzvorland. — Vogel und Umw 18: 25–61. (In German)

Newton, I., Davis, P. E. & Davis J. E. 1989: Age of first breeding, dispersal and survival of Red Kites *Milvus milvus* in Wales. — Ibis 131: 16–21. https://doi.org/10.1111/j.1474-919X.1989.tb02738.x

Newton, I., Davis, P. E. & Moss, D. 1994: Philopatry and population growth of red kites, *Milvus milvus*, in Wales. — Proceedings of the Royal Society 257(1350): 317–323. https://doi.org/10.1098/rspb.1994.0132

Newton, I., Davis, P. E. & Moss D. 1996: Distribution and Breeding of Red Kites *Milvus milvus* in Relation to Afforestation and Other Land-Use in Wales. — Journal of Applied Ecology 33: 210–224. https://doi.org/10.2307/2404744

Nur, N. 1988: The consequences of brood size for breeding blue tits. III. Measuring the cost of reproduction: survival, future fecundity, and differential dispersal. — Evolution 42: 351–362. https://doi.org/10.2307/2409238

Ortlieb, R. 1980: Der Rotmilan *Milvus milvus*. — Ziemsen Verlag, Wittenberg Lutherstadt (Ziemsen), Germany.

Pfeiffer, T. & Meyburg, B. U. 2015: GPS tracking of Red Kites (*Milvus milvus*) reveals fledgling number is negatively correlated with home range size. — Journal of Ornithology 156: 963–975. https://doi.org/10.1007/s10336-015-1230-5

Porstendörfer, D. 1994: Aktionsraum und Habitatnutzung beim Rotmilan *Milvus milvus* in Süd-Niedersachsen. — Vogelwelt 115: 293–298. (In German)

Porstendörfer, D. 1998: Untersuchungen zum Aktionsraum des Rotmilans (*Milvus milvus*) während der Jungenaufzucht. — Vogelkdl Ber Niedersachs 30: 15–17. (In German)

R Core Team 2022: R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Sergio, F., Blas, J., Forero, M., Ffernández, N., Donázar, J. A. & Hiraldo, F. 2005: Preservation of wide-ranging top predators by site protection: black and red kites in Doñana National Park. — Biological Conservation 125: 11–21. https://doi.org/10.1016/j.biocon.2005.03.002

Silverman, B.W. 1986: Density estimation for statistics and data analysis. — Chapman and Hall, London.

Soutullo, A., Urios, V., Ferrer, M. & López-López, P. 2008: Habitat use by juvenile Golden Eagles *Aquila chrysaetos* in Spain. — Bird Study 55: 236–40. https://doi.org/10.1080/00063650809461528

Trivers, R.L. 1972: Parental investment and sexual selection. — In Sexual Selection and the Descent of Man (ed. Campbell, B): 136–179. Aldine Publishing Company.

Urios, V., Romero, M. & Mellone, U. 2015: The use of satellite telemetry for the study of the movement ecology of raptors. — Publicaciones de la Universidad de Alicante, Spain.

Tucker, M.A., Alexandrou, O., Bierregaard, R.O., Bildstein, K.L., Böhning-Gaese, K., Bracis, C., Brzorad, J.N., Buechley, E.R., Cabot, D., Calabrese, J.M., Andre Chiaradia, C.C., Davenport, L.C., Davidson, S.C., Desholm, M., DeSorbo, C.R., Domenech, R., Enggist, P., Fagan, W.F., Farwig, N., Fiedler, W., Fleming, C.H., Franke, A., Fryxell, J.M., García-Ripollés, C., Grémillet, D., Griffin, L.R., Harel, R., Kane, A., Kays, R., Kleyheeg, E., Lacy, A.E., LaPoint, S., Limiñana, R., López-López, P., Maccarone, A.D., Mellone, U., Mojica, E.K., Nathan, R., Newman, S.H., Noonan, M.J., Oppel, S., Prostor, M., Rees, E.C., Ropert-Coudert, Y., Rösner, S., Sapir, N., Schabo, D., Schmidt, M., Schulz, H., Shariati, M., Shreading, A., Silva, J.P., Skov, H., Spiegel, O., Takekawa, J.Y., Teitelbaum, C.S., van Toor, M.L., Urios, V., Vidal-Mateo, J., Wang, Q., Watts, B.D., Wikelski, M., Wolter, K., Žydelis, R. & Mueller, T. 2019: Large Birds Travel Farther in Homogeneous Environments. — Global Ecology and Biogeography 28(5): 576–87. https://doi.org/10.1111/geb.12875

Veiga, J. P. & Hiraldo, F. 1990: Food Habits and the Survival and Growth of Nestlings in Two Sympatric Kites (*Milvus milvus* and *Milvus migrans*). — Holarctic Ecology 13: 62–71. https://www.jstor.org/stable/3682346

Vidal-Mateo, J., Romero, M. & Urios, V. 2019: How can the home range of the Lesser Kestrel be affected by a large civil infrastructure? — Avian Research 10: 10. https://doi.org/10.1186/s40657-019-0149-6

Villafuerte, R., Viñuela, J. & Blanco, J. C., 1998: Extensive predator persecution caused by population crash in a game species: The case of red kites and rabbits in Spain. — Biological Conservation 84: 181–188. https://doi.org/10.1016/S0006-3207(97)00094-3

Viñuela, J., Martí, R. & Ruiz, A. 1999: El Milano Real en España. Monografía nº6. — SEO/BirdLife, Madrid. (In Spanish)

Viñuela, J., De la Puente, J. & Bermejo, A. 2021. Milano real, *Milvus milvus*. — In Libro Rojo de las Aves de España (Ed. López-Jiménez, N.): 446–455. SEO/BirdLife, Madrid, Spain. (In Spanish)

Walz, J. 2001: Bestand, Ökologie des Nahrungserwerbs und Interaktionen von Rot- und Schwarzmilan 1996–1999 in verschiedenen Landschaften mit unterschiedlicher Milandichte: Obere Gäue, Baar und Bodensee. — Ornithologische Literatur mit Bezug auf Baden Württemberg 17: 1–212. (In German)

Williams, T.D. 2018: Physiology, activity and costs of parental care in birds. — Journal of Experimental Biology 221: jeb169433. https://doi.org/10.1242/jeb.169433

Worton, B. J. 1989: Kernel methods for estimating the utilization distribution in home-range studies. — Ecology 70: 164–8. https://doi.org/10.2307/1938423

Zar, J. H. 1999: Biostatistical analysis, 4th Ed. — Prentice Hall, Upper Saddle River, N.J. U.S.A.

Online supplementary material

Supplementary material available in the online version includes Tables S1 and S2 with metadata and information on individual parameters.

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Diet and grit characteristics in young Eurasian Bullfinches (*Pyrrhula pyrrhula*) inhabiting Iberian hedgerows

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For the first time, the diet of young Iberian Bullfinches (*Pyrrhula pyrrhula iberiae*) is studied, specifically in a hedgerow habitat in northwestern Spain, through stomach (younger nestlings up to 8 days of age, which died without researcher intervention) and faecal sac (older nestlings) analysis, and secondarily direct observation (nestlings and dependent juveniles). Also, for the first time, grit use by bullfinch nestlings is described in some detail. Bullfinches fed their young with a mixture of seeds and invertebrates, with greater quantitative importance of the former. The identity of the seeds varied considerably between spring and summer, and animal fraction gradually decreased from May to July for older nestlings, in both cases presumably because of the seasonal changes in food availability. Caterpillars and spiders were the most important arthropod prey in the diet. Apparently, the young were not fed non-arthropod invertebrates. The relative importance of invertebrates, which are very rich in proteins, was greater for younger nestlings than for older ones. Difficult to digest hard-bodied prey, such as beetles, were not present in the stomachs of the youngest nestlings. The frequency of occurrence and amount of grit in stomachs increased with nestling age, along with the need to grind food. There were no remarkable differences in number of units, size, or number of colour types of gastroliths between months. The high floristic diversity in the study area, which has great overall conservation value, provides a wide range of resources for bullfinches, including plenty of food for their young.

1. Introduction

The diet of finch (Fringillidae) nestlings in Europe usually consists of a mixture of seeds and invertebrates in variable proportions, the latter being the main source of proteins to favour growth, except for species in the subfamily Fringillinae whose nestlings are fed almost entirely on invertebrates, and some species in the subfamily Carduelinae whose nestlings are fed almost entirely on seeds (Newton 1967a, 1985, Cramp & Perrins 1994, Valera *et al.* 2005, Gil-Delgado *et al.* 2009).

Granivorous passerines select specific plant foods, mostly seeds in the broader sense, based mainly on their bill size and shape, including feeding of finch nestlings (Newton 1967a, 1985, Willson 1971, Pulliam 1985, review by Díaz 1996). Furthermore, the high proportion of caterpillars (Lepidoptera larvae) and spiders in the diet of passerine nestlings in wooded habitats in temperate and Mediterranean regions has been underlined (Pagani-Núñez *et al.* 2011, Ceia *et al.* 2016, Serrano-Davies & Sanz 2017, Nyffeler *et al.* 2018). In connection with avian diet, ingestion of small stones to break down food in the gizzard and enable digestion is widespread in granivorous, insectivorous, and omnivorous species (McLelland 1979, Best & Gionfriddo 1991, Gionfriddo & Best 1996, 1999, Luttik & de Snoo 2004, Møller & Erritzøe 2010), and parents provide this grit for their nestlings (Barrentine 1980, Alonso 1985, Marques *et al.* 2003, Orłowski *et al.* 2009, Ottens *et al.* 2014). Other secondary functions of bird gastroliths have been suggested, namely, as a supply of minerals such as calcium and potential detoxifying action (see Barrentine 1980, Orłowski *et al.* 2009, Møller & Erritzøe 2010).

Eurasian Bullfinches (*Pyrrhula pyrrhula*) (Carduelinae, Fringillidae) (hereinafter referred to as bullfinches) are considered generalist forest birds that readily accept heterogeneous semi-open landscapes (Cramp & Perrins 1994, Wilson *et al.* 2009, Clement 2010, Hernández 2021). Currently, there are nine recognized bullfinch subspecies, of which *iberiae* occupies southwest France (Pyrenees) and the mountains of northern Portugal and Spain (Clement 2010). The nestling diet composition of certain populations of the species, particularly those in northern, central and western Europe, including the British Isles, is known to some degree, at least with regard to main food types (Newton 1967b, 1985, Cramp & Perrins 1994). Summarizing this knowledge, bullfinches feed their nestlings mostly a mixture of seeds, insects, and spiders, and occasionally include some small terrestrial gastropods. The amount of invertebrates given tends to decrease in the final days of growth (less necessary proteins), at the end of the breeding season (lower availability of invertebrates), and in open country (lower availability of invertebrates than in woodland). Also, there may be some differences in diet composition between broods, even in the same habitat and time, due to very local environment variations, since adults generally forage near the nest. Compared to nestlings, food of plant origin forms the bulk of adult bullfinch diet. According to Newton (1967b), young bullfinches receive grit and free water from their parents, along with food, without providing further details. By contrast, to date, information available on nestling diet in the Iberian subspecies is practically non-existent, except for vague and imprecise references to the probable contribution of herb seeds and some invertebrates (Noval 2000, Díaz 2016). Occasionally, bullfinches have been observed pecking cherries and then feeding fledglings with pieces of pulp in northern Spain (Hernández 2008). Bernis (1957) found grit in the stomach of an adult male bullfinch from Galicia (NW Spain). However, according to the literature reviewed, no information has been published for Iberian bullfinch nestlings in this regard.

