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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 fixed

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.

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 21–22th 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).

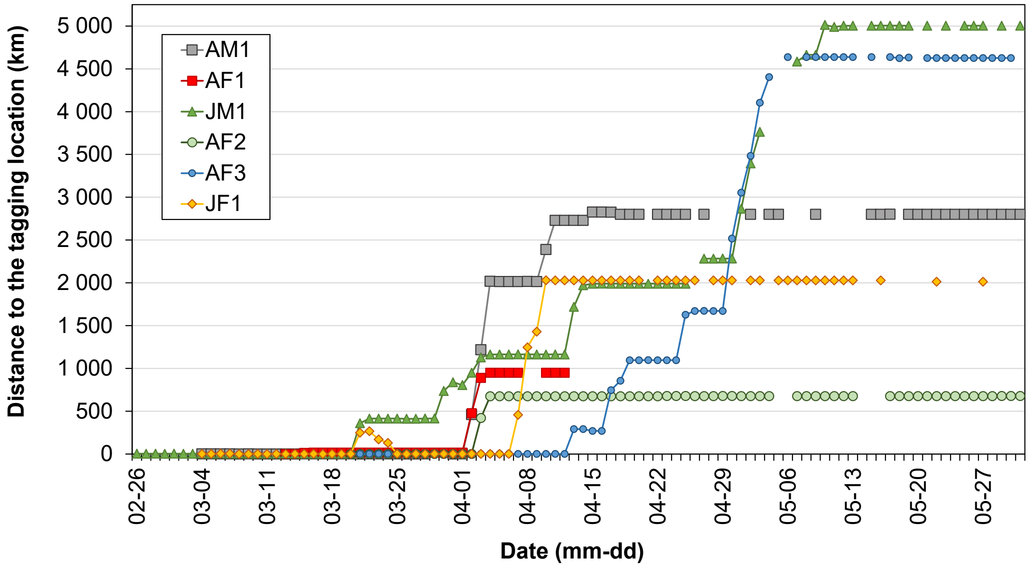

Fig. 1. Pre-nuptial migration dynamics of the tagged Woodcocks.

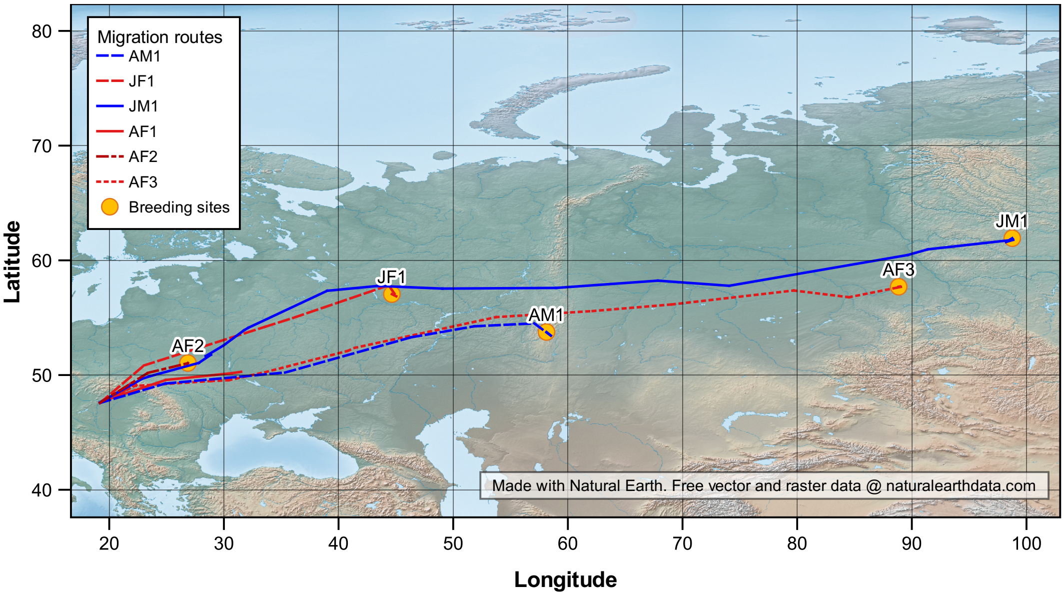

Fig. 2. Pre-nuptial migration routes and breeding areas of Woodcocks deployed with GPS transmitters in Hungary.

