

Ranging behaviour of an adult female greater spotted eagle (*Clanga clanga*) wintering in Sudan for 10 years, as revealed by satellite telemetry

Správanie dospelej samice orla hrubozobého (*Clanga clanga*) zimujúcej v Sudáne počas 10 rokov, ako ho odhalila satelitná telemetria

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Abstract: Using global position system (GPS) technology, we tracked an adult female greater spotted eagle (*Clanga clanga*) on its wintering grounds in the Sudan-South Sudan borderland during 2005–2015. There were 10 909 GPS locations for this bird in the non-breeding range. Throughout the study, the eagle showed fidelity to its wintering grounds. The non-breeding season coincided with the dry season. The median arrival date was 11 October ($n = 10$). The median departure date ($n = 10$) was 4 March, and was less variable than the arrival date. The 95% kernel density estimate (KDE) for all years was 33 838 km², and the 50% KDE encompassed 6 585 km². The wintering range was split between two areas, west and east, with the eagle typically arriving in the western area, where it stayed for some time. It then moved about 330 km to the eastern area, where it would remain for a few weeks before departing for Europe in the spring. In both the western and eastern subareas, the annual home ranges overlapped to a variable extent (14–99%). The high degree of fidelity to the wintering grounds shown by this bird was mirrored by the behaviours of two other adult greater spotted eagles that we tracked (using >1 tracking devices) for 15 years that wintered in South Sudan and Turkey. The number of greater spotted eagles that winter in Africa is a matter of speculation, although virtually all individuals are likely to pass through a narrow corridor near Suez, Egypt. Collectively, these tracking data and the findings of other studies suggest that greater spotted eagles from the western parts of the European breeding range often move to Africa. Further, the Sudd wetlands in South Sudan are important for greater spotted eagles and other rare bird species during the non-breeding season.

Abstrakt: Pomocou technológie globálneho polohového systému (GPS) sme sledovali dospelú samicu orla hrubozobého (*Clanga clanga*) na jej zimovisku na sudánsko-juhosudánskom pohraničí v rokoch 2005-2015. V nehniedznom areáli tohto vtáka bolo zaznamenaných 10909 GPS lokalizácií. Počas celej štúdie orol vykazoval vernosť svojmu zimovisku. Nehniedzne obdobie sa zhodovalo s obdobím sucha. Mediánový dátum priletu bol 11. október ($n = 10$). Mediánový dátum odletu ($n = 10$) bol 4. marec a bol menej variabilný ako dátum priletu. Kernelový odhad hustoty (KDE) pre všetky roky predstavoval 95 %, čo je 33838 km² a 50 % KDE zahŕňalo 6585 km². Zimovisko bolo rozdelené medzi dve oblasti, západnú a východnú, pričom orol zvyčajne prilietal do západnej oblasti, kde sa istý čas zdržiaval. Potom sa presunul asi 330 km do východnej oblasti, kde zostal niekoľko týždňov pred jarným odletom do Európy. V západnej aj východnej podoblasti sa ročné domovské okrsky prekrývali v rôznej miere (14 - 99 %). Vysoký stupeň vernosti zimoviskám, ktorý preukázal tento vták, sa odzrkadlil v správaní ďalších dvoch dospelých orlov hrubozobých, ktoré sme sledovali (pomocou >1 sledovacích zariadení) 15 rokov a ktoré zimovali v Južnom Sudáne a Turecku. O počte orlov hrubozobých, ktoré zimujú v Afrike, možno len špekulovať, hoci prakticky všetky jedince pravdepodobne prelietajú úzkym koridorom v blízkosti Suez v Egypte. Súhrnne tieto údaje o sledovaní a zistenia iných štúdií naznačujú, že orly hrubozobé zo západnej časti európskeho hniezdného areálu sa často presúvajú do Afriky. Okrem toho sú mokrade Sudd v Južnom Sudáne dôležité pre orly hrubozobé a iné vzácne druhy vtákov v mimohniedznom období.

Key words: Non-breeding season, site fidelity, ranging behaviour, Sudd wetlands, Sudan

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Acknowledgements: Many people, agencies, and institutions have enabled this study and the publication of these results. We would like to thank the following for making the research possible and for their comprehensive assistance: The Directorate and District Supervisors of the Biebrza National Park in Poland, and the Forest District Manager and services of the Rajgród Forest District involved in the protection of the eagles.

Conducting extensive fieldwork would have been impossible without the help of several colleagues: Paweł Baranowski, Kordian Bartoszek, Andrzej Batycki, Michał Białek, Michał Jankowski, Kai Graszynski, Antoni Kasprzak, Jan Kowalski, Jan Lontkowski, Joachim and Hinrich Matthes, Paweł Mirski, and Sylwester Aftyka. R. Buij and A. Kwarteng helped us obtain relevant remotely sensed vegetation information for the Sudd wetlands and helped us understand their importance to eagles. M. Oli provided advice regarding the analyses. The University of Florida provided funding for this study.

Introduction

Migration is a common phenomenon among birds, especially those that experience significant seasonal changes in temperature or rainfall or breed at higher latitudes. Migrations are typically driven by changes in food supply, both annually and evolutionarily (Bildstein 2006; Newton 2008). Historically, ecological data collection has focused on the breeding grounds as birds are often tied to nest sites, making their capture easier. Moreover, breeding success can often be determined at these locations. In addition, temperate countries—in which many long-distance migratory birds breed—often have more human and financial resources for bird research compared to countries at lower latitudes, where many of those same bird species overwinter. As a result, far more is known about the ecology of migratory birds in their breeding areas than during migration or in their wintering areas.

The greater spotted eagle (*Clanga clanga*) is a medium- to large-sized migratory species (Ferguson-Lees and Christie 2001; Meyburg and Meyburg 2005; Meyburg et al. 2005; Maciorowski et al. 2015) that breeds in wet forests in Eurasia and is a medium- to long-distance migrant. The global conservation status of the greater spotted eagle is vulnerable (Meyburg et al. 2016; BirdLife International 2022). It has a large breeding distribution, which extends from eastern Poland to the Pacific Ocean in southeast Siberia and Manchuria. However, human activities have caused severe fragmentation within this range (Väli et al. 2019; 2021; Karyakin 2008).

