J Ornithol (2015) 156:515–523
DOI 10.1007/s10336-014-1152-7

ORIGINAL ARTICLE

Solar/Argos PTTs contradict ring-recovery analyses: Woodcocks wintering in Spain are found to breed further east than previously stated

Juan Arizaga · Ariñe Crespo · Ibon Telletxea · Rubén Ibáñez · Felipe Díez · Joseba F. Tobar · Miguel Minondo · Zarbo Ibarrola · Juan J. Fuente · José A. Pérez

Received: 29 July 2014 / Revised: 16 September 2014 / Accepted: 3 December 2014 / Published online: 16 December 2014

Abstract The development of increasingly small devices for the satellite tracking of small birds allows us to explore aspects of avian migration that have never been studied before. Here, we provide the results of using 12- and 9.5-g platform transmitter terminals (PTTs) to track game birds of 300–385 g. Attaching PTTs to 20 Woodcocks (*Scolopax rusticola*), wintering in Spain from 2006 to 2012, allowed us to explore (1) migration strategies (timing, velocity and stopovers), (2) the identity of the breeding grounds; (3) inter-year site fidelity to wintering grounds. We provide details of the route, speed and timing of migration and the location of remote breeding sites that were unknown prior to this study. The departure from winter quarters (median date) was completed by 20 March. The spring migration period lasted 40 days, and our birds were found to travel from >5,000 to >10,000 km, with a mean total migratory speed (i.e., including stopovers) of 170 km/day. Woodcocks followed fairly direct routes of migration. Stopover duration tended to be shortened when birds were closer to their breeding areas, which were located further east than previously stated. The only bird that provided long-term data (>1 year) was observed to return to the same wintering area, suggesting high winter site fidelity. The use of small PTTs opens new research lines related to the study and management of small to medium-sized migratory birds.

Keywords Biological conservation · Hunting · Migratory game birds · Satellite tracking

Zusammenfassung

Solar/Argos PTT-Sender widersprechen Ringfundanalysen: In Spanien überwinternde Waldschnepfen brüten weiter östlich als bislang angenommen

Die Entwicklung zunehmend kleinerer Geräte zur Satellitenverfolgung kleiner Vögel gestattet es uns, zuvor noch nie untersuchte Aspekte des Vogelzuges zu erforschen. Hier stellen wir die Ergebnisse vor, die wir mit 12 g- und 9.5-g-PTT-Sendern (Platform Transmitter Terminals) an 300–385 g schwerem Federwild erzielten. Die Ausstattung von 20 in Spanien überwinternden Waldschnepfen *Scolopax rusticola* mit PTT-Sendern ermöglichte uns zwischen 2006 und 2012 (1) die Erforschung von Zugstrategien (zeitlicher Ablauf, Zuggeschwindigkeit und Rastaufenthalte); (2) die Ermittlung der Brutgebiete; (3) die Bestimmung der Winterquartiertreue von Jahr zu Jahr. Wir liefern Einzelheiten bezüglich Route, Geschwindigkeit und Zeitverlauf des Zuggeschehens sowie der Lage entfernterer Brutgebiete, die vor dieser Studie nicht bekannt waren. Der Abzug aus den Winterquartieren (Datumsmittelwert) war am 20. März abgeschlossen. Der Frühjahrszug dauerte 40 Tage, und unsere Vögel legten dabei zwischen über 5,000 bis über 10,000 km zurück, bei einer mittleren Zuggeschwindigkeit (d. h. einschließlich Zwischenstopps) von 170 km pro Tag. Die Waldschnepfen nutzten relativ direkte Zugrouten. Tendenziell verkürzte sich die Rastdauer, wenn die Vögel näher an ihre Brutgebiete kamen,

Communicated by N. Chernetsov.

J. Arizaga (✉) · A. Crespo
Department of Ornithology, Aranzadi Sciences Society, Zorroagagaina 11, 20014 Donostia-S. Sebastián, Spain
e-mail: jarizaga@aranzadi.eus

I. Telletxea · R. Ibáñez · F. Díez · J. F. Tobar · M. Minondo · Z. Ibarrola · J. J. Fuente · J. A. Pérez
Club de Cazadores de Becada, Avda. Schulz 8, 4 dcha, 33208 Gijón, Asturias, Spain

welche weiter östlich lagen als bislang angenommen. Der einzige Vogel, welcher längerfristige (>1 Jahr) Daten lieferte, kehrte ins selbe Winterquartier zurück, was eine hohe Treue zum Überwinterungsgebiet nahelegt. Der Einsatz kleiner PTT-Sender eröffnet neue Forschungsansätze für die Untersuchung und das Management kleiner bis mittelgroßer Zugvögel.

Introduction

Birds generally divide their migration into phases of flight and stopover, the latter being used to rest and gain the energy needed for the subsequent flight (Alerstam and Lindström 1990). Knowing how birds organize their migration, particularly in terms of the number, duration and location of stopovers, is of great value in disentangling migratory strategies and identifying key conservation areas (Newton 2008; Chernetsov 2012). Several aspects of the migration of small to medium-sized birds are still poorly understood (e.g., stopover duration, number of stopovers, route and speed of migration). This is mostly due to the lack, until recent times, of accurate methodological facilities.