Cardueline finches swallow food and then regurgitate it to nestlings without predigesting it (Newton 1967a, 1985). Differential digestion rates of dietary items, with soft items being digested more rapidly (*e.g.*, soft-bodied insects vs. hard seeds) and different passage times, with large hard items persisting for longer, impose the highest risk of bias in any study of bird gut contents (Rosenberg & Cooper 1990, Sutherland 2004). Nevertheless, gut content analysis is considered appropriate for reliably determining the presence of prey items in the nestling diet of small insect-eating songbirds (Kleintjes & Dahlsten 1992). Normally, 10 or fewer stomachs are adequate for assessing species-specific bird diets at particular sites within a collection period (Rosenberg & Cooper 1990, but see Kleintjes & Dahlsten 1992). Regarding bird dropping analysis, one of its disadvantages is the high degree of fragmentation and digestion of samples, making the identification of remains more difficult than stomach contents, together with unequal digestibility between food items (Rosenberg & Cooper 1990, Pulido & Díaz 1994, Stoate *et al.* 1998, Sutherland 2004). Nevertheless, no major differences have been found between the results – range of food items encountered – of the faecal and stomach analysis in passerines, and nestlings typically have lower digestive efficiency than adults, which, comparatively, enables better identification of fragments (Ralph *et al.* 1985, Rosenberg & Cooper 1990, Sutherland 2004). Faecal analysis is a feasible procedure to obtain a rough assessment of diet composition and relative proportion of prey items in nestlings of small insectivorous passerines (Kleintjes & Dahlsten 1992, Poulsen & Aebischer 1995, Moreby & Stoate 2000, Michalski *et al.* 2011). Obviously, dropping analysis is less intrusive than stomach analysis if the latter involves deliberately killing the birds. The direct observation technique is appropriate for assessing the diet and foraging tactics of frugivorous and granivorous birds that feed above the ground, for which species of food plants may be identified, but is less useful for insectivorous birds, especially in detecting inconspicuous prey (Rosenberg & Cooper 1990, Sutherland 2004, Yoshikawa & Osada 2015). Bullfinches accumulate food collected for their young, or for the female in the case of mate-feeding, in special pouches under the lower jaw (up to 1 cm^3 of food), with the consequent bulging of the throat (Newton 1967b, Hernández 2020, Á. Hernández pers. obs.).

The main aim of this study is to provide a first approach to the diet of bullfinch nestlings in an area located in northwestern Mediterranean Spain, close to the southwestern distribution limits of the species. The target population occupied a single general habitat, specifically a dense network of well-grown hedgerows surrounded by woodland. Well-tried techniques in avian research, namely, stomach content analysis – applied to nestlings found dead –, faecal sac analysis, and direct observation, following the usual procedures for each technique (Rosenberg & Cooper 1990, Hernández 1993, Hódar 1994, Sutherland 2004), were used to determine the diet of young bullfinches.

The following issues on nestling diet were assessed quantitatively: (1) relative importance of plant and animal fractions, (2) diversity of foods within these fractions, and (3) variations associated with timing of breeding and nestling age. Direct observation allowed some data on the diet of dependent juveniles to be obtained. Additionally, (4) the results obtained through the different analysis methods were compared, and (5) the relevance of the mineral fraction in stomachs was evaluated and the gastroliths found were described. Important bioecological aspects of this bullfinch population are already known, some of which are closely related to nestling diet, namely feeding habits of adults and independent juveniles (self-feeding), habitat use and space preferences, and breeding, including nestling stage characteristics except for diet composition (Hernández 2020, 2021, 2022, Hernández & Zaldívar 2021). Using part of this information, a secondary aim of the present study is to compare the general young provisioning diet with self-feeding.

Based on the background information set out above, the diet of nestling Iberian bullfinches is expected to be diverse (seeds plus invertebrates) with seasonal and age-related changes in composition, including a higher contribution of animal matter in younger nestlings and at the onset of the breeding season, certain food types being selected according to their size. No notable differences are expected between the general dietary patterns of young Iberian bullfinches and those of other European subspecies, but certain peculiarities associated with the regional and local ecological community are expected in the more detailed range of foods consumed. Caterpillars and spiders are expected to play an important role in nestling diet. The contribution of invertebrates should be greater in nestling diet than in self-feeding. Stomach analysis is expected to provide the most comprehensive results on diet in terms of taxonomic accuracy, and to allow grit use to be properly assessed, but the other techniques are expected to provide a reliable view of the major food categories.

2. Material and methods

2.1. Study area

The study area covers 78 ha and is located in the middle-lower Torío river valley, between Palacio and Manzaneda (42º 43’–42º 44’ N, 5º 30’–5º 31’ W; 900 m a.s.l.; León province, Castile and León autonomous community), in northwest Spain. Biogeographically, it forms part of the Carpetano-Leonese sector in the Mediterranean West Iberian province (Rivas-Martínez 2007). Hot summers (average temperature of *ca.* 20 ºC), cold winters (*ca.* 4 ºC) with some snowfall, and moderate rainfall (average annual precipitation of *ca.* 500 mm) with a relatively short dry summer season characterize the area. Details on the weather during the study period are available in Hernández (2020). The landscape is mainly composed of hedgerows that separate irrigated meadows grazed by livestock and cut for hay, bordered by riparian woodland on the west side and slopes covered in Pyrenean Oak (*Quercus pyrenaica*) woods interspersed with very small plantations of Scots Pine (*Pinus sylvestris*) on the east side (see Supplementary Material Fig. S1). Some hedgerows border Canadian Poplar (*Populus* x *canadensis*) plantations. Estimated hedgerow density is 3.3 km per 10 ha. The area is located in a transition zone to the Eurosiberian region, south of the Cantabrian Mountain range, in an extensive hedgerow network of great conservation value for flora and fauna (Hernández 2009, 2018, Hernández & Zaldívar 2013). About thirty species of broadleaved, chiefly deciduous shrubs, trees, and climbers are found in the hedgerows. The landscape and hedgerow density and structure are very similar throughout the study area and have hardly changed in recent years and decades, except for a moderate increase in the number of poplar plantations and an incipient abandonment of meadows and hedges.

2.2. General considerations

All the fieldwork was performed using non-invasive techniques which enabled sufficient data for the objectives of the study to be obtained without threatening the welfare of the birds, as neither live birds nor active nests were manipulated (see Dawkins 2007). Throughout 2001–2006, the bullfinches directly observed in the area and maximum details of these sightings were recorded during field trips conducted to investigate various aspects of their ecology. Bullfinches inhabited the area all year round. In particular, general fieldwork to study their breeding ecology was conducted between the months of March (when the first signs of probable breeding were observed) to October (when the last sightings of adults with dependent young were made) (Hernández 2020). In a systematic way, 113 trips were conducted in spring (March: 31, April: 33, May: 49), 155 in summer (June: 49, July: 54, August: 52), and 65 in autumn (September: 39, October: 26). The total number of trips in each season was equally distributed among the years of study as far as possible, except for 2006 when the sampling effort was considerably lower. Two trips were usually needed to cover the entire area: approximately half of the area (36 ha) on one trip, and the other (42 ha) the following day. On each trip, the corresponding zone was explored by slowly walking around it, stopping frequently, following the edge of the hedgerows and marginally (≈10% sampling effort) the edge of the oak woods. Small European birds generally show a bimodal pattern of daily locomotor activity, but mobility tends to decrease throughout the day (Bas *et al.* 2007). Consequently, more than 85% of field trips were conducted in the morning in all seasons, and the remainder in the afternoon. The morning trips lasted from one hour after sunrise to 12:00 h (solar time) and the afternoon trips from 12:00 h (solar time) to one hour before sunset, as there was insufficient light at dawn or dusk for sampling to be carried out. Standard optical equipment was used to observe birds, *i.e.*, binoculars and a telescope. Bullfinch density in the area and study period was approximately 2.5–3.5 pairs/10 ha during April–May (Hernández 2020). As far as the current situation is concerned, recent visits to the study area for other purposes in 2022 revealed that the bullfinches are still present and apparently in good conservation status.

More specifically, nests were searched for, found and monitored during April–August of the period 2001–2005 (n=56 nests found). Direct nest searching ("cold searching") is not usually effective for bird species that hide their nests (Green 2004), which is the case of the bullfinch. Thus, the search for nests was mainly by following adults showing signs of nest attendance. Apart from field trips made systematically to cover the entire area, as described above, short visits were made to increase the monitoring of active nests in an effort to identify, weekly at least, the breeding stage of each nest. The observer kept the maximum distance possible when visiting the nests to determine their content by visual inspection, with the help of a long-handle mirror if necessary. Immediately after these visits, the nests were usually checked by long-distance observation to verify whether they were still active, which always occurred, that is, the researcher did not apparently interfere in nest success. The earliest date of nest building was within 11–30 April for all years, and fledglings were recorded leaving the nest during all the ten-day periods from the end of May to mid-August (Hernández 2020; but a nest found in 2021, very close to the study area at the edge of the forest, contained nestlings until early September). Nest attendance, from the early building stage to when nestlings were ready to leave the nest, lasted approximately 36 days. The overall mean clutch size was 4.6 eggs. Bullfinches chose nesting zones with greater shrub and tree cover than that available, and nests were normally placed in hedgerows approximately 1.5 m above the ground, on a wide variety of plant species, but thorny species were selected (Hernández & Zaldívar 2021). Adult activity around the active nests was concentrated in a radius of 100 m, although it was not rare for them to move beyond this distance, sometimes flying out of sight (Hernández 2020).

Nesting success, *i.e.*, at least one young fledged, increased progressively from April–May (4% of 25 nests) to June–July (61% of 28) and August (100% of 3) (Hernández 2020). The principal proximate causes of nest failure were egg desertion/predation (18 of 35 failed nests, 51%), nest desertion during nest building (20%), and nestling desertion/predation (17%). In complete clutches with a known size (n=32), approximately half of the eggs became fledglings leaving the nest, no significant seasonal differences being observed for this parameter. In such clutches, individual losses (n=71) were due to deserted/predated eggs (49%), deserted/predated nestlings (31%), unhatched eggs (18%), and marginally natural death in nestlings in successful nests (<2%) (Hernández 2020).

Both males and females fed nestlings, fledglings, and dependent juveniles. Considering the total number of visits by males and females, parents visited the nest at intervals of *ca.* 17–23 min, resulting in 40–55 times a day (Hernández 2020). Concerning self-feeding, there was no significant difference between males and females in the frequency of plant and animal food records in spring, or in summer between males, females, and juveniles (Hernández 2022). In all, 84% of self-feeding records during spring–summer corresponded to plants (1046 of 1247) and 16% to arthropods, these values being used for comparison with those of parental provisioning of young. Self-feeding records were obtained by direct observation, similar to how the young provisioning records were obtained by direct observation (see below).