Greater spotted eagles prefer wet habitats in all seasons (Meyburg et al. 1995, Maciorowski et al. 2014, 2015, 2019), including wetlands in the non-breeding season and wet forests or forests adjacent to wetlands during the breeding season. However, during the non-breeding season, they are sometimes found in drier habitats (Brown et al. 1982, Meyburg et al. 1995) and at sites of anthropogenic waste disposal (Lobley 2007, Meadows 2011, Strick et al. 2011, McGrady et al. 2021).

Satellite telemetry has developed significantly in recent decades (Meyburg and Fuller 2007; Cagnacci et al. 2010), and its use has led to a significant advancement in our knowledge of the areas used by many bird species during the non-breeding season, especially birds of prey (Panuccio et al. 2021). The non-breeding (boreal winter, hereafter referred to as “wintering” or “non-breeding”) range of the greater spotted eagle covers a vast area in the subtropics and tropics of Eurasia and Africa (Väli et al. 2021). On wintering grounds, this species can be observed at many locales, which can be distant from one another and hold a few or dozens of individuals (Naoroji and Schmitt 2007; Jeyarajasingam 2012; Prakash 1988; Mallalieu 2007).

Greater spotted eagles spend more than one-third of the year on their wintering grounds. However, their ecology and habitat use within these areas have not been well studied, and very few telemetry studies of wintering birds have been conducted (Meyburg et al. 1995; Pérez-García et al. 2014; McGrady et al. 2021; Väli et al. 2021). In the last 30 years, the development of satellite-based

animal tracking has made it possible to follow bird species over large distances, through remote areas, and over several years (Meyburg and Fuller 2007). Tracking birds during migration and in their wintering grounds contributes to a better understanding of their year-round ecology, including the factors affecting their survival and reproduction. We fitted our first satellite-received transmitter (Platform Transmitter Terminal, PTT) to a nestling greater spotted eagle in North-East Poland in 1992. Over the years, we have deployed additional tags on adults and nestlings, including nine adults between 1995 and 2003. Location data from PTTs are typically less precise than tracking devices using Global Positioning System (GPS) technology.

Material and methods

On 14 July 2005, we captured an adult female greater spotted eagle nesting in the Biebrza River Valley in NE Poland (ca 53.3° N; 22.6° E). We collected a blood sample to determine its sex. Analysis of the sample confirmed that the bird was a greater spotted eagle, and not a *Clanga clanga* x *C. pomarina* hybrid. The eagle was fitted with a 45 g solar-powered GPS-PTT tag (Microwave Telemetry, Inc., USA; ID 57116) as a backpack (Meyburg and Fuller 2007). The transmitter accounted for 2.3% of the eagle's body mass. The bird was ringed (BN 3843 in the Polish ringing scheme; individual identification ring: 1 D) and released (Fig 1). It subsequently reared a chick in that year.

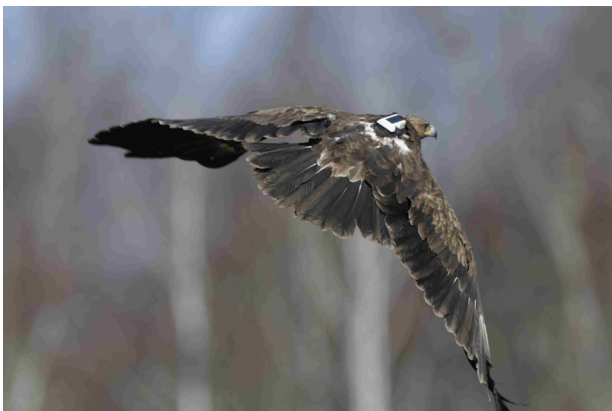


Fig. 1. Female greater spotted eagle with the longest record of fidelity to its wintering area (Göksu River Delta in Turkey (1999 – 2014) with its second transmitter (see page 46). (Photo by Kordian Bartoszek, 24.04.2013).

Obr. 1. Samica orla hrubozobého s najdlhším záznamom fidelity k svojmu zimovisku (delta rieky Göksu, Turecko (1999 - 2014) s druhým vysielateľom (pozri stranu 46). (Foto: Kordian Bartoszek 24.4.2013).

The transmitter uploaded the GPS locations via the Argos satellite system, and provided Argos-Doppler location estimates (http://www.argos-system.org/manual/3-location/34_location_classes.htm). The transmitter was programmed to collect GPS locations every hour during daylight hours. The GPS data collection rates and transmission could be affected by low solar charging, resulting in data collection gaps. GPS data gaps were rare in the early years of the study; however, they became more frequent with time. Moreover, the volume of collected data also declined with transmitter age. Therefore, the data collected during the winter 2014–2015 were excluded from between-year range comparisons due to the small sample size. We tracked this eagle until the PTT device failed on 12 January 2016.

We cleaned the GPS and Argos location datasets to remove outliers and implausible location estimates. The arrival times at and departure from the wintering grounds were objectively determined by applying piecewise regression to a plot of GPS-determined latitudes against the respective date (Limiñana et al. 2007). Arrivals and departures were recorded as the dates and times where the regression “broke,” indicating a change in the bird's flight behaviour between migration and wintering. Subsequently, we directly examined the Argos location data to improve the precision of arrival and departure estimates when there were gaps in the GPS data.

The non-breeding season spans from approximately late September to early April. Therefore, the locations were categorised by the year in which the non-breeding season began. For instance, the locations collected in January 2006 were considered part of the 2005 data because the bird arrived at the non-breeding grounds in the autumn of 2005. Additionally, because the bird generally split its time between two sub-areas within its non-breeding range (west and east), we conducted analyses to understand the characteristics of those sub-areas and elucidate any differences between them. Specifically, we visually inspected the locations in ArcMap (ESRI 2019) and categorised them into either sub-area or as instances of travelling between them (although the bird typically spent only one day or less travelling between sub-areas; see Figs. 2 and 3).

We estimated separately the non-breeding home ranges and core ranges of the bird for each sub-area using 95% and 50% utilisation distributions (UD) from the kernel density estimator (KDE; Worton 1989). We estimated the ranges using all non-breeding data combined for each year and each sub-area by year. We used the data of at least 30 locations in the dataset (year, sub-area, or

sub-area by year) to estimate the home range and the reference bandwidth (i.e. kernel smoothing parameter) to estimate the overall non-breeding home range. For all other home ranges, we first estimated home ranges using the reference bandwidth and then calculated the average bandwidths in each category. We calculated the yearly non-breeding home ranges, including both sub-areas (east and west), the overall home ranges by sub-area for all years combined, and home ranges for each sub-area by year. Then, we re-estimated the home ranges using the average reference bandwidth. We tested for differences in size between the east and west sub-areas by year using a paired t-test.