The development of new technologies has been invaluable with regard to the study of avian migration (Martell et al. 2001; Hake et al. 2003; Alerstam et al. 2006; Stutchbury et al. 2009). Although ring–recovery data have been (and still are) useful for disentangling bird migrations (Bairlein 2001; Wernham et al. 2002), they fail to track individual birds along the whole migration route, throughout the entire annual cycle, and in areas where there is no possibility of ring recoveries (Zwarts et al. 2009). Consequently, our knowledge of migration routes, relevant stopover sites, and the location of remote goal areas (winter/breeding quarters) remains relatively poor for many migrant species, especially small birds (Stutchbury et al. 2009; Bächler et al. 2010; Schmaljohann et al. 2012; Tøttrup et al. 2012; Kristensen et al. 2013).

The Eurasian Woodcock (*Scolopax rusticola*) is a widespread gamebird occurring over much of the Palaearctic (Cramp and Simmons 1983). It breeds mainly in boreal and temperate forested habitats, from Portugal to the east of Asia, and also in some sub-tropical Atlantic archipelagos in Macaronesia (Onrubia 2003; Machado et al. 2008). Northern Woodcocks are migratory and those breeding in the south are resident (Cramp and Simmons 1983; Hoodless 1995). Southern European countries host important wintering Woodcock populations. Understanding connectivity patterns between breeding and non-breeding areas is fundamental from both an ecological and a conservation viewpoint. The number of Woodcocks from each breeding population currently shot in Europe during the winter period remains uncertain. This is due to the fact that it is still not clear whether current data, which are obtained from ring–recovery analyses, properlyassess the origin region of wintering Woodcocks (Guzmán et al. 2011; Hobson et al. 2013).

Woodcocks are nocturnal birds whose migratory habits are still relatively unknown. Available data (mostly ring–recovery data) have been useful in revealing basic aspects of the timing and routes of migration (Hoodless and Coulson 1994; Spina and Volponi 2008; Guzmán et al. 2011; Péron et al. 2011), but are insufficient for describing crucial aspects of migration such as stopover strategies, flight distance between consecutive resting areas, etc. (Schmaljohann et al. 2012; Tøttrup et al. 2012). Furthermore, ring–recovery analyses (Guzmán et al. 2011) have shown different origin areas from those obtained using stable isotope analyses (Hobson et al. 2013). This highlights the need for more research to identify the chief breeding areas of this gamebird.

The use of PTTs on a number of Woodcocks wintering in Spain from 2006 to 2012 allowed us to track these birds for the whole annual cycle. We were therefore able to describe their migration routes and relevant stopover sites in detail, as well as to determine the locations of their breeding areas, until now circumscribed to the circum-Baltic and central-eastern European regions (Guzmán et al. 2011). Specific issues to be explored in this work are: (1) strategies of migration in autumn and spring (timing, velocity, stopovers), (2) identification of breeding grounds, (3) inter-year site fidelity to wintering grounds.

Methods

Ethics statement

All animals were handled in strict accordance with good animal practice, as defined by the Regional Administrations. These are the governmental bodies responsible for issuing the requisite permits for the capture and marking of wild animals in Spain.

Sampling methods and details

From 2006 to 2013, 20 Woodcocks wintering in several different regions in Spain were tagged with PTTs (Appendix Table 2; Fig. 1). Most birds were tagged in the north, where the wintering population is larger (Onrubia 2012).

Woodcocks were captured when foraging in meadows at night, using a 12-V 100-W lamp attached to a helmet (Ferrand and Gossmann 1988). Once a bird was detected, the observer (ringer) approached it very cautiously, walking in a straight line. The birds were captured with a large circular net attached to a 6-m-long pole. The PTT was attached to the bird with a home-made nylon harness. The Woodcocks' weight when caught ranged from 300 to 385 g