2.3. Nestling diet determination

2.3.1. Stomach content analysis

In all, the stomach contents of 13 nestling bullfinches from 5 nests were analysed. By month of death, 9 nestlings from 3 nests corresponded to May, and 4 from 2 to July. By year, 4 nestlings from 1 nest corresponded to 2001, 4 from 1 to 2002, and 5 from 3 to 2003. The nestlings died without researcher intervention in unsuccessful nests (*i.e.*, they were apparently nestlings abandoned due to factors such as weather or predation, so none of them fledged), except for one that died in a successful nest due to natural causes (the rest of the young fledged). None of the nestlings had reached 9 days old when they died, that is, some had, at most, slightly exceeded half of their growth period, as the nestling stage in bullfinches lasts 14–17 days (Hernández 2020). Nestlings with an estimated age of <5 days were differentiated from those with an estimated age of 5–8 days, through visual inspection of their body size and plumage development, and taking into account the approximate hatching date, if known. Nestlings of both ages were recorded in May and July. After verifying that nests were no longer active, dead nestlings were removed and placed in a labelled container with 70% ethanol. In the laboratory, the stomach of each nestling was removed using a scalpel and fine-tip scissors and preserved under the same conditions in individual labelled containers until their contents were analysed. The stomachs were then opened using the same surgical material, and the contents spread on a thin sheet of water in a Petri dish to identify and count food items by examining them under a Motic® SMZ-168 (7.5x–50x magnification range) trinocular stereo microscope equipped with a Moticam 580 (5.0 MP) digital camera. Photographs were taken so that analysis could continue later without depending on physical samples and microscope (as shown in Supplementary Material Fig. S2).

Three main components were considered, namely, plant remains, animal remains, and mineral fraction. For each stomach, plant, animal, and mineral contribution, in terms of volume, was visually estimated with 5% accuracy. Plant remains were mostly whole seeds/fruits, some fragmented, as well as skins and small fibrous pieces, presumably belonging to seeds/fruits ingested. The term "seed" will be used from now on in a broad sense (*e.g.*, it includes whole achene-type fruits found in the stomachs). For each stomach, all of the seeds were counted, the number of different seed types (at species/genus level) was estimated according to their morphology and size, and an attempt was made to identify them. Seeds were identifed by comparing them with pictures (photos/drawings) in botanical encyclopedias or guides (*e.g.*, Castroviejo 1986–2017, Torroba *et al.* 2013) and well-known online media file repositories (*e.g.*, Wikimedia Commons 2004–2021, Alamy 1999–2021, Arkive 2013–2019), together with prior knowledge of the flora in the study area and many of their fruits and seeds (Hernández & Zaldívar 2013, Hernández 2021, Á. Hernández pers. obs.). A large number of the seeds, but not all of them, were identified at species/genus level; thus, the analysis carried out at this level is not quantitative but semi-quantitative. Seed length attributed to each stomach is the mean value of the respective length range found.

All of the animal remains found belonged to small arthropods, and were identified to order level when possible. They were mainly heads, jaws, thoraxes, wings, elytra, legs, and long hairs, in the case of insects; and prosomata, chelicerae, and spinnerets, in the case of spiders. Some prey, such as caterpillars, were found almost whole. The stomachs also contained unidentifiable tiny fragments of arthropods. The contribution of the different arthropod orders was estimated as frequency of occurrence in stomachs.

Mineral fraction was formed by small stones, *i.e.*, gastroliths. For each stomach, all of the gastroliths were counted and the number of gastrolith colours estimated, differentiating between colourless (translucent), whitish, pinkish, reddish, brownish, and blackish, *i.e.*, the six differentiated colour types found in the stomachs as a whole. Gastrolith length attributed to each stomach is the mean value of the respective length range found. Tiny mineral fragments, resembling fine sand, found in one stomach were excluded from the analysis.

2.3.2. Faecal sac analysis

In all, the content of 103 faecal sacs from 15 nests was analysed. The faecal sacs came from a maximum of 46 nestlings. In the case of nests containing more nestlings than faecal sacs collected, the number of faecal sacs was taken as the maximum number of nestlings involved. Faecal sacs were assigned to 20 May–10 June (47 sacs from a maximum of 13 nestlings, 4 nests), 11–30 June (34, 16, 6), and 1–31 July (22, 17, 5), corresponding to the years 2002 (5 nests), 2003 (6), 2004 (2), and 2005 (2). For 14 successful nests, the date assigned was the estimated day when the young fledged, and the faecal sacs were collected when the nest was no longer active. For the remaining nest, which was unsuccessful, it was the day when it was verified that the nestlings, which were at least half-grown, had been predated. Faecal sacs were collected from the nest rim, where the droppings of more developed mobile European finch nestlings, including bullfinches, usually accumulate as parents no longer remove them at the end of the nestling stage (Newton 1985, Ferguson-Lees *et al.* 2011, Hernández 2020). Therefore, the faecal sacs corresponded to older nestlings. Each one was collected with fine-tip tweezers and placed in a small labelled plastic bag. In the laboratory, they were removed from the bags, placed on absorbent paper, left to dry at room temperature and then returned to their respective bags until analysis. Each sac was placed and broken up on a thin sheet of water in a Petri dish for purposes of identification of food items using the same optical equipment as that described for stomach content analysis.

The analysis only considered two main components, namely, plant remains and animal remains, as the presence of small stones was negligible (a few were found in only one faecal sac). For each faecal sac, plant and animal contribution, in terms of volume, was visually estimated with 5% accuracy. Plant remains were above all vegetable matter, highly fragmented by digestion, small fibrous pieces, and, very exceptionally, some small seeds whole or in pieces (a few were found in two faecal sacs). The plant remains were not taxonomically identified.

All of the animal remains found belonged to small arthropods, and were identified to order level when possible. They were mainly heads, antennae, jaws, wings, elytra, hemelytra, legs/leg segments, abdomen segments, and long hairs, in the case of insects; and prosomata, chelicerae, legs/leg segments, and opisthosomata, in the case of spiders. The faecal sacs also contained unidentifiable tiny arthropod fragments. The contribution of the different arthropod orders was estimated as frequency of occurrence in faecal sacs.

2.3.3. Direct observation

Sightings of adults searching for food, filling their buccal pouches, and immediately feeding nestlings or dependent juveniles (all this in a maximum time of 10 min), were recorded during the fieldwork period in 2001–2006 (June: 9 records, July: 36, August: 15). Focal sampling, *i.e.*, watching foraging individual birds for a specific time, is a standard method in studies on avian feeding habits (Sutherland 2004). Each record refers to an individual, differentiating between male and female, entering a nest to feed nestlings or feeding juveniles that had left the nest, regardless of number of nestlings or juveniles fed on each feeding visit. More than one record could occur for the same individual if it collected more than one food type during 10 min prior to feeding. As far as possible, the records were independent of one another, at least those for each sampling day, since the birds were successively left behind during the visits. In addition, the study period covering many years, bullfinch movements – which can even affect some pairs during their long breeding season (Newton 2000 for British birds) – and the short lifespan of this species, averaging 2 years (Robinson 2005), together ensure a high degree of independence between records. The records came from 20 males and 19 females, considering the sum of apparently different individuals from each sampling day.

For each record, food was identified a) visually while the birds ate (*e.g.*, fleshy fruits), b) by inspection immediately after *in situ* (*e.g.*, caterpillars that build communal silken nests), and/or c) by collecting a sample and identifying it in the laboratory (*e.g.*, most herbs). In all cases, it was confirmed whether the food was vegetable or animal (arthropods), but not always identified to lower taxonomic levels. It cannot be completely ruled out that the bullfinches used part of the food collected in this way for self-feeding or to feed females (in the case of males).

2.4. Statistical analysis

The *Z*-score test was used to compare two independent proportions; the Mann–Whitney *U* test to compare two mean ranks of two independent groups; the Kruskal–Wallis test (*H*) to compare three mean ranks of three independent groups; the chi-square test (χ^2), with Yates correction for one degree of freedom, to compare series of absolute frequencies for two variables; and the Spearman's correlation coefficient (r_s) to assess association between two ranked variables; considering the two-tailed way wherever possible (Fowler *et al.* 1998, Lowry 1998–2022). For rows by columns chi-square tests, the total sample size was not smaller than 50, at least 80% of the cells had an expected frequency equal to or greater than 5, and no cell had an expected frequency smaller than 1. In addition, for 2 x 2 tables, the chi-square test was only used if all expected cell frequencies were equal to or greater than 5. Consequently, for 2 x 2 tables, two-tailed Fisher's exact test was used instead of the chi-square test if any the above requirements were not met (Lowry 1998–2022). In some comparisons between techniques for determining diet, percentages relating to volume were assumed to be sufficiently equivalent to those relating to feeding records and both were considered as absolute frequencies, although this should be taken with caution. For several comparisons in the stomach content analysis, the ratio between two means was used so as not to overuse statistical tests having small sample sizes. The ratio between two means simply refers to the division of the mean with the highest value by the other. Standard deviation (SD) was estimated as a measurement of dispersion. Probability $p<0.05$ was considered statistically significant. All years were pooled together, mainly to avoid analysing small sample sizes. As stated above, the sampling effort in each season was equally distributed among the years of study. Also, little changing environmental conditions from year to year seemed to promote steady breeding population densities during the main study period, nest success and breeding productivity rates were fairly constant from one year to the next, and interannual variation in adult and independent juvenile diet was not remarkable (Hernández 2020, 2022, Á. Hernández unpubl.). All of the nests were in an area characterized by a landscape invariably composed of hedgerows between meadows, which did not allow considering a habitat stratification.

3. Results

3.1. Stomach content analysis

All nestling stomachs contained both plant and arthropod remains (Table 1). Frequency of occurrence of grit was similar in May (56% of 9 stomachs) and July (50% of 4) (*Z*-score = 0.18, p=0.85), but much less in nestlings <5 days old (14% of 7 stomachs) than 5–8 days old nestlings (100% of 6) (*Z*-score = –3.09, p=0.002) (Table 1). Taking all of the stomachs into account (n=13), mean percent volume was 66 ± 26% (range = 10–90%) for plant remains, 31 ± 26% (range = 5–90%) for animal remains, and 3 ± 3% (range = 0–10%) for grit. Mean percent volume ratio between May and July was low for plant (1.2), animal (1.3), and mineral (1.3) fractions (Fig. 1). Comparing ages, such ratio was low for plant (1.2) and animal (1.2) fractions, but high for mineral fraction (8.3), grit accounting for less than 1% on average in nestlings <5 days old and almost 6% in those aged 5–8 days (*U*=2.5 , p<0.01, n=7 and 6 stomachs respectively) (Fig. 1).

Regarding plant remains for the 14 total stomachs, the mean number of seed types was 4, mean number of seeds approximately 70, and mean seed length slightly over 2 mm (Fig. 2). Mean ratios between months (May and July) and between ages (<5 d and 5–8 d old nestlings) were low or moderately low for these variables (seed types: 1.3 and 1.2, respectively; number of seeds: 1.8 and 2.3; size: 1.4 and 1.3) (Fig. 2). Fourteen seed species belonging to 10 families (Asteraceae, Caprifoliaceae, Caryophyllaceae, Fabaceae, Geraniaceae, Polygonaceae, Ranunculaceae, Rosaceae, Urticaceae, Violaceae) were identified. Most of the seeds corresponded to dry fruits of herb species, except for a few Common Honeysuckle

	Nest	Nestling	Plant remains	Animal remains	Gastroliths
<5 days old	Nest 1 (May 2002)	1	85	15	0
		2	90	10	0
		3	85	15	0
		4	90	10	0
	Nest 2 (July 2003)	1	50	50	0
		2	10	90	0
		3	90	5	5
5−8 days old	Nest 3 (May 2001)	1	45	50	5
		2	55	40	5
		3	40	55	5
		4	50	45	5
	Nest 4 (May 2003)	1	85	10	5
	Nest 5 (July 2003)	1	85	5	10

Table 1. Individualized percent volume of plant, animal, and mineral fractions in stomachs of Iberian bullfinch nestlings in northwest Spain, regarding estimated age at death, and month and year of death. For each stomach, plant, animal, and mineral contribution was visually estimated with 5% accuracy.