To estimate the degree of winter site fidelity exhibited by the bird among years in the east and west sub-areas, we calculated the overlap between yearly home ranges (95% KDE) at each sub-area using Bhattacharyya’s affinity (BA; Fieberg and Kochanny 2005). A value of 0 indicated no overlap in the total UD, whereas a value of 1 indicated complete overlap. Considering that the values at each site were not normally distributed, we tested for a difference in the overlap between the east and west sub-areas using a Wilcoxon rank sum test.

We calculated the distance travelled between successive hourly locations (hourly step length) to describe the bird’s movements. We log-transformed hourly step lengths and used a generalised linear model with a step length response to test for the effects of year, sub-area, and the interaction between them. We excluded step lengths from periods when the bird was categorised as travelling between the west and east sub-areas owing to low sample sizes in most years. Based on Akaike’s information criterion corrected for a small sample size (AICc; Burnham and Anderson 2002), the only supported model included interactions between years and sub-areas.

To investigate whether the bird’s movements were related to the onset of drier conditions during winter, we examined the monthly averages of enhanced vegetation indices (Africa Soil Information Service: <http://www.africasoils.net/data/datasets?page=1>) within annual KDEs. However, no obvious relationship could be discerned as our data were from a single individual. Therefore, we did not pursue further habitat analyses.

All analyses were performed using R statistical software (version 3.4.4; R Core Team, 2019). We estimated the bird’s home ranges using the “adehabitat” package (Calenge 2006) and calculated step lengths using the “adehabitatLT” package in R (Calenge 2006). All statistical tests were performed using base R functions.

Results

In all years (N = 10 winter seasons), the eagle wintered within a narrow latitudinal range (9.2°–10.7° N) in two sub-areas (west and east) centred at approximately 9.9° N; 27.8° E in the Sudan-South Sudan border region. The western sub-area was situated along the Bahr al Arab (the Kiir River) in Scharq Darfur, one of the five states in the Darfur region. The Bahr al Arab flows through southwest Sudan, marks a portion of the international border between Sudan and South Sudan, and becomes part of the Nile River system. The eastern sub-area was located along the Bahr al Gazal, which flows into the White Nile. Wintering coincided with the dry season (November to March), with the driest months being December–February (average rainfall = 0 mm). Precipitation increased significantly within the sites used by this bird from the

Tab. 1. Movement of an adult female greater spotted eagle between two sub-areas of its winter range in the Sudan-South Sudan borderlands, 2005–2015.
Tab. 1. Pohyb dospelej samice orla hrubozobého medzi dvoma podoblastami jeho zimoviska na sudánsko-juhosudánskom pohraničí v rokoch 2005-2015.

Year	Arrival at wintering ground in west	Departure from west sub-area		Arrival at east sub-area		Departure from east sub-area		Arrival at west sub-area again		Departure from west sub-area again		Arrival at east sub-area again		Migration departure	
		Departure from west sub-area	Arrival at east sub-area	Departure from east sub-area	Arrival at west sub-area	Departure from west sub-area	Arrival at east sub-area	Departure from west sub-area	Arrival at east sub-area	Departure from west sub-area	Arrival at east sub-area	Departure from west sub-area	Arrival at east sub-area	Migration departure	
2005–2006	22-Oct	27.12	28.12	30.12	6.1	4.3	NA	4.3	NA	4.3	NA	4.3	NA	4.3	
2006–2007	13-Oct	18.1	20.1	3.3	NA	NA	NA	NA	NA	NA	NA	NA	NA	3.3	
2007–2008	03-Oct	14.1	15.1	5.3	NA	NA	NA	NA	NA	NA	NA	NA	NA	5.3	
2008–2009	07-Oct	4.1	5.1	28.2	NA	NA	NA	NA	NA	NA	NA	NA	NA	28.2	
2009–2010	14-Oct	8.12	12.12	28.12	30.12	3.1	4.1	3.1	4.1	3.1	4.1	3.1	4.1	7.3	
2010–2011	10-Oct	27.12	29.12	2.3	NA	NA	NA	NA	NA	NA	NA	NA	NA	2.3	
2011–2012	08-Oct	19.12	24.12	28.2	NA	NA	NA	NA	NA	NA	NA	NA	NA	28.2	
2012–2013	21-Oct	6.1	9.1	4.3	NA	NA	NA	NA	NA	NA	NA	NA	NA	4.3	
2013–2014	23-Sep	10.1	13.1	3.3	NA	NA	NA	NA	NA	NA	NA	NA	NA	3.3	
2014–2015	15-Oct	-	-	6.3	NA	NA	NA	NA	NA	NA	NA	NA	NA	6.3	
Mean	10 Oct ± 8.1 days													3 March ± 2.4 days	
Median	11 Oct													4 March	