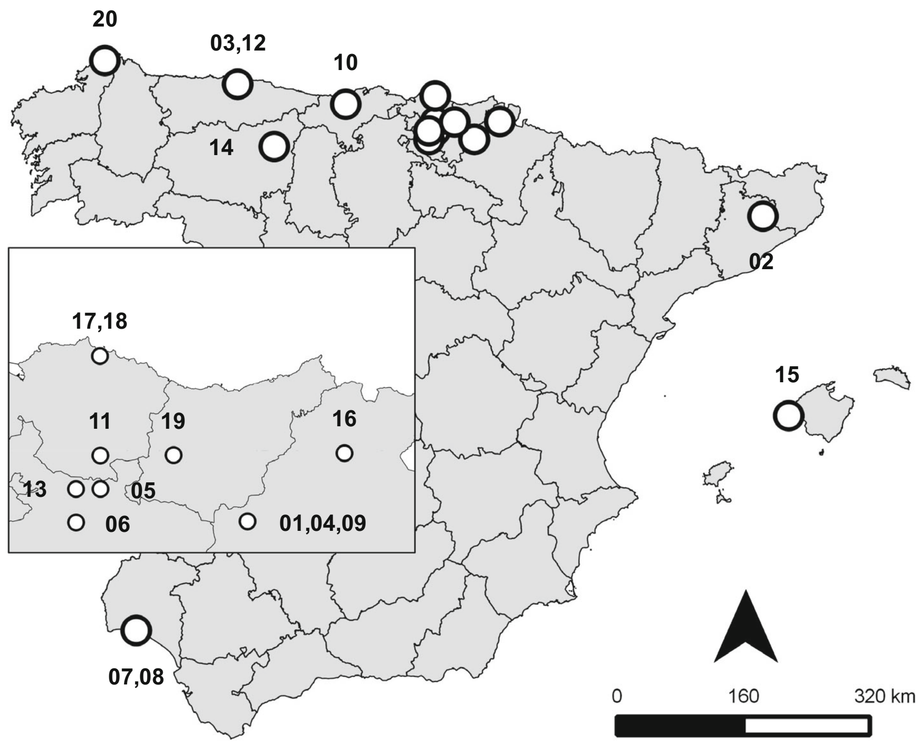

Fig. 1 The locations in northern Spain where 20 Eurasian Woodcocks (*Scolopax rusticola*) were tagged with PTTs from 2006 to 2013. The enlarged area shows the location of 11 birds in a high-concentration tagging area in the Basque Country and Navarra. *Numbers* (bird IDs) are as shown in Appendix Table 2

(mean ± SE: 332 ± 24 g), hence the weight of the PTT did not exceed 3.2 % (mean: 2.8 %) of body mass.

Most Woodcocks were tagged at the end of the winter period, once the hunting season had finished in the region (range 11 January–19 March; Appendix Table 2). This procedure was followed in order to avoid tagged birds being shot before the spring migration (Guzmán 2013).

Characteristics of the PTTs

PTTs have been found to be a very useful tool for tracking birds that are too small to carry a GPS device. The development of PTTs has paralleled that of the Argos satellites. In contrast to a GPS device, the position of a bird carrying a PTT is calculated on the Doppler effect basis.

The PTTs were produced by MTI, Columbia (USA). Woodcocks tagged in 2006 were equipped with 12-g PTTs, whilst those tagged from 2007 onwards were equipped with 9.5-g PTTs. PTT dimensions were 43 × 18 × 14 mm for the 12-g PTT, and 38 × 17 × 12 mm for the 9.5-g PTT. All the PTTs were equipped with a battery charged by a solar array, so in theory they had the capacity to last for several years. Most PTTs ($n = 15$) were programmed to charge energy over a 48-h period, which was followed by a 10-h emission period (i.e., a 48:10 cycle). Alternative duty cycles were also used (55:08, $n = 4$, and 72:10, $n = 1$; for details, see Appendix Table 2). Accordingly, most PTTs had 2-day "gaps" before each 10 h of emission. If the satellite did not pass over the PTT during that 10-h period (or the signal was too low to be detected), then the temporal gap was extended to a minimum of 106 h (i.e., 4.4 days).

The data provided by the satellites were: (1) platform (bird) identification, (2) date and hour when the signal was obtained (actual position of a bird), (3) accuracy of the position, and (4) position (latitude, longitude). Argos provides location accuracies denoted as: Z; B; A; 0 (>1,500 m); 1 (500–1,500 m); 2 (250–500 m); and 3 (<250 m). The Z category indicates that the satellite was able to detect the PTT but unable to assess a geographic position (no accuracy). Categories A and B have no accuracy estimation, and errors can exceed 1° (i.e. >100 km).

Data selection

The data considered in this study were taken from the 0–3 categories only (i.e., good quality data; categories Z, B and A were excluded). This resulted in 1,240 points, pertaining to 20 Woodcocks (Appendix Table 2). However, not all Woodcocks provided data that were useful for all the analyses, due to a lack of points provided during the lifetime of the PTTs (Appendix Table 2). In Appendix Table 3, we show which birds were used to calculate the different parameters considered in this study.

Analyses of routes and timing of migration

The departure date from the winter quarters was calculated as the median date between the last signal from the winter area and the first one on migration. When we detected more than a 10-day gap between these signals, the departure date was not calculated (Martell et al. 2001). The same approach was used to estimate the date of arrival at breeding quarters.

At wintering sites, the distance from one position to the next did not exceed 0.3° (ca. ~30 km). To be conservative, we considered that subsequent points (positions) situated at a distance <0.4° belonged to the same site (i.e. a wintering, stopover or breeding site). Points situated farther apart were assumed to be after a phase of migratory flight. When more than one location was obtained for a particular site, we calculated the median value in order to obtain a more realistic position for the bird. Thus, during the migration period, we determined a stopover site to be the median position of a number (≥2) of subsequent points situated at a distance of <0.4°. However, some of such "apparent" stopovers related to stopping periods of <24 h, and in some cases it was difficult to confirm whether the bird was really stationary or was still on migration. Therefore, to estimate stopover duration, we only considered stopovers ≥2 days. Considering each bird as a random factor, we used generalized linear mixed models (GLMMs) to examine whether the stopover duration was constant or varied across the season. Stopover duration was the object variable (with a linear-link function) and date was included as a covariate. The departure date from the winter site was also included as a covariate, since late birds could be under pressure to migrate faster (Kokko 1999).

The migration distance was estimated as the sum of the distances between segments, including the distance from the last stopover to the breeding/wintering area. The duration of migration was estimated as the time (in days) taken to travel from the wintering to the breeding quarters in spring, and conversely in the autumn. The mean distance travelled per day is thus calculated as the distance of migration divided by the duration of migration.