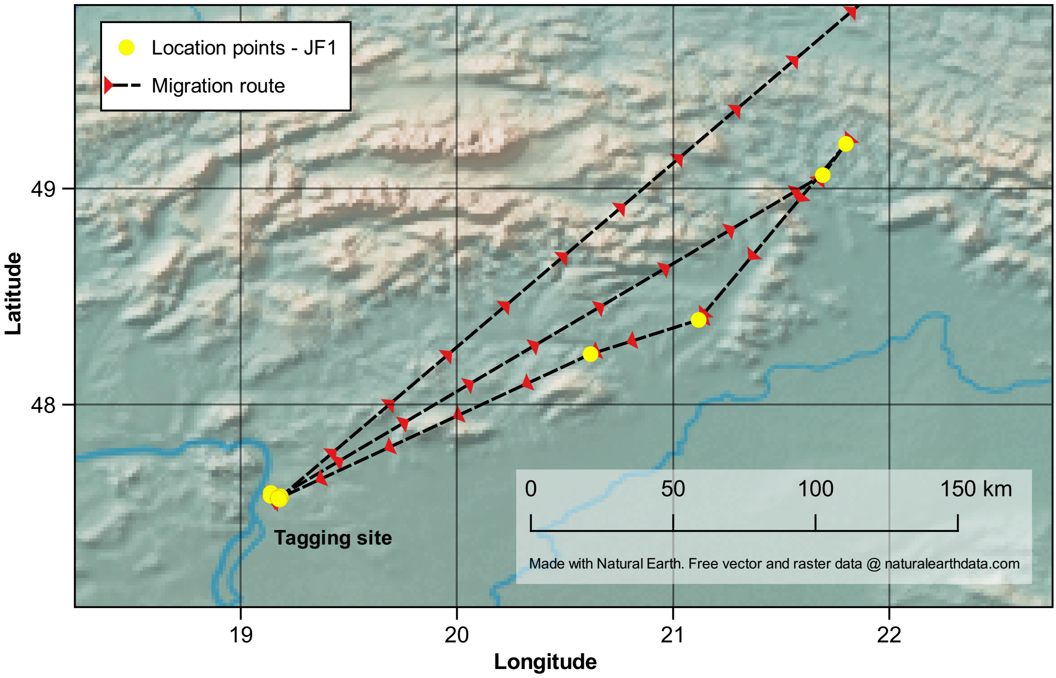

Fig. 3. Interrupted and return migration of the Woodcock JF1 to the tagging site.

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.

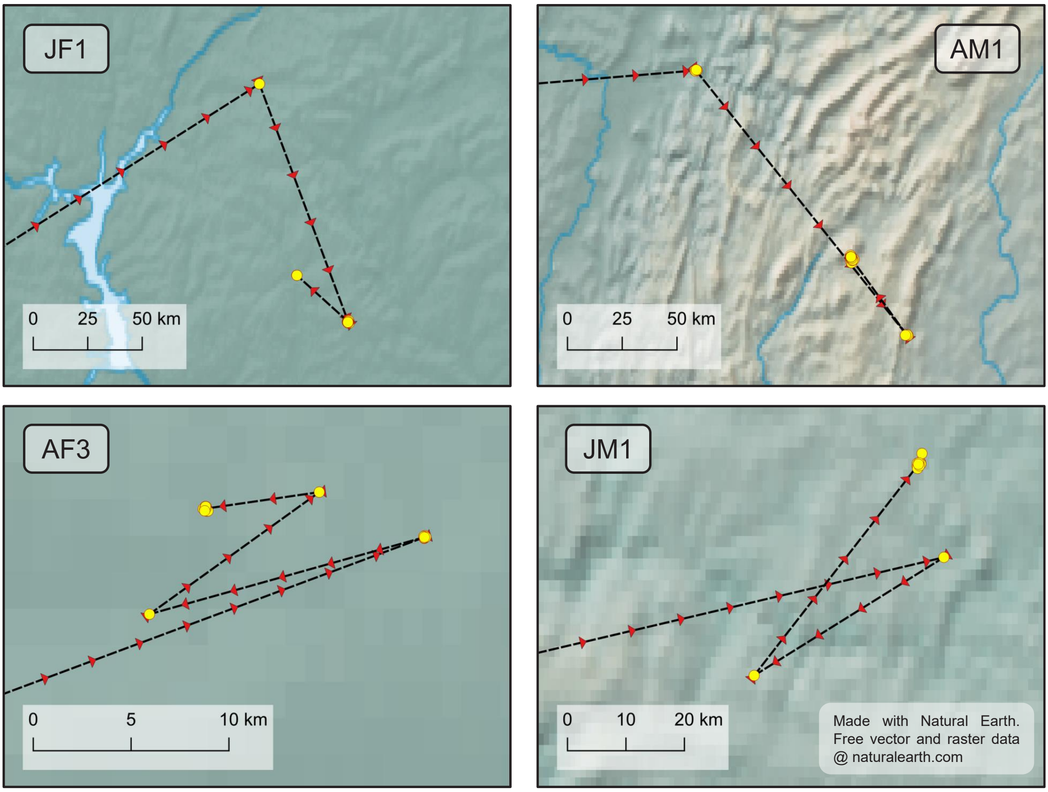

Fig. 4. Examples of the patterns of arrival at the breeding sites by the tracked Woodcocks.

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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