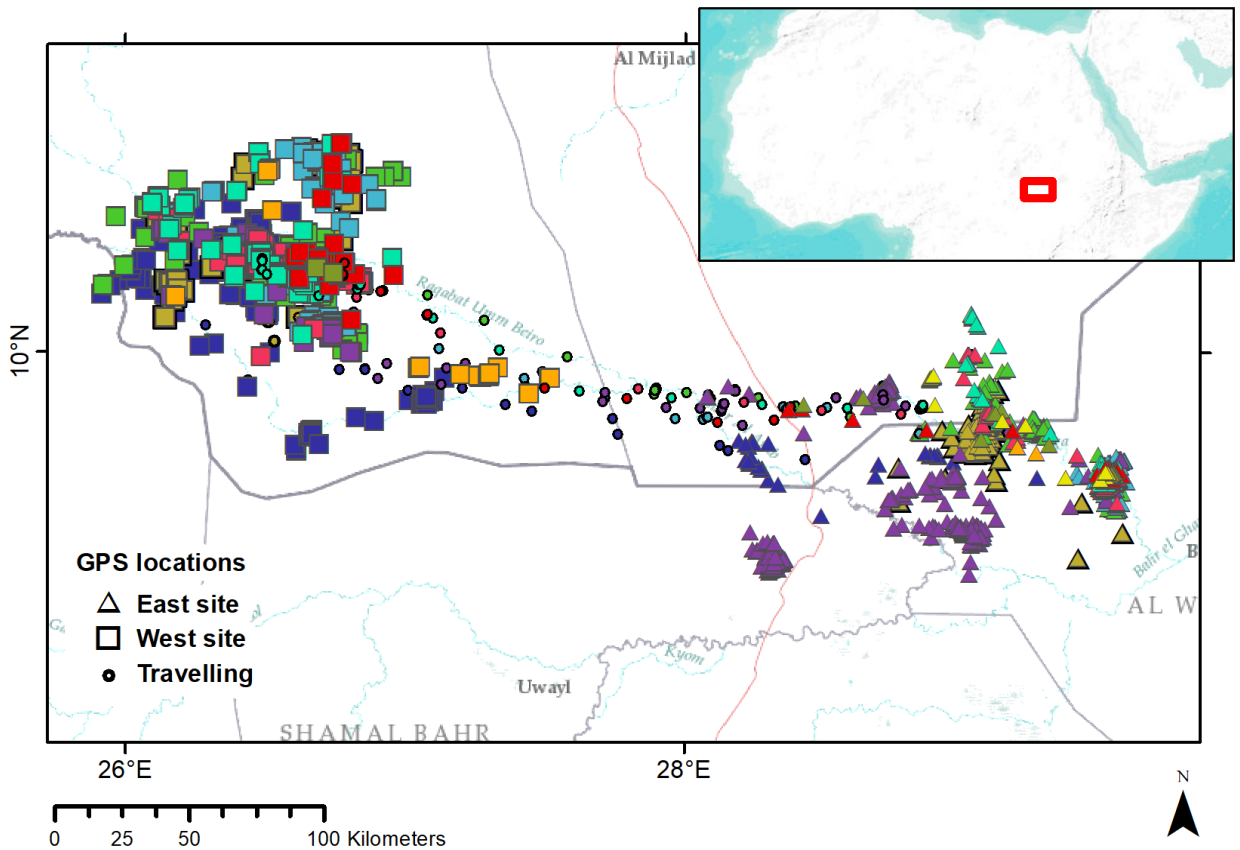


Fig. 2. Global Positioning System (GPS) locations of a tracked adult female greater spotted eagle on its non-breeding grounds in Sudan-South Sudan during 2005–2016. Squares are locations in the western sub-area; triangles are locations in the eastern sub-area; circles are locations of the bird as it moves between the sub-areas. Colours represent different years.

Obr. 2. Lokalizácie globálneho polohového systému (GPS) sledovanej dospeljej samice orla hrubozobého v mimohniezdnom území v Sudáne a Južnom Sudáne v rokoch 2005 - 2016. Štvorce reprezentujú miesta v západnej podoblasti; trojuholníky sú miesta vo východnej podoblasti; kruhy sú miesta, kde sa vták pohybuje medzi podoblastami. Farby predstavujú rôzne roky.

northwest to the southeast. The arrival dates were in September and October and were more variable than the spring departure dates, which occurred during 10 days in February–March (Table 1, Fig. 2). The median autumn arrival and spring departure dates were 11 October and 4 March, respectively. The eagle showed fidelity to its general wintering area (Fig. 2), where it was tracked each year.

The eagle arrived at the western end of its winter range every year during autumn migration. Throughout the winter, it moved between the two sub-areas (Tables 1 and 2, Fig. 2). In seven of the nine years, the bird arrived and settled in the western sub-area in Scharq Darfur (Sudan). It then moved approximately 330 km (from late December to early January) to an eastern sub-area in South Sudan, where it settled until the spring migration. In the winter of 2005, it moved from the west to the east and back to the

west, from where it migrated north. In 2009, it moved from the west to the east, back to the west, and then again to the east before migrating (Tables 1 and 2, Figs. 2 and 3). The eagle typically travelled between the western and eastern sub-areas in a single day, but sometimes the journey lasted as much as four days (Table 1, Fig 3).

From 2005 to 2016, we recorded 10 909 GPS locations for the greater spotted eagle in its non-breeding range (Table 2, Fig. 2). Using data from all years and sub-areas, the non-breeding 95% and 50% KDE home range estimates were 33 838 km² and 6 585 km², respectively. The estimates and averages for the years and sub-areas are listed in Table 2 and plotted in Fig. 4; maps are shown in Figs. 1 and 4. Both the 95% and 50% home ranges in the western sub-area were significantly larger than those in the eastern sub-area (paired t-tests: 95% KDE: $t = -3.10$, $df = 8$, $p = 0.01$; 50% KDE: $t = -2.28$, $df = 8$, $p = 0.05$).

Year	Site	n locations	Home ranges (km ²)		n step- lengths	Average step-length ± SE (km)
			95% KDE	50% KDE		
2005	Overall	1471	32544	4467	1296	1.80 ± 0.00
	West	1369	3776	493	1203	1.40 ± 0.00
	East	82	2944	443	75	3.81 ± 0.10
	Travelling	20	-	-	18	2.05 ± 0.09
2006	Overall	1412	29742	6452	1220	1.25 ± 0.00
	West	926	2355	238	795	0.78 ± 0.00
	East	480	1087	221	420	2.11 ± 0.01
	Travelling	6	-	-	5	4.18 ± 1.19
2007	Overall	1421	37247	8068	1243	1.32 ± 0.00
	West	783	3466	336	669	1.22 ± 0.01
	East	618	2213	342	556	1.07 ± 0.00
	Travelling	20	-	-	18	13.01 ± 0.72
2008	Overall	1511	32833	7187	1320	1.50 ± 0.00
	West	814	3146	485	707	1.13 ± 0.01
	East	671	823	186	588	1.42 ± 0.00
	Travelling	26	-	-	25	13.95 ± 0.58
2009	Overall	1481	46580	11419	1289	1.78 ± 0.00
	West	468	2986	520	397	1.17 ± 0.01
	East	941	4027	594	832	1.82 ± 0.01
	Travelling	72	-	-	60	5.40 ± 0.17
2010	Overall	1236	35085	7920	1069	1.07 ± 0.00
	West	567	1822	285	482	1.08 ± 0.01
	East	637	1691	292	557	0.56 ± 0.00
	Travelling	32	-	-	30	10.56 ± 0.49
2011	Overall	1124	34606	6620	960	1.24 ± 0.00
	West	353	3102	478	279	1.48 ± 0.01
	East	726	1391	179	639	0.80 ± 0.00
	Travelling	45	-	-	42	6.44 ± 0.28
2012	Overall	651	31890	4199	543	0.50 ± 0.00
	West	120	3563	559	90	0.93 ± 0.04
	East	531	736	159	453	0.42 ± 0.00
	Travelling	0	-	-	0	-
2013	Overall	546	30659	4541	448	1.66 ± 0.01
	West	99	2089	336	70	2.81 ± 0.09
	East	428	753	155	363	1.17 ± 0.01
	Travelling	19	-	-	15	8.14 ± 0.82
2014	Overall	47	27193	4980	30	3.22 ± 0.25
	West	2	-	-	1	6.50 ± NA
	East	45	2910	306	29	3.10 ± 0.26
	Travelling	0	-	-	0	-
2015	Overall	9	-	-	7	11.36 ± 1.44
Average among years ± SE	Overall		33838 ± 5308	6585 ± 2227		1.41 ± 0.00
	West		2923 ± 684	415 ± 115		1.19 ± 0.00
	East		1857 ± 1130	288 ± 142		1.25 ± 0.00
	Travelling		-	-		9.50 ± 0.06