To assess whether routes of migration to breeding quarters were more or less straight, we calculated the 'total detour ratio' (TDR), i.e., how much longer the routes were than a straight line (loxodrome) connecting the wintering and breeding quarters. The TDR ranges from 0 to 1. Values closer to zero indicate long detours, whereas values closer to 1 indicate relatively straight, direct migration routes to the breeding grounds (Klaassen et al. 2010; Mellone et al. 2013).

Statistical procedures were carried out using SPSS v.21.0 and QGIS.

Results

Spring migration

The Woodcocks departed (median) on 20 March (range 14 March–3 April, $n = 8$), and the spring migration lasted a mean of 40 days (SE = 5 days, range 24–62 days, $n = 7$).

All the Woodcocks arriving at the breeding areas ($n = 12$) provided data along the route of migration. Of these, 11 provided data from "single-position" points (overall: 39 points; mean per bird: 3.3 points; range 0–7 points), whilst 10 birds provided data from sites where we obtained >1 position (i.e. potential stopovers; overall: 49 points; mean per bird: 4.1 points; range 0–14 points) (Table 1). Twenty-three of the stopovers were found to be shorter than 24 h, and 26 lasted for more than 24 h (Table 1). Considering only the stopovers ≥2 days, we obtained a mean stopover duration of 5 days (SE = 1 day, range 2–16 days). However, the stopover duration was affected by the date in the season (B parameter: −0.094, $P = 0.008$), not by the departure date from the wintering site (B parameter: −0.120, $P = 0.306$). Thus, the Woodcocks tended to reduce their stopover periods when they were closer to their breeding areas (Fig. 2).

The mean straight-line distance from the wintering to the breeding quarters was 6,522 km (SE = 434 km, range 5,168–10,560 km, $n = 12$). The mean TDR was almost 1 (0.95 ± 0.01; range 0.80–1.00), indicating that Woodcocks tended to follow a fairly direct route to their breeding sites in Russia. The TDR was not correlated to the number of points provided by each bird along its route of migration ($r = 0.260$, $P = 0.415$, $n = 12$).

Two birds were found to attempt sea crossings, and in such cases they seemed to minimize the distance when they were flying over the water (Woodcocks ID = 06 and 16 crossed the Baltic Sea; Fig. 3). The time elapsed from the last position on one of the shores and the first one on the other shore ranged from 2 days (ID = 06) to 5 days (ID = 16). Moreover, a Woodcock that overwintered in northwestern Iberia (Galicia, ID = 20) did not fly over the

Table 1 Number of Eurasian Woodcocks (*Scolopax rusticola*) locations during the spring migration

ID	1 position	Stopovers (<24 h)	Stopovers (>24 h)
01	3	0	0
03	1	0	0
04	1	0	1
05	4	0	1
06	7	1	0
09	2	0	3
10	3	3	2
11	6	8	6
16	3	5	4
17	0	2	2
19	6	3	4
20	3	1	3

Bay of Biscay but instead migrated parallel to the coast and the Pyrenees, to the east of Iberia. Two days later, from there, the bird was detected in Croatia. This is compatible with either a crossing over the Mediterranean and, perhaps, a 1-day stopover in Italy, or a migration along the coast of southern France and then through northern Italy to Croatia (Fig. 3). Interestingly, all three birds had a lower TDR than birds that migrated through inland regions (TDR <0.95, which is below the mean).

Considering the seven cases where we were able to accurately estimate the timing of migration, we obtained a total mean speed of migration (i.e. including stopovers) of 170 ± 14 km/day (range 100–256 km/day).

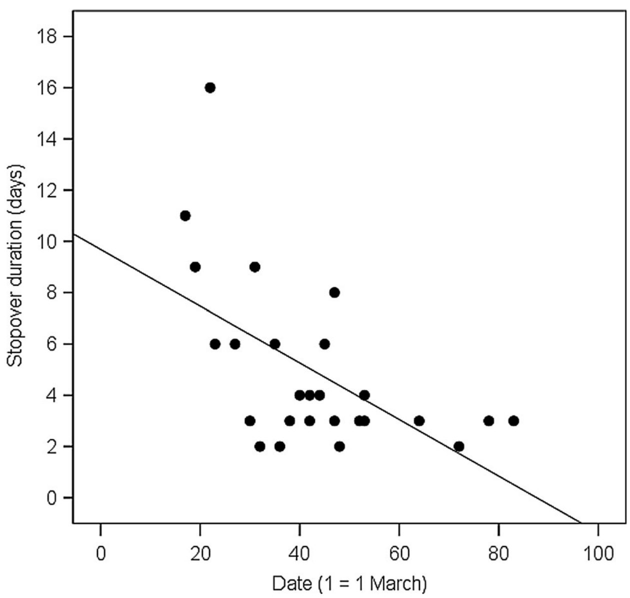

Fig. 2 Relationship between the minimum stopover duration and the starting date of each stopover. All individuals pooled

Breeding grounds

The arrival date (median) at the breeding quarters was 29 April (range 19 April–25 May; $n = 11$). The location of the breeding quarters ranged from the circum-Baltic region (Finland) to Central Siberia (Fig. 3; mean ± SE: latitude 58.9 ± 0.9°N, longitude 44.0 ± 4.5°E; $n = 12$).