(*Lonicera periclymenum*) and Bramble (*Rubus* spp.) seeds (fleshy fruits of shrub species). In May, seeds appearing in a higher number of stomachs and/or in greater quantity were Daisy (*Bellis perennis*), Mouse-eared Chickweed (*Cerastium fontanum*), Chickweed (*Stellaria media*), Dandelion (*Taraxacum* gr. *officinale*), Common Nettle (*Urtica dioica*), and Violet (*Viola* spp.). In July stomachs, the seeds of Cranesbill (*Geranium* spp.) predominated, but those of Common Honeysuckle, Medick (*Medicago* spp.), Buttercup (*Ranunculus* spp.), Dock (*Rumex* spp.), and Common Nettle were also found. Dandelion seeds were particularly abundant in some May stomachs (as many as 130 units in one). Only two seed types (Cranesbill and Common Nettle) coincided in May and July stomachs. However, five seed types coincided in the stomachs of <5 days and 5–8 days old nestlings, namely, Bramble, Chickweed, Dandelion, Common Nettle, and Violet.

Both insects and spiders were found in ≥75% of stomachs in any month and at any age, with no significant differences in the occurrence of either prey types between May and July (Fisher's exact test, $p=0.99$) or between nestlings <5 days and 5–8 days old (Fisher's exact test, $p=0.99$) (Fig. 3). Insects could only be identified at the order level in May stomachs (Fig. 3). Lepidoptera remains, belonging to caterpillars, appeared very frequently in this month (8 of 9 stomachs, 89%) regardless of nestling age. Coleoptera remains, belonging to adult beetles, were only found for nestlings 5–8 days old (4 of 6 stomachs, 67%). Diptera remains, belonging to adult flies, only appeared in the stomach of one nestling <5 days old. As for the relative abundance of remains of different arthropod orders in particular stomachs, in some cases where this could be established with certain consistency, spiders predominated, or caterpillars and spiders in equal proportion, with lower number of beetles and negligible proportion of flies. Individual prey could not usually be counted accurately due to fragmentation, but, for example, at least eight caterpillars were found in one stomach.

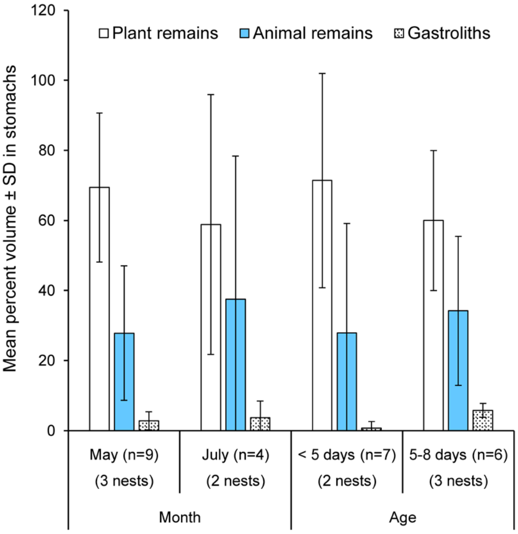

Fig. 1. Mean percent volume of plant, animal, and mineral fractions in stomachs of Iberian bullfinch nestlings in northwest Spain, regarding month of death and estimated age at death. Sample size (n) is the number of nestlings. For each stomach, plant, animal, and mineral contribution was visually estimated with 5% accuracy. Pooled data for 2001–2003.

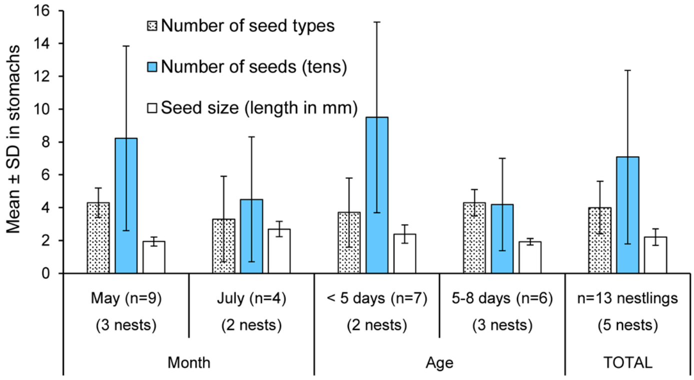

Fig. 2. General attributes of seed presence in stomachs of Iberian bullfinch nestlings in northwest Spain, regarding month of death and estimated age at death. Sample size (n) is the number of nestlings. Seed types refers to the number of plant species. The number of seeds is expressed as the number of tens (groups of 10 seeds). Pooled data for 2001–2003.

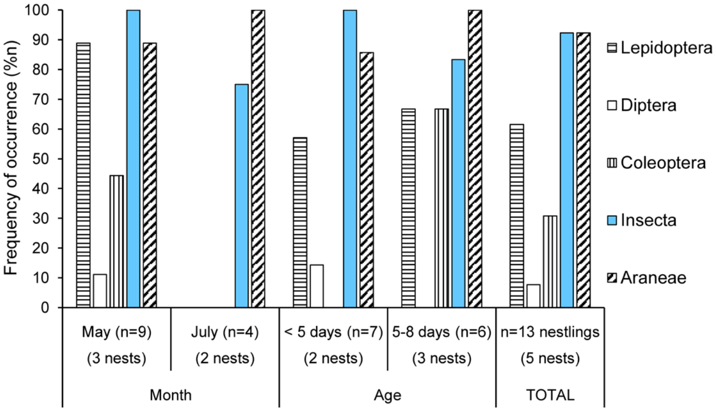

Fig. 3. Frequency of occurrence of arthropod remains in stomachs of Iberian bullfinch nestlings in northwest Spain, regarding month of death and estimated age at death. Sample size (n) is the number of nestlings. Insecta includes all stomachs containing remains of insects, whether or not identified to order level. All stomachs contained arthropod remains. Pooled data for 2001–2003.

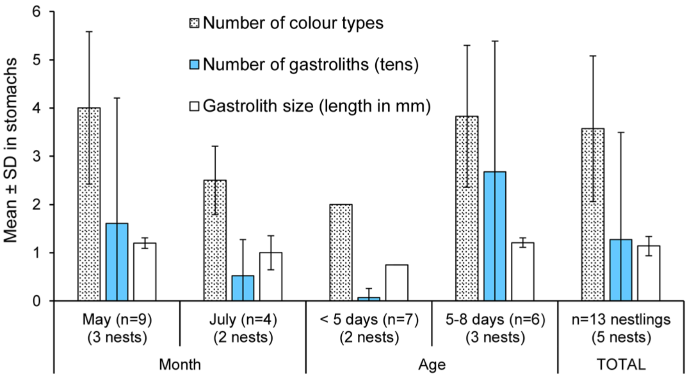

Fig. 4. General attributes of gastrolith presence in stomachs of Iberian bullfinch nestlings in northwest Spain, regarding month of death and estimated age at death. Sample size (n) is the number of nestlings. Possible colour types: colourless (translucent), whitish, pink, reddish, brownish, and blackish. Restrictions: no gastroliths were found in 6 of the 13 total stomachs. These stomachs were included in the calculation of the number of gastroliths (with a value of 0), but not in that of size and colour type. Therefore, the sample size for these two variables is n=5 nestlings from 2 nests (May); n=2 nestlings from 2 nests (July); n=1 nestling from 1 nest, SD=0 (<5 d old); n=6 nestlings from 3 nests (5–8 d old). The number of gastroliths is expressed as the number of tens (groups of 10 gastroliths). Pooled data for 2001–2003.

With regard to mineral fraction for total stomachs (n=13), the mean number of gastroliths was approximately 12 (range = 0–81), and, considering only stomachs containing them (n=7), mean gastrolith length was just over 1 mm and mean number of gastrolith colours just under 4 (Fig. 4). The mean number of gastroliths in the stomachs containing them was 23.7 ± 24.2 (range = 5−81, n=7). Mean ratios between months (May and July) and between ages (<5 d and 5–8 d old nestlings) were generally low or moderate for these variables (colour types: 1.6 and 1.9, respectively; size: 1.2 and 1.7; number of units: 3.2 between months), but mean ratio between ages was very high for number of gastroliths (38.3), grit accounting for 0.7 units on average in nestlings <5 days old and 26.8 in those aged 5–8 days (U=0, p<0.01, n=7 and 6 stomachs respectively) (Fig. 4). The number of colour types in the grit was positively and significantly correlated with the number of grit particles (r_s=0.95, p=0.001, n=7 stomachs). Six colour types were observed in the stomach containing the most grit particles (n=81 gastroliths). Gastroliths were irregular in shape, but compact and not very elongated, some even almost spherical.

3.2. Faecal sac analysis

Significant differences were observed in percent volume of plant and animal remains among faecal sacs from different periods of the breeding season (H_2=6.29, p=0.04, n=4, 6, and 5 nests; both for plant and animal remains), with a progressive decrease in the importance of animal fraction, from a mean of just over 10% during 20 May–10 June to approximately 4% in July (Fig. 5). Plant remains were found in all faecal sacs in all time periods (n=103). Arthropod remains were found in all of the 20 May–10 June faecal sacs (n=47), in 82% of the 34 corresponding to 11–30 June, and in 64% of the 22 corresponding to July (Fig. 6). Similarly, the frequency of occurrence of the main arthropod orders, *i.e.*, Lepidoptera (caterpillars), Coleoptera (adults), and Araneae, decreased from May−early June to July (Fig. 6). Nevertheless, in all nests (n=15), at least part of the faecal sacs removed contained arthropod remains. Taking into account the frequency of occurrence in faecal sacs, there was no significant association between time periods (the three already mentioned) and main prey types (insects and spiders) (χ^2_2=2.72, p=0.25), even though the relative importance of spiders tended to increase and that of insects to decrease from May−early June to July (from 44% to 62%, and from 56% to 38%, respectively). Considering three prey types (lepidopteran caterpillars, the remaining insects identified at the order level together, and spiders), this same analysis also resulted in non-significant association (χ^2_4=5.72, p=0.22).

3.3. Direct observation

According to direct observations, bullfinches provisioned the young (nestlings and dependent juveniles) with plant (82% of 60 feeding visits) and animal (18%) food. They used at least 10 plant species belonging to 6 families (Asteraceae, Caprifoliaceae, Geraniaceae, Polygonaceae, Ranunculaceae, Rosaceae), mainly seeds corresponding to dry fruits of herb species, but also flower buds of herb species and seeds/pulp of fleshy fruits of shrub/tree species (Table 2).

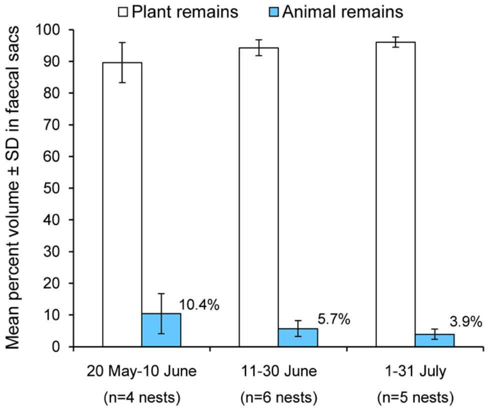

Fig. 5. Mean percent volume of plant and animal remains in faecal sacs of Iberian bullfinch nestlings in northwest Spain during the breeding season. The faecal sacs belonged to older nestlings. Sample size (n) is the number of occupied nests. For each faecal sac, plant and animal contribution was visually estimated with 5% accuracy. The volume values (plant vs. animal) for each nest are the mean values corresponding to its respective faecal sacs. 20 May–10 June: 47 faecal sacs from a maximum of 13 nestlings; 11–30 June: 34 faecal sacs from a maximum of 16 nestlings; 1–31 July: 22 faecal sacs from a maximum of 17 nestlings. Pooled data for 2002–2005.