Tab 2. Kernel density estimator (KDE) home range sizes (95% and 50%), and average step-lengths (distance between successive hourly locations) of an adult female greater spotted eagle during the non-breeding season (boreal winter) 2005 – 2015 in the Sudan-South Sudan borderlands. Analyses are for all winter locations, locations in the western sub-area, locations in the eastern sub-area and locations as the eagle travelled between the sub-areas. A bandwidth of 26.43 km was used to estimate the overall home range, 6.27 km to estimate the home range of the western sub-area and 5.74 to estimate the home range of the eastern sub-area. A minimum of 30 locations was required to estimate a home range.

Tab. 2. Veľkosti domovského okrsku (95% a 50%) metódou odhadu jadrovej hustoty (KDE) a priemerné dĺžky krokov (vzdialenosti medzi po sebe nasledujúcimi hodinovými lokalitami) dospelej samice orla hrubozobého počas nehniedznej sezóny (boreálna zima) v rokoch 2005 - 2015 na sudánsko-juhosudánskom pohraničí. Analýzy sa týkajú všetkých zimných lokalít, lokalít v západnej podoblasti, lokalít vo východnej podoblasti a lokalít, keď orol putoval medzi podoblasťami. Na odhad celkového domovského okrsku sa použila honnota vyhladzovacieho parametra 26,43 km, na odhad domovského okrsku západnej podoblasti 6,27 km a na odhad domovského okrsku východnej podoblasti 5,74 km. Na odhad domovského okrsku bolo potrebných minimálne 30 lokalít.

Tab. 3. Degree of overlap (Bhattacharyya's affinity; 1 = total overlap, 0 = no overlap) of western and eastern wintering sub-areas used by an adult female greater spotted eagle in the Sudd Wetlands of Sudan/South Sudan, 2005–2013.

Tab. 3. Stupeň prekrytia (Bhattacharyyaho afinita; 1 = úplné prekrytie, 0 = žiadne prekrytie) západných a východných podoblastí zimovania využívaných dospelou samicou orla hrubozobého v Suddských mokradiach v Sudáne/Južnom Sudáne v rokoch 2005-2013.

West	2005	2006	2007	2008	2009	2010	2011	2012	2013
2005	NA	NA	NA	NA	NA	NA	NA	NA	NA
2006	0.84	NA	NA	NA	NA	NA	NA	NA	NA
2007	0.31	0.33	NA	NA	NA	NA	NA	NA	NA
2008	0.62	0.81	0.61	NA	NA	NA	NA	NA	NA
2009	0.76	0.76	0.71	0.84	NA	NA	NA	NA	NA
2010	0.72	0.81	0.53	0.83	0.84	NA	NA	NA	NA
2011	0.65	0.73	0.75	0.81	0.9	0.82	NA	NA	NA
2012	0.28	0.22	0.53	0.32	0.37	0.32	0.46	NA	NA
2013	0.17	0.35	0.82	0.58	0.49	0.53	0.62	0.55	NA

East	2005	2006	2007	2008	2009	2010	2011	2012	2013
2005	NA	NA	NA	NA	NA	NA	NA	NA	NA
2006	0.22	NA	NA	NA	NA	NA	NA	NA	NA
2007	0.2	0.56	NA	NA	NA	NA	NA	NA	NA
2008	0.23	0.03	0.16	NA	NA	NA	NA	NA	NA
2009	0.2	0.13	0.1	0.15	NA	NA	NA	NA	NA
2010	0.25	0.48	0.53	0.79	0.14	NA	NA	NA	NA
2011	0.22	0.15	0.3	0.96	0.15	0.86	NA	NA	NA
2012	0.23	0.07	0.22	0.99	0.15	0.79	0.96	NA	NA
2013	0.24	0.06	0.2	0.99	0.16	0.78	0.96	0.99	NA
2014	0.24	0.39	0.49	0.81	0.24	0.87	0.88	0.84	0.84

The BA measurements of overlap of the annual UD_s at the east sub-areas averaged 0.45 ± 0.05 (range: 0.03–0.99), and those at the west sub-areas averaged 0.60 ± 0.04 (range: 0.17–0.90; Table 3). The annual home ranges in the western sub-area exhibited a significantly greater overlap than those in the eastern sub-area (Wilcoxon rank sum test: $W = 573$, $p = 0.02$).

Hourly step lengths ranged from 0 to 51 km (mean = 17.6 km across all years, see Fig. 6). The averages for all data from all years, and the averages by year and by sub-area, are listed in Table 2. The step lengths from the west site were shorter than those from the east site, with variation observed over the years (Table 4).

Discussion

In this study, a breeding adult female greater spotted eagle was tracked during ten consecutive boreal winters. Although these data are from a single individual, they are unique as no other greater spotted eagle has been followed during so many consecutive winters using a GPS tag. Nor, as far as we know, has any other eagle species, apart from the lesser spotted eagle (Meyburg 2021), been tracked for such a long duration. The data presented in this study provide novel insights regarding the wintering ecology of the greater spotted eagle, providing a theoretical basis for further investigations with larger sample sizes.