Of the 12 Woodcocks detected arriving at their breeding areas, 10 birds emitted their last known position before starting their autumn migration (range 25 May–16 October).

One Woodcock (ID = 04, Appendix Table 3) was found to return to the same breeding area in two consecutive years.

Autumn migration

It was impossible to assess departure dates from the breeding quarters in autumn because most devices either failed or stopped providing data before the start of the autumn migration period. We only obtained data from two birds after their first recorded breeding period. One bird (ID = 04) provided data from 5 February (i.e. we missed the autumn migration period) to 5 August, and a second individual (ID = 10) provided data from 29 August to 28 October. Its last breeding position was recorded on 7 July, so once again we were not able to calculate the departure date.

During the autumn migration period, the positions of bird ID = 10 moved along an axis from 57.3°N, 84.1°E to 56.4°N, 53.9°E, i.e. the PTT stopped providing data before this bird reached its wintering site (Fig. 4). Moreover, one

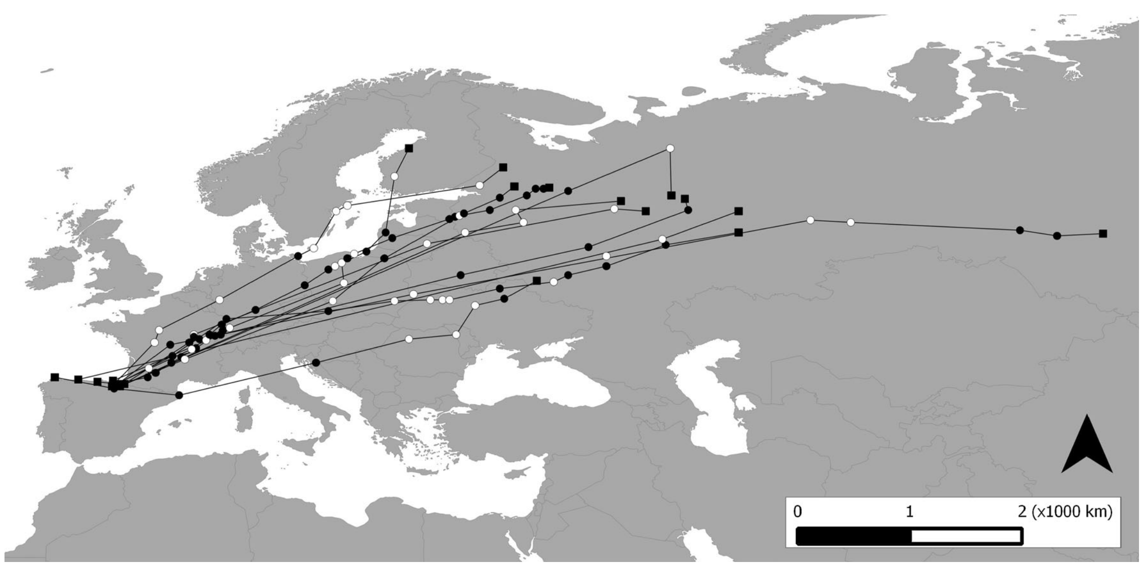

Fig. 3 Detailed spring migration routes of 12 Woodcocks. *Open dots* sites where we obtained a single position. *Filled dots* sites where we obtained >1 position; n this last case, median values of longitude and latitude were calculated. *Squares* wintering (Spain) and breeding localities

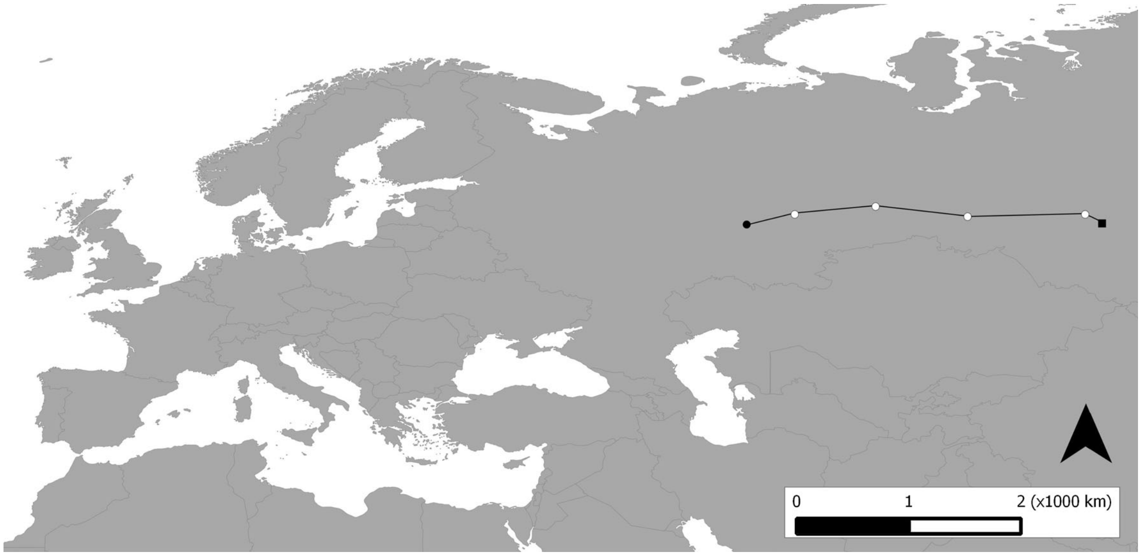

Fig. 4 Detailed autumn migration of one of the Woodcocks (ID = 10). The signal of this bird was lost before the end of its migration. *Open dots* sites where we obtained a single position. *Filled dots* sites where we obtained >1 position. *Square* breeding site

bird (ID = 20) was shot on 14 November 2013, just 1.5 km (coordinates: 42°45′N, 2°34′W) from one of the spring stopover places in northern Iberia (communicated by the hunters who shot the bird to J.F. Tobar).