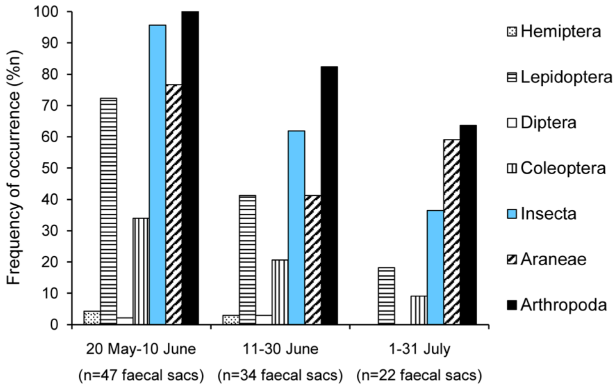

Fig. 6. Frequency of occurrence of arthropod remains in faecal sacs of Iberian bullfinch nestlings in northwest Spain during the breeding season. The faecal sacs belonged to older nestlings. Sample size (n) is the number of faecal sacs. All faecal sacs collected are considered, including those containing plant remains only. In the case of Insecta, all faecal sacs containing insect remains are considered, whether or not identified to order level. In the case of Arthropoda, all faecal sacs containing arthropod remains are considered, whether or not identified to order level. 20 May–10 June: faecal sacs from a maximum of 13 nestlings, 4 nests; 11–30 June: faecal sacs from a maximum of 16 nestlings, 6 nests; 1–31 July: faecal sacs from a maximum of 17 nestlings, 5 nests. Pooled data for 2002–2005.

Table 2. Direct observations of adult Iberian bullfinches searching for food, filling their buccal pouches, and immediately feeding nestlings or dependent juveniles, in northwest Spain during summer months. Each record corresponds to one adult, distinguishing between male and female, entering a nest to feed nestlings or feeding juveniles outside the nest, regardless of number of nestlings and juveniles fed on each visit. One adult could produce more than one record if it collected more than one food type during a maximum of 10 min foraging prior to feeding nestlings or juveniles. Data for June (9 records), July (36 records), and August (15 records). Pooled data for 2001–2006.

Food types	Males		Females	
	Feeding nestlings (%n)	Feeding juveniles (%n)	Feeding nestlings (%n)	Feeding juveniles (%n)
Prunus avium (pulp)	0.0	16.8	0.0	0.0
Lonicera periclymenum (seeds)	0.0	0.0	0.0	29.3
Unidentified fleshy fruit	0.0	0.0	0.0	11.8
Rumex spp. (seeds)	0.0	0.0	9.1	0.0
Polygonum bistorta (seeds)	0.0	27.9	0.0	5.9
Ranunculus spp. (seeds)	21.5	0.0	9.1	5.9
Filipendula ulmaria (seeds)	7.1	0.0	9.1	5.9
Geum urbanum (seeds)	21.5	22.2	27.2	23.5
Geranium molle (seeds)	7.1	11.1	9.1	0.0
Lactuca serriola (seeds)	7.1	0.0	9.1	0.0
Unidentified herb seeds	7.1	5.5	9.1	0.0
Agrimonia eupatoria (flower buds)	0.0	0.0	9.1	0.0
Total food of plant origin	71.4	83.5	89.9	82.3
Hemiptera nymphs	0.0	5.5	0.0	5.9
Lepidoptera caterpillars	0.0	5.5	0.0	5.9
Unidentified arthropods	28.6	5.5	9.1	5.9
Total food of animal origin	28.6	16.5	9.1	17.7
Number of records (n)	14	18	11	17

Regarding arthropod prey, only hemipteran nymphs and lepidopteran caterpillars were identified at order level. There was no significant association between food type (plant vs. animal origin) and sex of the adult (male vs. female) that fed the young (χ^2_1=0.18, p=0.67, nestlings and dependent juveniles together), or between food type (the same types) and age of the young birds (nestlings vs. dependent juveniles) (Fisher's exact test, p=1, males and females together).

3.4. Comparison between techniques

Considering only plant and animal fractions, *i.e.*, ignoring grit, their relative importance in the young provisioning diet was 68% vs. 32% (overall mean percent volume), respectively, according to the stomach analysis (n=13 stomachs), 93% vs. 7% (overall mean percent volume) according to the faecal analysis (n=3 time periods, encompassing 103 droppings belonging to a maximum of 46 nestlings in 15 nests), and 82% vs. 18% (percentage of records) according to direct observations (n=60 feeding visits), resulting in significant differences between techniques when percentage values are considered as absolute frequencies (overall: χ^2_2=20.40, $p<0.001$; for each couple of techniques: χ^2_1, $p<0.05$). Plant remains were found in all stomachs (n=13) and all faecal sacs (n=103), and arthropod remains in all stomachs and 86% of faecal sacs. No significant differences were observed between stomachs and faecal sacs in frequency of occurrence (occurrence vs. no occurrence) of insect remains (Fisher's exact test, p=0.18), but they were observed for spiders (Fisher's exact test, p=0.03). Both prey types were found in a higher percentage of stomachs than faecal sacs (insects: 92% of 13 stomachs, 72% of 103 faecal sacs; spiders: 92% and 61%, respectively). Gastroliths were found in just over half of the stomachs (7 of 13, 54%), but their occurrence in faecal sacs was negligible (1 of 103, <1%).

3.5. Comparison between young provisioning diet and self-feeding

Self-feeding during spring–summer (84% plants and 16% arthropods, relating to feeding records, as stated in the methods section) was significantly different to the young provisioning diet when compared with stomach analysis (68% and 32%, respectively, by volume) (χ^2_1=6.17, p=0.01), but not when compared with faecal analysis (93% and 7%, respectively, by volume) (χ^2_1=3.14, p=0.08) or, especially, direct observation (82% and 18%, respectively, relating to feeding records) (χ^2_1=0.04, p=0.85), considering percentage values as absolute frequencies. Nor were there significant differences in the latter comparison considering actual absolute frequencies, with very similar statistical results (self-feeding: 1046 plants and 201 arthropods; young provisioning according to direct observation: 49 plants and 11 arthropods; χ^2_1=0.08, p=0.78). Self-feeding during spring–summer and young provisioning diet, considering all of the different techniques used as a whole, coincided in 11 plant taxa at species/genus level with regard to seeds consumed.

4. Discussion

Of the three methods used to determine the diet of young Iberian bullfinches in a hedgerow habitat, faecal sac analysis provided the best results, weighing advantages (relatively non-invasive, large sample sizes) against drawbacks (lack of detail in taxonomic identification due to digestion). As expected, their diet was formed by a blend of seeds and invertebrates, and the importance of the animal fraction decreased during the breeding season and with age. Dietary changes were apparently associated with seasonal variations in the availability of different food types and with variations in the requirements (*e.g.*, protein intake) or handicaps (*e.g.*, difficulty digesting hard-bodied prey) of growing nestlings. For the first time, a qualitative and quantitative characterization of grit use by bullfinch nestlings is provided. Gastrolith occurrence and abundance was positively related to nestling age, probably owing to an increasing need to crush food. As expected, the importance of arthropod prey was higher in the diet of younger nestlings than in that of adults or independent juveniles during spring–summer.

4.1. Effects of the techniques used on findings about diet

The values obtained by faecal analysis in estimating the contribution of the animal fraction were lower (overall percent volume averaged only 7%) than those for stomach analysis and direct observation. Assuming that faecal sacs corresponded exclusively to older nestlings, these results could partly reflect an age-related variation in diet, as bullfinch nestlings are fed on fewer invertebrates towards the end of their growth period, even on seeds alone during the last days prior to leaving the nest, according to research from Britain (Newton 1967b, 1985). A distorting effect of the method used should not be ruled out, since soft-bodied insects and spiders are digested more easily and quickly than seeds (Rosenberg & Cooper 1990, Sutherland 2004), and therefore the presence of their remains could be more unlikely in faecal sacs than in stomachs. However, faecal analysis provides similar results to other techniques, such as neck collars or gut analysis, when used simultaneously on the same passerine nestlings, in regard to important groups of invertebrates (Kleintjes & Dahlsten 1992, Poulsen & Aebischer 1995, Moreby & Stoate 2000). Insects and spiders appeared in a higher proportion of stomachs than droppings, but differences were not significant for the former. Using direct observation, a high percentage of plant food items were identified at genus or species level, but animal foods could usually only be identified as arthropods, and to a lesser extent to insect order – they were not reliably observed to catch spiders – as could be expected from this technique (Rosenberg & Cooper 1990, Sutherland 2004, Yoshikawa & Osada 2015, see methods section).

In sum, faecal analysis enabled large sample sizes to be obtained relatively rapidly and effortlessly, and their analysis provided sufficiently reliable and accurate results for major food categories, in line with findings for nestlings of other passerine bird species. Faecal sacs could be collected directly from younger nestlings in the nest, but it is nevertheless advisable to collect those of older nestlings on the nest-rim after fledging, as they tend to jump out of the nest prematurely ("exploding") over the age of 10 days if disturbed (Cramp & Perrins 1994, Ferguson-Lees *et al.* 2011). Younger bullfinch nestlings digest insects more easily than seeds, many of the latter being passed whole into the droppings (Newton 1967b, 1985), which could not be verified in the present study since the faecal sacs analysed were from older nestlings and contained seeds that were not normally recognisable.

Stomach analysis was, as expected, the most reliable and accurate method at a more detailed level, but it is unpredictable in its application if it only relies, as ethics advises, on dead nestlings without researcher intervention, and direct observations were costly to obtain and imprecise in the determination of animal food. In contrast, over half of the plant species recorded by direct observation as nestling food were not found in stomachs, including soft food that bullfinches probably digest readily, such as Wild Cherry (*Prunus avium*) pulp, Common Agrimony (*Agrimonia eupatoria*) flower buds, and Meadowsweet (*Filipendula ulmaria*) seeds, some of which were unripe when consumed. Logically, stomach analysis was the only useful technique for studying gastroliths. Birds replace grit from time to time, often every few days in the case of small passerines, because it wears out progressively (McLelland 1979, Alonso 1985, Gionfriddo & Best 1995), so its appearance in droppings seems to be rare.

4.2. Seasonal and age-related variations in diet

Overall, bullfinches fed their young with a mixture of seeds and invertebrates, with greater quantitative importance of the former, as is usual in finches and expected in this species (Newton 1985, Cramp & Perrins 1994). Animal fraction decreased gradually and significantly, considering both frequency of occurrence and percent volume, from May to July for older nestlings (faecal analysis). This result is largely in agreement with what Newton (1967b) observed in British bullfinches, that is, a decline in the proportion of invertebrates in nestling diet at the end of the breeding season associated with lower availability. In the case of stomach contents (younger nestlings), there were apparently no noticeable monthly differences in this respect, but without a consistent statistical basis due to the small sample sizes. Perhaps bullfinches actually fed younger nestlings with invertebrates regardless of the month, despite the increasing effort to obtain them as the breeding season progressed, due to their higher protein requirements. It should not be ruled out that the most frequent invertebrates in the July diet, *i.e.*, spiders, probably reflecting their temporal availability, were still underestimated in faecal sacs as they were more easily digested. According to Pulido and Díaz (1994), spiders are amongst the most difficult soft-bodied arthropods to detect in the droppings of insectivorous passerines. On the contrary, in the May–June diet, insects as a whole were the most commonly found arthropods, in particular caterpillars and beetles. Similarly, in England, caterpillars predominated in the June diet of bullfinch nestlings among invertebrates, whereas spiders (as well as small slugs and snails) did so in the July diet (Newton 1967b by using neck collars, which allow identifying food not yet completely ingested by nestlings). In temperate and Mediterranean forest ecosystems, abundance and biomass of insects and spiders reach their peak in spring (May–June), followed in summer by a marked decrease in insects, but less so in spiders (Southwood *et al.* 2004, Cardoso *et al.* 2007). Both are an optimal diet for passerine birds, especially nestlings, on account of their high protein content and, in the case of spiders, high taurine content, both organic compounds playing a vital role in their early development (see reviews by Gunnarsson 2007, Nyffeler *et al.* 2018).