Among the “spotted eagles” (i.e., both greater and lesser) that migrate from Europe to Africa via Suez, the proportion which is greater spotted eagle is unknown. However, this proportion is probably larger than that suggested by observations reported from Lebanon, Israel, and Egypt (Meyburg et al. 2020). This is because most

Tab. 4. Results from the most supported model for step length by a female greater spotted eagle during the non-breeding season (boreal winter) during 2005–2014.

Tab. 4. Výsledky najviac podporovaného modelu pre dĺžku kroku samice orla hrubozobého v mimohniezdnom období (boreálna zima) v rokoch 2005-2014.

Predictor variable		Estimate ± SE	95% Confidence Interval
Sub-area:	West	-0.7 ± 0.06	(-0.83, -0.57)
Year:	2006	-0.18 ± 0.11	(-0.4, 0.04)
	2007	-0.52 ± 0.11	(-0.74, -0.3)
	2008	0.02 ± 0.11	(-0.2, 0.23)
	2009	-0.05 ± 0.12	(-0.28, 0.18)
	2010	-0.88 ± 0.12	(-1.11, -0.64)
	2011	-0.5 ± 0.13	(-0.74, -0.25)
	2012	-0.92 ± 0.15	(-1.21, -0.62)
	2013	0.42 ± 0.16	(0.1, 0.73)
	2014	0.69 ± 0.51	(-0.31, 1.69)

Too few data existed to include 2015.

The categorical predictor variable Sub-area: West was in reference to East, and the years were in reference to 2005.

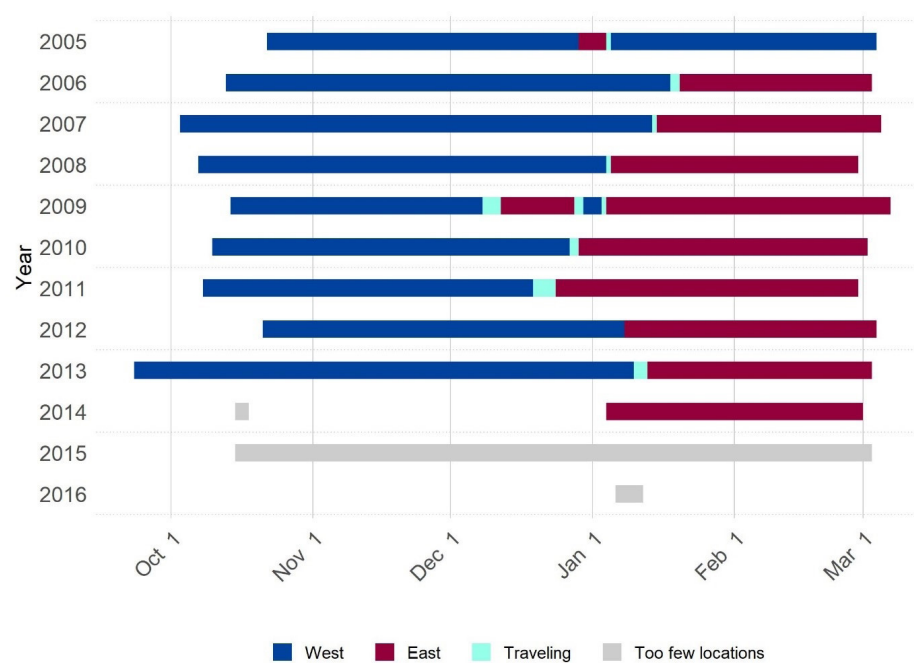


Fig. 3. Temporal use by an adult female greater spotted eagle of western and eastern sub-areas within its wintering grounds in the Sudan-South Sudan borderlands during 2005–2014.
Obr. 3. Časové využívanie západných a východných podoblastí dospelou samičou orla hrubozobého na jeho zimovisku v sudánsko - juhosudánskom pohraničí v rokoch 2005 - 2014.

greater spotted eagles that use this route along the eastern Mediterranean coast may go unrecorded by observers, as they are mistaken for the much more common lesser spotted eagle (Bijlsma 1983). Over 11 days in September–October 2019 only, 8 751 raptors were counted in Lebanon, 80 identified as *C. clanga* and 2 682 as *C. pomarina*. In 42 other cases, it was not possible to determine the species, as these eagles are often difficult to distinguish (Meyburg et al. 2020). Approximately 5% of the spotted eagles that migrated over the Suez in autumn were determined by us to be *C. clanga* (B.-U. Meyburg, unpublished data). Of the seven adult greater spotted eagles we had tracked from Poland, five wintered in Africa, and only two in Greece and Turkey (Meyburg et al. 1998). Dombrovski et al. (2018) tracked eight individuals, four of which wintered in the Nile Valley.

Habitat

Greater spotted eagles winter in Europe, Africa, and southern Asia. However, little is known about the relative importance of these areas to wintering birds. In Europe, greater spotted eagles winter in Spain, France, Italy, and the Balkan Peninsula (Maciorowski et al. 2019; Pérez-García et al. 2014; Meyburg et al. 2020). Further east, this species winters mostly in Turkey (Kirwan et al. 2008), the Middle East and the Arabian Peninsula (Lobley 2007; McGrady et al. 2021), the north of the Indian subcontinent (Naoraji