Bird ID = 04 wintered in the same site as the previous year, when it was caught and tagged with the PTT.

Discussion

This work is the first European study to show the spring migration routes and identify the breeding quarters of Woodcocks tagged with Solar/Argos PTTs. Birds were tagged during the winter period in Spain, this being one of the main wintering regions for the species in Europe (Guzmán et al. 2011). Our study shows the great value of small-sized Solar/Argos PTTs for tracking medium-sized migratory birds and determining the location of remote breeding sites. We gained much more information on Woodcock migration by using 20 PTTs than has been obtained from all the Woodcocks ever ringed in Spain (more than 1,200). The PTTs allowed us to meet our goals, which were to describe the routes and timing of migration, including potential stopovers, and to identify breeding quarters. Although the PTTs are provided with a small solar panel, and in theory should last for more than a year, most birds were observed to stop emitting within 12 months of activation. The particular behavior of the Woodcock (a nocturnal shorebird that lives in dense forest vegetation) (Cramp and Simmons 1983) is likely to have hampered the charging of the PTT batteries.

The departure from winter quarters (median date) was completed by 20 March. This date is within the temporal window reported in Woodcocks wintering in Iberia, with most birds leaving in February or March (Hidalgo and Rocha 2001; Arroyo and Guzmán 2010; Mendiburu and Arizaga 2010). Thus, our birds were found to depart relatively late. Causes explaining these results could be: (1) tagging was carried out as late as possible (Appendix Table 2) to minimize hunting of the birds, so we inevitably selected birds that were still at their wintering sites at the end of the winter period, whilst other Woodcocks might have already departed; (2) tagged birds might delay their departure from wintering sites in order to accumulate some extra fuel reserves due to the weight/impact of the PTT; (3) a random effect cannot be fully rejected since our sample size was quite small and the proportion of Woodcocks wintering in Iberia which leave the region in February (or even before), as opposed to March, is still unknown.

The spring migration period lasted a mean of 40 days, and our birds were found to travel from >5,000 to >10,000 km, with a mean total migratory speed (i.e., including stopovers) of 170 km/day. Overall, the speed was similar to the speed found for other birds of broadly similar size including shorebirds performing long-distance migrations (132 km/day in spring; Battley et al. 2012), raptors (170 km/day when crossing Europe; Hake et al. 2003) and the European Hoopoe (*Upupa epops*) (122 km/day in spring; Bächler et al. 2010).

Woodcocks followed fairly direct routes of migration, avoiding detours. This strategy fits with the rule that the spring migration is generally fast, and birds fly as directly as possible when travelling to breeding sites (Newton 2008). It also fits with the idea that there is competition to reach breeding sites as soon as possible (Kokko 1999). Stopover duration tended to be shortened when birds were closer to their breeding areas, providing further support for the competition theory.

An important, new finding revealed by our study is that Woodcocks were found to breed much further east than any previous results have shown (Guzmán et al. 2011; Hobson et al. 2013). In a study based on ring–recovery data, Guzmán et al. (2011) concluded that 80 % of the Woodcocks wintering in Spain originated from the circum-Baltic region. Using stable isotopes (deuterium), Hobson et al. (2013) determined that most Woodcocks wintering in Spain came from breeding areas situated in central-eastern Europe and the Baltic region. However, we observed only one bird (8 % of the birds for which we knew their breeding sites) that bred within the circum-Baltic region, whilst most birds bred far to the east of Moscow, and one bird was tracked passing over the Urals to breed in Central Siberia (85.6°E). Hence, our data from Woodcocks tagged with PTTs contradict the conclusions of the two previous studies. This shows that further work is required to identify the main breeding quarters of Woodcocks wintering in Spain. Our results might in fact be compatible with the ring–recovery study since there is a lack of ringing in broad areas of Russia, hence an absence of recoveries in Spain (Guzmán et al. 2011).

If our results can be extrapolated to the majority of Woodcocks wintering in Spain, then these birds belong to a management stock which is different from the Woodcock population wintering in France (Bauthian et al. 2007). Our results support the leap-frog migration pattern suggested for the Woodcock: that is, Woodcocks wintering in Spain come from areas that are further to the east and more northern than those wintering in France (Ferrand and Gossmann 2009).

Finally, the only bird that provided long-term data (>1 year) was observed to return to the same wintering area, suggesting high winter site fidelity. Although our contribution to this aspect of the species' biology can only be classified as anecdotal, fidelity to both wintering and breeding quarters from year to year is likely. This confirms what has been obtained in survival analyses (Tavecchia et al. 2002).