Regarding the apparent non-consumption of small non-arthropod invertebrates by young Iberian bullfinches, perhaps the techniques used overlooked them, since neck collars were not placed, or their absence was actually due to very sporadic use of this food resource. No remains of snail shells were found either in the examination of the building materials of 23 bullfinch nests that were already inactive (Hernández & Zaldívar 2021). Species richness and abundance of terrestrial gastropods in the study area is unknown, although they are indeed present. Most passerines need calcium-rich materials, in addition to their normal food, for eggshell formation and growth of nestling skeleton, making use mainly of snail shells and calcareous grit (Barrentine 1980, Graveland & van Gijzen 1994). Some specific prey, such as woodlice (Isopoda) and millipedes (Diplopoda), can also fulfill this function (Bureš & Weidinger 2003). Paradoxically, according to Newton (1967b), bullfinches remove the shells from snails, by handling them in the bill, before feeding the nestlings. Therefore, the role of gastropods and gastroliths as calcium sources for bullfinch nestlings needs to be investigated.

In the study area, herb seed availability increased from early spring to summer (Hernández & Zaldívar 2013), as did their general consumption by bullfinches (Hernández 2022), which could have led to a progressive increase in their use to feed nestling. According to stomach analysis, most of the seed types making up the diet of bullfinch nestlings in spring were not present in their summer diet, and vice versa, largely reflecting seasonal variation in the presence/fruiting of herb species in the study area (Hernández & Zaldívar 2013, Á. Hernández pers. obs.). Temporal variation in the diet of nestling passerines is common, and is generally associated with seasonal changes in the abundance and affordability of food at different taxonomic levels (Hernández 1993, Iglesias *et al.* 1993, Marques *et al.* 2003, Zeng & Lu 2009). Even so, the mean length of the seeds was consistently less than 3 mm. Granivorous passerines choose plant foods based principally on their bill size and shape (review by Díaz 1996). Some genera and species of seeds found in the diet of the young Iberian bullfinches match those found in that of subspecies of the western Palearctic further north (*e.g.*, *Taraxacum*, *Stellaria media*), but some others do not, presumably due primarily to geographic variations in floristic composition. For example, Spruce (*Picea*) and Blueberry (*Vaccinium*) seeds may be common in the diet of bullfinch nestlings from central Europe and western Russia (Cramp & Perrins 1994), but these plants are absent from the study area, the former due to its global distribution and the latter only inhabiting the valley at somewhat higher elevations.

With regard to age-related variation, as noted above, the relative importance of invertebrates was lower in faecal sacs (older nestlings) than stomachs (younger nestlings), but apparently there were no remarkable differences between stomachs belonging to nestlings <5 days and 5–8 days old in the percent volume of the plant and animal fractions. This pattern is in line with findings by Newton (1967b, 1985) for Britain, where the percent volume of animal matter in the food of nestling bullfinches did not clearly decrease until day 11 or 12. According to this author, protein requirements for nestling growth are better supplied by animal than vegetable matter, particularly during the first days, when young digest arthropods more effectively than seeds in overall terms. The relative contribution of invertebrates to the diet of nestlings of granivorous passerines, including several finches and sparrows, usually decreases markedly with age, and after about the tenth day they often receive seeds only (Newton 1967b, 1985, MacMillan 1981, Klvaňová *et al.* 2012). A relative uniformity in the general diet of the nestling bullfinches until day 8 was also the case for main types of invertebrates (frequency of occurrence of insects and spiders), and for seeds (quantity, range of variety, and identity). More specifically, however, hard-bodied prey such as beetles were found in the stomachs of nestlings aged 5–8 days but not in those aged <5 days. According to Orłowski *et al.* (2015), the youngest Barred Warbler (*Sylvia nisoria*) nestlings, which received the highest proportions in number and biomass of soft-bodied prey, may be physiologically limited as regards their ability to digest more heavily chitinised arthropods.

4.3. Seasonal and age-related variations in gastrolith presence

Considering both number of gastroliths and volume, the frequency of occurrence and amount of grit in stomachs were clearly associated with nestling age and not with season. Although parents may begin to provide the nestlings with grit practically after hatching in passerine birds, it has been found that the percentage of stomachs containing it increases with nestling age, and there is also a positive correlation between nestling age/weight and number of gastroliths in the stomach (Barrentine 1980 for Barn Swallows (*Hirundo rustica*), Alonso 1985 for Spanish Sparrows (*Passer hispaniolensis*), Orłowski *et al.* 2009 for Rooks (*Corvus frugilegus*)). Alonso (1985) noted a positive correlation between nestling age and the mean size of grit particles. There may be several reasons for greater importance of grit in older passerine nestlings, mainly retention of some grit in stomachs as age increases, and changes in diet (increasing number and mean size of food elements) (Alonso 1985, Orłowski *et al.* 2009). In the case of bullfinch nestlings, the progressive increase in the hardness of the arthropods ingested perhaps influenced the increasing role of grit for more efficient grinding action. It should also be considered that nestlings ingest most calcium-rich items at a time of maximum skeletal growth (Graveland & van Gijzen 1994, Bureš & Weidinger 2003). For birds in general, gizzards of granivores normally contain more and larger grit particles than those of insectivores, omnivores and frugivores, linked to food hardness and coarseness (Gionfriddo & Best 1996, Luttik & de Snoo 2004). In adult and nestling sparrows, the digestion of soft-bodied insects (*e.g.*, caterpillars, aphids) may require relatively little grit, whereas the breakdown of hard plant food and hard-bodied insects (*e.g.*, adult coleopterans) may require large amounts (Gionfriddo & Best 1995 and references therein, Marques *et al.* 2003).

Avian species that change their diet composition seasonally can also change the corresponding grit use (Gionfriddo & Best 1995, 1996 and references therein), which did not occur in bullfinch nestlings presumably because there were no significant monthly variations in the main food types received by nestlings up to 8 days old. Seeds ingested by these nestlings changed quite a bit taxonomically from May to July, but the difference in their mean length between both months was less than 1 mm. Also, at first glance the hardness of the food items in general did not seem to vary considerably from one month to another, but this quality was not assessed quantitatively.

The number and size of gastroliths generally correlate positively with the body size of bird species (Best & Gionfriddo 1991, Gionfriddo & Best 1996, Luttik & de Snoo 2004). Compared to other small songbirds, the mean number of gastroliths per stomach, without differentiating ages, was higher in bullfinch nestlings (≈12) than in wholly insectivorous Barn Swallow nestlings (≈5) (Barrentine 1980 for USA), but lower, differentiating between ages, than in largely insectivorous Spanish Sparrow nestlings (≈1 vs. 8 for nestlings *ca.* <5 days old, ≈26 vs. 90 for nestlings *ca.* 5–10 days old) (Alonso 1985 for Spain). In another study of Spanish Sparrows, the mean number of gastroliths in nestlings aged 5–10 days was only 2.2 (Marques *et al.* 2003 for Portugal), not referring to stomachs but to samples obtained using the ligature method, that is, restricted feeding events. In terms of size, mean gastrolith length is usually within 1.0–1.5 mm in small passerine nestlings, namely, Barn Swallow (Barrentine 1980), Spanish Sparrow (Alonso 1985), Eurasian Skylark (*Alauda arvensis*) (Ottens *et al.* 2014 for The Netherlands), and bullfinch (present study). This is probably an optimal size for them. Therefore, among small songbird species, the number of grit particles given to nestlings seems more flexible than the size of each one. The number of grit colours per nestling stomach was high (averaging approximately 4 out of 6 possible), with no seasonal variations to note, and increased with the number of gastroliths. There was no apparent predominance of any particular colour types in frequency of occurrence or quantity, and the selection of colours, with respect to those available in the field, was not evaluated. The shape of bird gastroliths usually ranges from spherical to, more commonly, slightly oblong, with sub-rounded corners (Best & Gionfriddo 1991, Gionfriddo & Best 1996, present study).

4.4. Nestling diet vs. self-feeding

Arthropods contributed significantly more to the diet of younger nestlings (stomach analysis) than to self-feeding (direct observation) during spring–summer, which is normal in other bullfinch subspecies and several European finch species (Newton 1967b, 1985, Cramp & Perrins 1994, Clement *et al.* 1993, Del Hoyo *et al.* 2010). Most temperate-zone passerines, including many typical seed-eaters, feed their young a protein-rich diet dominated by insects, at least for the first few days of life (Winkler 2004). The similarity found between self-feeding and diet of older nestlings or dependent juveniles was due to the decrease in importance of arthropod prey for the latter two in comparison with younger nestlings. Nevertheless, estimated diet composition of bullfinches in spring and summer by direct observation, both for nestlings and dependent juveniles and for adults, is not completely accurate as it was not always possible to determine whether or not they stored food for their young in the buccal pouches whilst eating – the bulging throat was only visible under optimal watching conditions – and neither was it possible to verify whether all of the food collected while they filled their pouches was destined for young individuals. According to Newton (1967b, 1985), British bullfinches normally only capture invertebrate prey to provide their young with a diet rich in proteins, which promotes growth, but in the study area their consumption was not necessarily associated with nestlings/fledglings, as adults regularly ate arthropods in autumn, after the breeding season, and independent juveniles in summer–autumn (Hernández 2022).

Nestlings, independent juveniles, and adults all fed on small insects and spiders, and coincided in the consumption of many seed species. According to Newton (1976b), adult bullfinches consume the same seed types that they feed their nestlings on. Although tree buds were an important component of the spring diet of adult bulfinches in March–April, when seed abundance was lower, they consumed very few from May onwards (Hernández 2022) and they were not found in the nestling diet. Bullfinches clearly preferred certain plant species, and avoided others, as a food resource in each season, and favourite herb seeds were generally contained in small achenes and capsules, probably easy to handle and dehusk (Hernández 2022, present study).

It is interesting to note that parent bullfinches often eat the faecal sacs removed from the nest, particularly during the first days of the nestling stage, seemingly implying the reuse of food that had not been digested by younger nestlings, mainly seeds – then they usually attach the sacs to branches and twigs and later ignore them – (Newton 1967b, 1985, Hernández 2020). In this way, the dividing line between the diet of nestlings and adults becomes even more diffuse. Removing faeces from the nest is common behaviour in passerines for nest-cleaning purposes or to hide the nest from predators, the parents also benefitting from ingesting the sacs (*e.g.*, energetically or nutritionally), which they can do even without leaving the nest (Hurd *et al.* 1991, McGowan 1995, Düttmann *et al.* 1998, Winkler 2004, Quan *et al.* 2015). The specific reasons for parental consumption of nestling faeces in bullfinches remain to be determined.