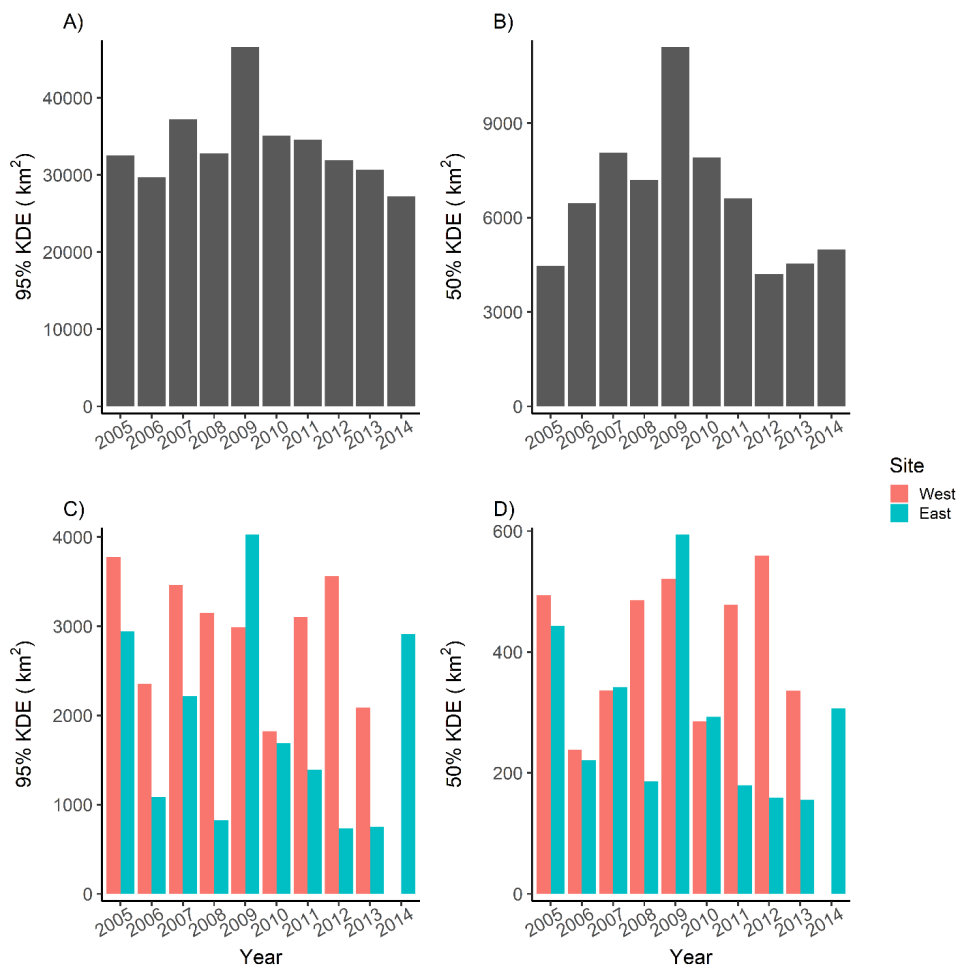
and Schmitt 2007), and Southeast Asia and southern China (Mallalieu 2007; Jeyarajasingam 2012) and exceptionally in Japan and Taiwan (Meyburg et al. 2020).

Each year, the tracked eagle wintered in an area west of the Sudd wetlands, one of the largest wetlands on the planet and a Ramsar site (<https://rsis Ramsar.org/ris/1622>). The eastern sub-area is located in the Bahr al Ghazal drainage basin (a region in the Sudd and the largest of the Nile's sub-basins: 520 000 km²). The Bahr al Ghazal feeds into the White Nile (Bahr al Dschabal). The wetlands are fed seasonally by variable volumes of water flowing from Lake Victoria but are also subject to seasonal rains (Zwarts et al. 2009, Williams 2019). The western sub-area is situated along the Bahr al Arab.

In seven of the nine winters for which we have data, the eagle arrived in the western sub-area, Bahr al Arab, which marks part of the international border between Sudan and South Sudan. In all but one year, it spent the latter part of the winter in the eastern sub-area, from where it also departed in the spring. Unlike the western sub-area, the eastern sub-area has permanently flowing rivers. In the western sub-area, the rivers usually dry up as the dry season (winter) progresses. Thus, desiccation in the western sub-area may have caused the eagle to spend most of the second half of its wintering period in the eastern sub-area, which is a part of the Sudd wetlands. The distribution of plant species in the Sudd depends on

Fig. 4. Sizes of annual non-breeding home ranges (95% and 50% kernel density estimator, KDE) of an adult female greater spotted eagle by year (A and B) and by sub-area (east and west) by year (C and D), during 2005–2014.

Obr. 4. Veľkosti ročných mimohniezdnych domovských okrskov (95% a 50% odhad jadrovej hustoty, KDE) dospelé samice orla hrubozobého podľa rokov (A a B) a podľa podoblastí (východná a západná) podľa rokov (C a D), počas rokov 2005 - 2014.



the water's permanence and depth. Plant diversity and the existence of water result in high numbers and diversity of wild animals (Zwarts et al. 2009). Between November and April, seasonal grasslands are an “extremely favourable habitat for birds” (Howell et al. 1988), including raptors and their potential prey species.

The extensive wintering home range of the tracked eagle

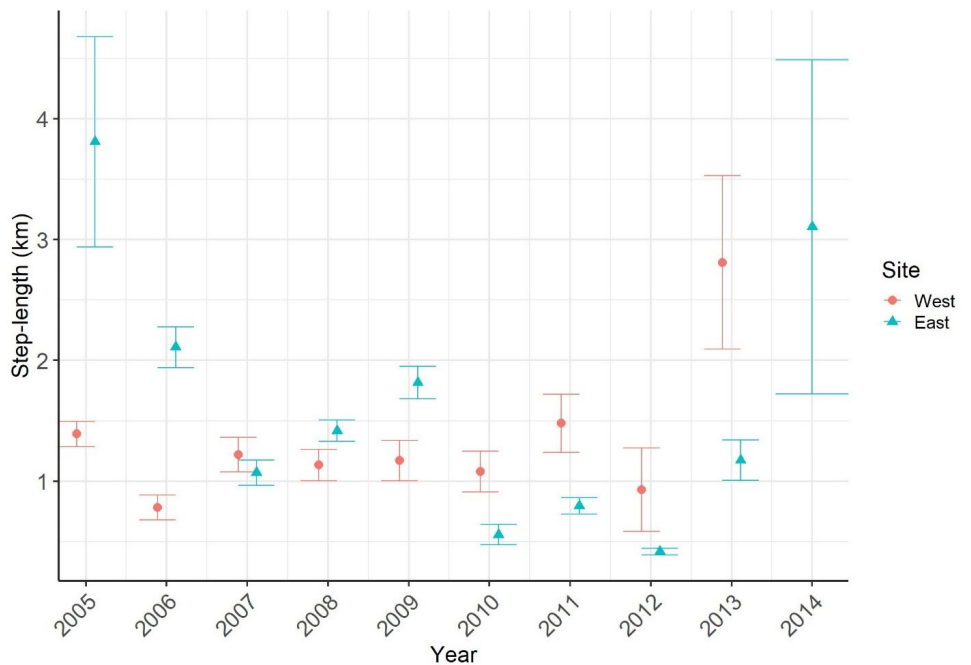
The winter home range of this eagle was larger than that of most other greater spotted eagles that have been tracked (see below). This was mainly due to the distance between the west and east sub-areas; in any given year, each sub-area typically covered <10% of the total winter range (Table 2, Fig. 4). In both sub-areas, the home range size fluctuated between years. The western sub-region in the Sharq Darfur region of Sudan receives less rainfall than the eastern sub-region in South Sudan (M.E.