Acknowledgments This work was funded by: Regional Councils or Governments of Gipuzkoa, Cataluña, Baleares, Bizkaia and Navarra; FEDENCA, IREC (CSIC-University of Castilla-La Mancha), Microwave Telemetry Inc., Urdaibai Bird Center-Sociedad de Ciencias Aranzadi, Club de Cazadores de Becada (CCB), CAM. Thanks to the people who collaborated during the flied work, especially to the CCB members. Authorizations to capture, ring and mark Woodcocks with PTTs were provided by Regional Councils or Governments of: Asturias, Gipuzkoa, Cataluña, Baleares, Castilla y León, Andalucía, Galicia, Bizkaia and Navarra. I.V. Iljinsky and one more reviewer provided valuable comments that helped us to improve an earlier version of this work.

Appendix

See (Tables 2, 3).

Table 2 Characteristics of the PTTs used in each bird, age (*Jv* juvenile; *Ad* adult) and body mass of the bird when captured, date of the first and last signal, and number of good-quality points obtained from each PTT

ID	PTT type (g)	Duty cycle	Age	Body mass (g)	Starting date	Last signal	Elapsed time (days)	No. points (0–3)
01	12	48:10	Jv	320	03/03/2006	16/06/2006	105	12
02	12	72:10	Jv	316	08/03/2006	19/03/2006	11	1
03	9.5	48:10	Ad	320	23/02/2007	05/08/2007	163	5
04	9.5	48:10	Ad	360	02/03/2007	12/08/2008	529	47
05	9.5	55:08	Jv	385	08/03/2008	08/08/2008	153	23
06	9.5	55:08	Jv	335	10/03/2008	14/09/2008	188	70
07	9.5	48:10	Ad	330	11/01/2009	09/03/2009	57	6
08	9.5	48:10	Ad	300	11/01/2009	21/01/2009	10	1
09	9.5	55:08	Ad	325	10/02/2010	25/05/2010	104	45
10	9.5	55:08	Ad	350	19/02/2010	13/11/2010	267	57
11	9.5	48:10	Jv	350	15/03/2010	06/09/2010	175	154
12	9.5	48:10	Jv	322	18/03/2010	19/04/2010	32	6
13	9.5	48:10	Ad	345	19/03/2010	20/03/2010	1	3
14	9.5	48:10	Jv	302	11/02/2011	31/05/2011	109	8
15	9.5	48:10	Jv	310	16/02/2011	02/04/2013	776	5
16	9.5	48:10	Ad	340	10/02/2012	16/10/2012	249	441
17	9.5	48:10	Ad	340	18/02/2013	11/09/2013	205	119
18	9.5	48:10	Ad	300	18/02/2013	23/05/2013	94	31
19	9.5	48:10	Ad	320	20/02/2013	24/08/2013	185	89
20	9.5	48:10	Ad	370	01/03/2013	11/09/2013	194	117

Table 3 List of the Woodcocks wintering in Spain that provided data (0–3 quality) useful to calculate the different migration-associated parameters considered in this work: departure from wintering site, spring migration period (timing, stopover sites and route), arrival at breeding quarters, identification of breeding site, autumn migration period

ID	Departure winter	Spring migration	Arrival breeding	Breeding location	Autumn migration	Winter location	Breeding location[a]
01		X	X	X			
02							
03		X		X			
04		X	X	X		X	X
05	X	X	X	X			
06		X	X	X			
07							
08							
09	X	X	X	X			
10	X	X	X	X	X		
11	X	X	X	X			
12							
13							
14							
15							
16	X	X	X	X			
17	X	X	X	X			
18							
19	X	X	X	X			
20	X	X	X	X			

[a] 2 years after being tagged with the PTT

References

Alerstam T, Lindström Å (1990) Optimal bird migration: the relative importance of time, energy and safety. In: Gwiner E (ed) Bird migration: the physiology and ecophysiology. Springer, Berlin, pp 331–351

Alerstam T, Hake M, Kjellen N (2006) Temporal and spatial patterns of repeated migratory journeys by ospreys. Anim Behav 71:555–566

Arroyo B, Guzmán JL (2010) Estudio inter-autonómico sobre la becada (*Scolopax rusticola*) en España. Instituto de Investigación de Recursos Cinegéticos (IREC), Ciudad Real

Bächler E, Hahn S, Schaub M, Arlettaz R, Jenni L, Fox JW, Afanasyev V, Liechti F (2010) Year-round tracking of small trans-saharan migrants using light-level geolocators. Plos ONE 5:e9566

Bairlein F (2001) Results of bird ringing in the study of migration routes. Ardea 89:7–19

Battley PF, Warnock N, Tibbitts TL, Gill RE, Piersma T, Hassell CJ, Douglas DC, Mulcahy DM, Gartrell BD, Schuckard R, Melville DS, Riegen AC (2012) Contrasting extreme long-distance migration patterns in bar-tailed godwits Limosa lapponica. J Avian Biol 43:21–32

Bauthian I, Gossmann F, Ferrand Y, Julliard R (2007) Quantifying the origin of Woodcock wintering in France. J Wildl Manag 71:701–705

Chernetsov N (2012) Passerine migration: stopovers and flight. Springer, Berlin

Cramp S, Simmons KEL (1983) Handbook of the Birds of Europe, the Middle East and North Africa, vol 3. Oxford University Press, Oxford