4.5. Brief comment on conservation

The high floristic diversity of the dense hedgerow network in the study area provides a wide range of resources for bullfinches, including plenty of suitable nest sites (Hernández & Zaldívar 2021) and food for their young. Its conservation and that of the rest of the valley with similar landscape characteristics, where bullfinches also live, is therefore highly advisable. For many typical passerine bird species in forested areas, hedgerows play an important role as foraging habitats or steppingstones for movement between woods, even providing the necessary resources both during and outside the breeding season (Gregory & Baillie 1998, Newton 1998, Robinson & Sutherland 1999, Hinsley & Bellamy 2000, Tellería *et al.* 2008, Wilson *et al.* 2009).

Nuorten Iberian punatulkkujen ruokavaliosta

Tässä tutkimuksessa dokumentoin ensimmäistä kertaa Iberian punatulkun (*Pyrrhula pyrrhula iberiae*) ruokavaliota pensaikkoympäristössä

luoteis-Espanjassa. Tutkittava aineisto koostui pienten (alle kahdeksan päivän ikäisten) poikasten vatsasisällöistä, ulostepussinsisällöistä (vanhemmat poikaset), sekä lisäksi suorista havainnoista (vanhemmat poikaset ja nuoret yksilöt). Dokumentoin myös ensimmäistä kertaa yksityiskohtaisemmin punatulkkupoikasten soran (tai mahalaukun kivien) käyttöä osana ruokavaliota. Punatulkut ruokkivat poikasiaan erilaisilla siemenillä ja selkärangattomilla, siementen ollessa merkittävämmässä roolissa poikasten ruokavaliossa. Erilaisten siementen käyttö vaihteli huomattavasti kevään ja kesän välillä, samoin kuin selkärangattomien osuus pieneni toukokuusta heinäkuuhun. Havaitut muutokset johtuvat todennäköisesti ravinnon saatavuudesta. Hämähäkit ja perhostoukat olivat tärkeimpiä niveljalkaisravintoa. Poikasille ei ilmeisesti syötetty niveljalkaisten lisäksi muita selkärangattomia. Runsasproteiiniset selkärangattomat olivat lisäksi suhteellisesti tärkeämpää ravintoa nuoremmille verrattuna vanhempiin poikaisiin. Kovakuoriaisia, jotka ovat vaikeasti sulatettavia, ei löytynyt pienimpien poikasten vatsoista lainkaan. Soraa havaittiin vatsojen sisällössä sitä enemmän, mitä vanhempia poikaset olivat. Mahalaukun kivien määrässä, koossa tai värissä ei havaittu eroja eri ajankohtina. Tutkimusalueen kasvillisuuden vaihtelevuus ja monimuotoisuus tarjoaa punatulkuille laajan valikoiman ravintoa poikasille, mikä myös nostaa alueen suojeluarvoa.

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References

Alamy 1999–2021: Online supplier of image material: https://www.alamy.com. — Alamy Ltd., Abingdon-on-Thames.

Alonso, J.C. 1985: Grit in the gizzard of Spanish Sparrows (*Passer hispaniolensis*). — Vogelwarte 33: 135–143.

Arkive 2013–2019: Images of life on earth: https://www.wildscreen.org/arkive-closure. — Wildscreen, Bristol. Current status: stored offline.

Barrentine, C.D. 1980: The ingestion of grit by nestling Barn Swallows. — Journal of Field Ornithology 51: 368–371. https://sora.unm.edu/node/50850

Bas, J.M., Pons, P. & Gómez, C. 2007: Daily activity of Sardinian Warbler *Sylvia melanocephala* in the breeding season. — Ardeola 54: 335–338. https://www.ardeola.org/uploads/articles/docs/1330.pdf

Bernis, F. 1957: The status of *Pyrrhula pyrrhula* in Spain. — Ardeola 3: 243–251. (In Spanish with English summary) https://www.ardeola.org/uploads/articles/docs/646.pdf

Best, L.B. & Gionfriddo, J.P. 1991: Characterization of grit use by cornfield birds. — Wilson Bulletin 103: 68–82. https://sora.unm.edu/sites/default/files/journals/wilson/v103n01/p0068-p0082.pdf

Bureš, S. & Weidinger, K. 2003: Sources and timing of calcium intake during reproduction in flycatchers. — Oecologia 137: 634−641. https://doi.org/10.1007/s00442-003-1380-7

Cardoso, P., Silva, I., De Oliveira, N.G. & Serrano, A.R.M. 2007: Seasonality of spiders (Araneae) in Mediterranean ecosystems and its implications in the optimum sampling period. — Ecological Entomology 32: 516–526. https://doi.org/10.1111/j.1365-2311.2007.00894.x

Castroviejo, S. 1986–2017: Flora iberica. — Real Jardín Botánico, CSIC, Madrid. (In Spanish)

Ceia, R.S., Machado, R.A. & Ramos, J.A. 2016: Nestling food of three hole-nesting passerine species and experimental increase in their densities in Mediterranean oak woodlands. — European Journal of Forest Research 135: 839–847. https://doi.org/10.1007/s10342-016-0977-4

Clement, P. 2010: Eurasian Bullfinch *Pyrrhula pyrrhula*. — In Handbook of the birds of the world, vol. 15: weavers to New World warblers (ed. Del Hoyo, J., Elliott, A. & Christie, D.A.): 609–610. Lynx Edicions, Barcelona.

Clement, P., Harris, A. & Davis, J. 1993: Finches and sparrows. — Helm, London.

Cramp, S. & Perrins, C.M. 1994: The birds of the western Palearctic, vol. 8: crows to finches. — Oxford University Press, Oxford.

Dawkins, M.S. 2007: Observing animal behaviour. Design and analysis of quantitative data. — Oxford University Press, Oxford.

Del Hoyo, J., Elliott, A. & Christie, D.A. 2010: Handbook of the birds of the world, vol. 15: weavers to New World warblers. — Lynx Edicions, Barcelona.

Díaz, M. 1996: Food choice by seed-eating birds in relation to seed chemistry. — Comparative Biochemistry and Physiology A: Molecular and Integrative Physiology 113: 239–246. https://doi.org/10.1016/0300-9629(95)02093-4

Díaz, L. 2016: Camachuelo común *Pyrrhula pyrrhula*. — In Enciclopedia virtual de los vertebrados españoles (ed.

Salvador, A. & Morales, M.B.): http://www.vertebradosibericos.org/aves/pyrpyr.html. Museo Nacional de Ciencias Naturales, Madrid. (In Spanish)

Düttmann, H., Bergmann, H.H. & Engländer, W. 1998: Development of behavior. — In Avian growth and development (ed. Starck, J.M. & Ricklefs, R.E.): 223–246. Oxford University Press, New York.

Ferguson-Lees, J., Castell, R. & Leech, D. 2011: A field guide to monitoring nests. — British Trust for Ornithology, Thetford.

Fowler, J., Cohen, L. & Jarvis, P. 1998: Practical statistics for field biology. Second edition. — Wiley, Chichester.

Gil-Delgado, J.A., Guijarro, D. & Vives-Ferrándiz, C. 2009: The nestling diet of greenfinch *Carduelis chloris* in orange groves of Eastern Spain. — Ardeola 56: 205–214. https://www.ardeola.org/uploads/articles/docs/1436.pdf

Gionfriddo, J.P. & Best, L.B. 1995: Grit use by House Sparrows: effects of diet and grit size. — Condor 97: 57–67. https://www.jstor.org/stable/4163749

Gionfriddo, J.P. & Best, L.B. 1996: Grit-use patterns in North American birds: the influence of diet, body size, and gender. — Wilson Bulletin 108: 685–696. https://www.jstor.org/stable/4163749

Gionfriddo, J.P. & Best, L.B. 1999: Grit use by birds: a review. — In Current ornithology, vol. 15 (ed. Nolan, V. Jr., Ketterson, E.D. & Thompson, C.F.): 89–148. Kluwer Academic-Plenum Plubishers, New York.

Graveland, J. & van Gijzen, T. 1994: Arthropods and seeds are not sufficient as calcium sources for shell formation and skeletal growth in passerines. — Ardea 82: 299−314. https://doi.org/10.5253/arde.v82.p299

Green, R.E. 2004: Breeding biology. — In Bird ecology and conservation. A handbook of techniques (ed. Sutherland, W.J., Newton, I. & Green, R.E.): 57–83. Oxford University Press, Oxford.

Gregory, R.D. & Baillie, S.R. 1998: Large-scale habitat use of some declining British birds. — Journal of Applied Ecology 35: 785–799. https://doi.org/10.1046/j.1365-2664.1998.355349.x

Gunnarsson, B. 2007: Bird predation on spiders: ecological mechanisms and evolutionary consequences. — Journal of Arachnology 35: 509–529. https://doi.org/10.1636/RT07-64.1

Hernández, Á. 1993: Nestling diet of three sympatric shrike species (*Lanius* spp.): age-related, seasonal, and interspecific variations. — Doñana Acta Vertebrata 20: 145–163. (In Spanish with English summary) http://hdl.handle.net/10261/128272

Hernández, Á. 2008: Cherry removal by seed-dispersing mammals: mutualism through commensal association with frugivorous birds. — Polish Journal of Ecology 56: 127–138. https://www.miiz.waw.pl/pliki/article/ar56_1_11.pdf

Hernández, Á. 2009: Summer–autumn feeding ecology of pied flycatchers *Ficedula hypoleuca* and spotted flycatchers *Muscicapa striata*: the importance of frugivory in a stopover area in north-west Iberia. — Bird Conservation International 19: 224–238. https://doi.org/10.1017/S0959270909008351

Hernández, Á. 2018: Diet of Eurasian sparrowhawks *Accipiter nisus* in a Northwest Iberian hedgerow habitat throughout the year. — Ornithological Science 17: 95–101. https://doi.org/10.2326/osj.17.95

Hernández, Á. 2020: Breeding ecology of Eurasian bullfinches *Pyrrhula pyrrhula* in an Iberian hedgerow habitat. — Journal of Natural History 54: 2613–2645. https://doi.org/10.1080/00222933.2020.1860263

Hernández, Á. 2021: Habitat use and space preferences of Eurasian Bullfinches (*Pyrrhula pyrrhula*) in northwestern Iberia throughout the year. — Avian Research 12: 8. https://doi.org/10.1186/s40657-021-00241-0

Hernández, A. 2022: Seasonal feeding habits of the Iberian bullfinch *Pyrrhula pyrrhula iberiae* in northwestern Spain. — Ornithology Research 30: 155–173. https://doi.org/10.1007/s43388-022-00100-6

Hernández, Á. & Zaldívar, P. 2013: Epizoochory in a hedgerow habitat: seasonal variation and selective diaspore adhesion. — Ecological Research 28: 283–295. https://doi.org/10.1007/s11284-012-1014-9

Hernández, Á. & Zaldívar, P. 2021: Nest-site selection and nest design of Iberian bullfinches *Pyrrhula pyrrhula iberiae* in northwestern Spain. — Avian Biology Research 14: 124–142. https://doi.org/10.1177/17581559211037501

Hinsley, S.A. & Bellamy, P.E. 2000: The influence of hedge structure, management and landscape context on the value of hedgerows to birds: a review. — Journal of Environmental Management 60: 33–49. https://doi.org/10.1006/jema.2000.0360

Hódar, J.A. 1994: La alimentación de *Sylvia undata* y *Sylvia conspicillata* en una zona semiárida del sureste de la península Ibérica. — Ardeola 41: 55–58. (In Spanish) https://www.ardeola.org/uploads/articles/docs/270.pdf

Hurd, P.L., Weatherhead, P.J. & McRae, S.B. 1991: Parental consumption of nestling feces: good food or sound economics? — Behavioral Ecology 2: 69–76. https://doi.org/10.1093/beheco/2.1.69

Iglesias, D.J., Gil-Delgado, J.A. & Barba, E. 1993: Diet of Blackbird nestlings in orange groves: seasonal and age-related variation. — Ardeola 40: 113–119. https://www.ardeola.org/uploads/articles/docs/255.pdf

Kleintjes, P.K. & Dahlsten, D.L. 1992: A comparison of three techniques for analyzing the arthropod diet of Plain Titmouse and Chestnut-backed Chickadee nestlings. — Journal of Field Ornithology 63: 276–285. https://sora.unm.edu/sites/default/files/journals/jfo/v063n03/p0276-p0285.pdf

Klvaňová, A., Lusková, M., Hořák, D. & Exnerová, A. 2012: The condition of nestling House Sparrows *Passer domesticus* in relation to diet composition and the total amount of food consumed. — Bird Study 59: 58–66. https://doi.org/10.1080/00063657.2011.643291

Lowry, R. 1998–2022: VassarStats, website for statistical computation: http://vassarstats.net. — Vassar College, Poughkeepsie.