Elshamy, personal communication). This may explain why the eagle shifted its activity to the east sub-region during the second (drier) half of the wintering season. As with other species (Ferguson-Lees and Christie 2001, Newton 2008), it is likely that the availability of suitable habitat and food affects the winter home range size of the greater spotted eagle. Some areas within the winter home range of the tracked bird may have been inaccessible due to dense vegetation or may have held only low densities of potential prey (Howell et al. 1988; Zwarts et al. 2009), which may have contributed to the large home range size. Moreover, the degree of overlap between years was moderately high, suggesting some degree of concentration in the availability of food resources across years.

We speculate that the tracked eagle moved between sub-areas because of seasonal changes in water availability. This view is bolstered by the eagle's relatively consistent timing of movement from west to east, mostly in January.

Fig. 6. Average hourly step-lengths of an adult female greater spotted eagle on its wintering grounds in Sudan-South Sudan by year and by sub-area.

Obr. 6. Priemerné hodinové dĺžky krokov dospelkej samice orla hrubozobého na jeho zimovisku v Sudáne a Južnom Sudáne podľa rokov a podoblastí.



However, data from other tracked greater spotted eagles suggest that winter-ranging behaviour varies between individuals, even when they winter relatively close to one another. For instance, a male greater spotted eagle that we tracked consecutively using two tags (PTT IDs: 23895 and 60550) spent the winters from 2000 to 2015 in and near the Abyei region (approx. 9.545° N; 28.558° E), which is situated between the two sub-areas used by our tracked female. In contrast to the female, the range of the male bird was not bipartite, and the home range was commensurately smaller. However, the tracking results of the two eagles are not directly comparable for the following reasons: the male was tracked using less precise Doppler tracking technology, and the tracking was not continuous for the entire period of 2000–2015 (B.-U. Meyburg and Maciorowski, unpublished data).

The size of the Sudd is highly variable throughout the year. During the wet season (April–October), it may extend to over 130 000 km², comprising 13% of the total area of South Sudan. Flood levels and areas of inundation (i.e., the extent of the wetlands) depend mostly on discharge from equatorial lakes and Lake Victoria, which peak in late summer and early autumn. At this time, the Sudd is at its largest. As winter progresses, the western areas dry out. This can affect food availability and may have forced the tracked eagle to move eastwards and closer to the main river (i.e., the White Nile, Bahr al Jabel), where the landscape was still flooded (M.E.

Elshamy, personal communication). However, in specific years, the eagle moved more than once between the sub-areas, suggesting a scenario more complicated than seasonal drying from the west. Furthermore, the ca 330 km move between the western and eastern sub-areas was accomplished in a brief period, which could suggest that the food availability or habitat conditions along the transit route were not ideal, although the male mentioned above also wintered in the area between the two sub-areas.

Previous telemetry studies

Despite its rarity, the greater spotted eagle was among the earliest raptor species tracked via satellite telemetry (Meyburg et al. 1995; Meyburg and Meyburg 2005). Despite this long history of tracking, we are aware of only a few publications that use telemetry data to provide information on the home ranges and movements of this species in wintering areas. In October 1993, a greater spotted eagle of unknown gender was caught in western Saudi Arabia and fitted with a transmitter. It then moved south into Yemen, where it remained from 28 November 1993 to 2 February 1994, approximately 104 km east of Sana. Its home range covers approximately 50 km² (Meyburg et al. 1995). Meanwhile, an Estonian-reared, male greater spotted eagle tracked during the first four years of its life exploited a small area (12.7 km², 95% KDE) in Spain during winter and showed high inter-annual fidelity to the wintering area (Pérez-García et al.

2014). Another study reported that the ranges of a non-adult greater spotted eagle in southwestern Yemen during three consecutive winters overlapped considerably. In that case, the range size estimates averaged 47.5 ± 5.3 km² for the 50% KDE, and $1\,658 \pm 357$ km² for the 95% isopleth KDE (McGrady et al. 2021). Dombrovski et al. (2018) tracked eight *C. clanga*, four of which wintered in the Nile Valley. Moreover, Maciorowski et al. (2019) collected data from nine eagles (one adult and eight juveniles) during one entire wintering period in southern Europe and reported home ranges of $6.7\text{--}1\,522$ km² (mean 89.7 km²). Five juveniles were tracked by Mischenko et al. (2022) for 14 months, of which one eagle wintered on the southern border of Sudan with South Sudan on the White Nile. However, no information was provided regarding their home range size.

Fidelity to the wintering area

The bird tracked in this study joins the ranks of other adult eagles that show longstanding fidelity to their wintering site. Since 1995, we have tagged adult greater spotted eagles and hybrids (*C. clanga* × *pomarina*) in North-East Poland using Argos-Doppler tracking transmitters (PTTs). The female reported herein was the first to be fitted with a GPS device. All six *Clanga clanga* tagged since 1995—for which we could identify the wintering grounds in at least two years—showed inter-annual fidelity to their respective wintering grounds (B.-U. Meyburg, unpublished data).

To our knowledge, the 15 consecutive winter use of the same area on the Göksu River Delta in Turkey (1999 – 2014; 36.296°N; 33.979°E) by an adult female is the longest record of greater spotted eagle fidelity to its wintering area. That bird was tracked (using two different devices, IDs: 08138 and 003), and visually observed, photographed and filmed on the wintering grounds (B.-U. Meyburg and Maciorowski, unpublished data). Moreover, a male greater spotted eagle that we had tracked using two tags consecutively (IDs: 23895 and 60550) spent an equally long time during 2000–2015 on its wintering grounds in and near the Abyei region (9.545° N; 28.558° E) in the Sudan/ South Sudan border area (B.-U. Meyburg and Maciorowski, unpublished data).

As with many species, the wintering ecology of the greater spotted eagle has not been studied in detail. This knowledge gap undermines conservation efforts, as does a similar lack of detailed information regarding its migration across its wide range. Thus, addressing these gaps is essential, and requires further studies, including data from more individuals.

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Received: 5.10.2022

Accepted: 25.6.2023