Ferrand Y, Gossmann F (1988) Repartition spatiale des Bécasses des bois sur leurs habitats nocturnes en Bretagne. In: Havet P, Hirons G (eds) 3ème Symposium Européen sur la Bécasse et la Bécassine, Paris, pp 53–59

Ferrand Y, Gossmann F (2009) La Bécasse des bois. Histoire naturelle, Saint-Lucien Effet de Lisière

Guzmán J.L. (2013). Factores que modulan la abundancia poblacional de la becada (*Scolopax rusticola*): implicaciones para su gestión y conservación.Universidad de Castilla La Mancha

Guzmán JL, Ferrand Y, Arroyo B (2011) Origin and migration of woodcock *Scolopax rusticola* wintering in Spain. Eur J Wildl Res 57:647–655

Hake M, Kjellén N, Alerstam T (2003) Age-dependent migration strategy in honey buzzards Pernis apivorus tracked by satellite. Oikos 103:385–396

Hidalgo S, Rocha G (2001) Distribución y fenología de la Becada *Scolopax rusticola* (Linnaeus, 1758) (Charadriiformes, Scolopacidae) durante la invernada en Extremadura. Zool Baet 12:37–48

Hobson KA, Van Wilgenburg SL, Guzman JL, Arroyo B (2013) Origins of juvenile Woodcock (Scolopax rusticola) harvested in Spain inferred from stable hydrogen isotope (delta H-2) analyses of feathers. J Ornithol 154:1087–1094

Hoodless AN (1995) Eurasia Woodcock. Br Birds 88:578–592

Hoodless AN, Coulson JC (1994) Survival rates and movements of British and continental woodcock *Scolopax rusticola* in the British Isles. Bird Study 41:48–60

Klaassen RHG, Strandberg R, Hake M, Olofsson P, Tottrup AP, Alerstam T (2010) Loop migration in adult marsh harriers Circus aeruginosus, as revealed by satellite telemetry. J Avian Biol 41:200–207

Kokko H (1999) Competition for early arrival in migratory birds. J Anim Ecol 68:940–950

Kristensen M, Tøttrup AP, Thorup K (2013) Migration of the common Redstart (*Phoenicurus phoenicurus*): a Eurasian songbird wintering in highly seasonal conditions in the West African Sahel. Auk 130:258–264

Machado AL, Brito JC, Medeiros V, Leitao M, Moutinho C, Jesus A, Ferrand Y, Goncalves D (2008) Distribution and habitat preferences of Eurasian woodcock *Scolopax rusticola* in S. Miguel island (Azores) during the breeding season. Wildl Biol 14:129–137

Martell MS, Henny CJ, Nye PE, Solensky MJ (2001) Fall migration routes, timing, and wintering sites of North American Ospreys as determined by satellite telemetry. Condor 103:715–724

Mellone U, López-López P, Limaña R, Piasevoli G, Urios V (2013) The trans-equatorial loop migration system of Eleonora's falcon: differences in migration patterns between age classes, regions and seasons. J Avian Biol 44:417–426

Mendiburu A, Arizaga J (2010) Patrones de distribución espacial y temporal de la becada (*Scolopax rusticola*) en Gipuzkoa, durante el periodo de migración e invernada. Munibe 58:187–195

Newton I (2008) The migration ecology of birds. Academic, London

Onrubia A (2003) Chocha perdiz, *Scolopax rusticola*. In: Martí R, Del Moral JC (eds) Atlas de las aves reproductoras de España. DGCN-SEO/BirdLife, Madrid, pp 258–259

Onrubia A (2012) Chocha perdiz Scolopax rusticola. In: Atlas de las aves en invierno en España 2007–2010 (Ed SEO/BirdLife), Ministerior de Agricultura, Alimentación y Medio Ambiente-SEO/BirdLife Madrid, pp 260–261

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. Behav Ecol Sociobiol 65:1949–1955

Schmaljohann H, Buchmann M, Fox J, Bairlein F (2012) Tracking migration routes and the annual cycle of a trans-Sahara songbird migrant. Behav Ecol Sociobiol 66:915–922

Spina F, Volponi S (2008) Atlante della migrazione degli uccelli in Italia. vol 1 non-Passeriformi. ISPRA-MATTM, Roma

Stutchbury BJM, Tarof SA, Done T, Gow E, Kramer PM, Tautin J, Fox JW, Afanasyev V (2009) Tracking Long-distance songbird migration by using geolocators. Science 323:896

Tavecchia G, Pradel R, Gossmann F, Bastat C, Ferrand Y, Lebreton JD (2002) Temporal variation in annual survival probability of the Eurasian woodcock *Scolopax rusticola* wintering in France. Wildl Biol 8:21–30

Tøttrup AP, Klaassen RHG, Strandberg R, Thorup K, Kristensen MW, Jargensen PS, Fox J, Afanasyev V, Rahbek C, Alerstam T (2012) The annual cycle of a trans-equatorial Eurasian-African passerine migrant: different spatio-temporal strategies for autumn and spring migration. Proc R Soc Lond B 279:1008–1016

Wernham C, Toms M, Marchant J, Clark JA, Siriwardena GM, Baillie S (2002) The migration atlas: movements of the birds of Britain and Ireland. Poyser, London

Zwarts L, Bijlsma RG, van der Kamp J, Wymenga E (2009) Living on the edge: Wetlands and birds in a changing Sahel. KNNV, Zeist