Luttik, R. & de Snoo, G.R. 2004: Characterization of grit in arable birds to improve pesticide risk assessment. — Ecotoxicology and Environmental Safety 57: 319–329. https://doi.org/10.1016/S0147-6513(03)00034-4

MacMillan, B.W.H. 1981: Food of house sparrows and greenfinches in a mixed farming district, Hawke's Bay, New Zealand. — New Zealand Journal of Zoology 8: 93–104. https://doi.org/10.1080/03014223.1981.10427946

Marques, P.M., Boieiro, M., Canário, F. & Vicente, L. 2003: Variation of nestling diet across the breeding season in Spanish Sparrow *Passer hispaniolensis* in southern Portugal. — Ardeola 50: 71–75. https://www.ardeola.org/uploads/articles/docs/523.pdf

McGowan, K.J. 1995: A test of whether economy or nutrition determines fecal sac ingestion in nesting corvids. — Condor 97: 50–56. https://doi.org/10.2307/1368982

McLelland, J. 1979: Digestive system. — In Form and function in birds, vol. 1 (ed. King, A.S. & McLelland, J.): 69–181. Academic Press, London.

Michalski, M., Nadolski, J., Marciniak, B., Loga, B. & Bańbura, J. 2011: Faecal analysis as a method of nestling diet determination in insectivorous birds: a case study in Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major*. — Acta Ornithologica 46: 164–172. https://doi.org/10.3161/000164511X625937

Møller, A.P. & Erritzøe, J. 2010: Why birds eat colourful grit: colour preferences revealed by the colour of gizzard stones. — Journal of Evolutionary Biology 23: 509–517. https://doi.org/10.1111/j.1420-9101.2009.01918.x

Moreby, S.K. & Stoate, C. 2000: A quantitative comparison of neck-collar and faecal analysis to determine passerine nestling diet. — Bird Study 47: 320–331. https://doi.org/10.1080/00063650009461192

Newton, I. 1967a: The adaptive radiation and feeding ecology of some British finches. — Ibis 109: 33–98. https://doi.org/10.1111/j.1474-919x.1967.tb00005.x

Newton, I. 1967b: The feeding ecology of the Bullfinch (*Pyrrhula pyrrhula* L.) in Southern England. — Journal of Animal Ecology 36: 721–744. https://doi.org/10.2307/2822

Newton, I. 1985: Finches. Limpback edition. — Collins, London.

Newton, I. 1998: Population limitation in birds. — Academic Press, San Diego.

Newton, I. 2000: Movements of Bullfinches *Pyrrhula pyrrhula* within the breeding season. — Bird Study 47: 372–376. https://doi.org/10.1080/00063650009461196

Noval, A. 2000: Guía de las aves de Asturias. — Alfredo Noval, Gijón. (In Spanish)

Nyffeler, M., Şekercioğlu, Ç.H. & Whelan, C.J. 2018: Insectivorous birds consume an estimated 400–500 million tons of prey annually. — Science of Nature 105: 47. https://doi.org/10.1007/s00114-018-1571-z

Orłowski, G., Kasprzykowski, Z., Zawada, Z. & Kopij, G. 2009: Stomach content and grit ingestion by Rook *Corvus frugilegus* nestlings. — Ornis Fennica 86: 117–122. https://lintulehti.birdlife.fi:8443/pdf/artikkelit/160/tiedosto/of_86_117-122_artikkelit_160.pdf

Orłowski, G., Wuczyński, A. & Karg, J. 2015: Effect of brood age on nestling diet and prey composition in a hedgerow specialist bird, the barred warbler *Sylvia nisoria*. — PLoS ONE 10(6): e0131100. https://doi.org/10.1371/journal.pone.0131100

Ottens, H.J., Kuiper, M.W., Flinks, H., van Ruijven, J., Siepel, H., Koks, B.J., Berendse, F. & de Snoo, G.R. 2014: Do field margins enrich the diet of the Eurasian Skylark *Alauda arvensis* on intensive farmland? — Ardea 102: 161–174. https://doi.org/10.5253/arde.v102i2.a6

Pagani-Núñez, E., Ruiz, Í., Quesada, J., Negro, J.J. & Senar, J.C. 2011: The diet of Great Tit *Parus major* nestlings in a Mediterranean Iberian forest: the important role of spiders. — Animal Biodiversity and Conservation 34.2: 355–361. https://doi.org/10.32800/abc.2011.34.0355

Poulsen, J.G. & Aebischer, N.J. 1995: Quantitative comparison of two methods of assessing diet of nestling Skylarks (*Alauda arvensis*). — Auk 112: 1070–1073. https://sora.unm.edu/sites/default/files/journals/auk/v112n04/p1070-p1073.pdf

Pulido, F.J.P. & Díaz, M. 1994: Diet and prey type selection by adult and young Blue Tits *Parus caeruleus*: the effect of correcting for prey digestibility. — Ardeola 41: 151–159. https://www.ardeola.org/uploads/articles/docs/280.pdf

Pulliam, H.R. 1985: Foraging efficiency, resource partitioning, and the coexistence of sparrow species. — Ecology 66: 1829–1836. https://doi.org/10.2307/2937378

Quan, R.C., Li, H., Wang, B. & Goodale, E. 2015: The relationship between defecation and feeding in nestling birds: observational and experimental evidence. — Frontiers in Zoology 12: 21. https://doi.org/10.1186/s12983-015-0116-y

Ralph, C.P., Nagata, S.E. & Ralph, C.J. 1985: Analysis of droppings to describe diets of small birds. — Journal of Field Ornithology 56: 165–174. https://sora.unm.edu/sites/default/files/journals/jfo/v056n02/p0165-p0174.pdf

Rivas-Martínez, S. 2007: Mapa de series, geoseries y geopermaseries de vegetación de España. — Itinera Geobotanica 17: 1–436. (In Spanish)

Robinson, R.A. 2005: BirdFacts: profiles of birds occurring in Britain and Ireland. Bullfinch *Pyrrhula pyrrhula*: https://app.bto.org/birdfacts/results/bob17100.htm. — British Trust for Ornithology, Thetford.

Robinson, R.A. & Sutherland, W.J. 1999: The winter distribution of seed-eating birds: habitat structure, seed density and seasonal depletion. — Ecography 22: 447–54. https://doi.org/10.1111/j.1600-0587.1999.tb00581.x

Rosenberg, K.V. & Cooper, R.J. 1990: Approaches to avian diet analysis. — Studies in Avian Biology 13: 80–90. https://sora.unm.edu/node/139273

Serrano-Davies, E. & Sanz, J.J. 2017: Habitat structure modulates nestling diet composition and fitness of Blue Tits *Cyanistes caeruleus* in the Mediterranean region. — Bird Study 64: 295–305. https://doi.org/10.1080/00063657.2017.1357678

Southwood, T.R.E., Wint, G.R.W., Kennedy, C.E.J. & Greenwood, S.R. 2004: Seasonality, abundance, species richness and specificity of the phytophagous guild of insects on oak (*Quercus*) canopies. — European Journal of Entomology 101: 43–50. https://doi.org/10.14411/eje.2004.011

Stoate, C., Moreby, S.J. & Szczur, J. 1998: Breeding ecology of farmland Yellowhammers *Emberiza citrinella*. — Bird Study 45: 109–121. https://doi.org/10.1080/00063659809461084

Sutherland, W.J. 2004: Diet and foraging behavior. — In Bird ecology and conservation. A handbook of techniques (ed. Sutherland, W.J., Newton, I. & Green, R.E.): 233–250. Oxford University Press, Oxford.

Tellería, J.L., Ramírez, A., Galarza, A., Carbonell, R., Pérez-Tris, J. & Santos, T. 2008: Geographical, landscape and habitat effects on birds in northern Spanish farmlands: implications for conservation. — Ardeola 55: 203–219. https://www.ardeola.org/uploads/articles/docs/1407.pdf

Torroba, P., Zaldívar, P. & Hernández, A. 2013: Semillas de frutos carnosos del norte ibérico. Guía de identificación. — Ediciones Universidad de Valladolid, Valladolid. (In Spanish)

Valera, F., Wagner, R.H., Romero-Pujante, M., Gutiérrez, J.E. & Rey, P.J. 2005: Dietary specialization on high protein seeds by adult and nestling serins. — Condor 107: 29–40. https://doi.org/10.1093/condor/107.1.29

Wikimedia Commons 2004–2021: Media files: https://commons.wikimedia.org. — Wikimedia Foundation, Inc., San Francisco.

Willson, M.F. 1971: Seed selection in some North American finches. — Condor 73: 415–429. https://doi.org/10.2307/1366663

Wilson, J.D., Evans, A.D. & Grice, P.V. 2009: Bird conservation and agriculture. — Cambridge University Press, Cambridge.

Winkler, D.W. 2004: Nests, eggs, and young: breeding biology of birds. — In Handbook of bird biology (ed. Podulka, S., Rohrbaugh, R.W. Jr. & Bonney, R.): 8.1-8.152. Cornell Lab of Ornithology-Princeton University Press, Ithaca.

Yoshikawa, T. & Osada, Y. 2015: Dietary compositions and their seasonal shifts in Japanese resident birds, estimated from the analysis of volunteer monitoring data. — PLoS ONE 10(2): e0119324. https://doi.org/10.1371/journal.pone.0119324

Zeng, X. & Lu, X. 2009: Breeding ecology of a burrow-nesting passerine, the white-rumped snowfinch *Montifringilla taczanowskii*. — Ardeola 56: 173–187. https://www.ardeola.org/uploads/articles/docs/1434.pdf

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Figures and drawings can be inserted in the end of the document at initial submission, each on a separate page. Every figure must be identified with the name of the first author and the number of the figure. Plan your figures and drawings to suit the journal's standard widths 69, 107 or 142 mm. Relate the font size, the thickness of lines, and the size of other parts of a figure, to the size of the figure itself in order to make sure that figure is intelligible. Explain all graphic symbols within the figure in the caption. Identify parts of a composite figure with letters, not numbers. Do not use fine rasters for filling of columns or areas. Only solid (white and/or black) or line-type fillings should be used. Avoid fancy design (e.g., 3-D). Figures produced using a computer program should be provided in PDF (or other high-quality) format with all fonts included. Arial as the font is preferred in all figures. Scanned figures should be bitmap files in the file formats TIFF or JPG, resolution at least 1,000 dpi.

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