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Revealing unexpected uses of space by wintering *Aquila pomarina*: how does satellite telemetry identify behaviour at different scales?

Bernd-Ulrich Meyburg, Stephie Mendelsohn, John Mendelsohn and Helen Margret de Klerk

B.-U. Meyburg, World Working Group on Birds of Prey, PO Box 33 04 51, DE-14199 Berlin, Germany. – S. Mendelsohn and H. M. de Klerk (hdeklerk@sun.ac.za), Stellenbosch Univ., Geography and Environmental Studies, Stellenbosch, Western Cape, South Africa. – J. Mendelsohn, Research and Information Services of Namibia (RAISON), Windhoek, Namibia.

Little is understood about the dispersion and movements of Palaearctic migrant raptors while wintering in southern Africa. The high temporal and spatial resolution of GPS telemetry data provided the opportunity to describe how space is used by one such migratory raptor in its wintering range, the lesser spotted eagle *Aquila pomarina*. Kernel density estimation was used to map the distribution of three individuals at various spatial scales. In addition to their extremely large overall wintering range (up to 112 000 km^2), three finer levels of spatial concentration were identified: favoured activity zones where the birds spent much of the winter, smaller core areas to which the birds returned each year, and tiny intensive foraging clusters. Philopatry was demonstrated by one bird which revisited core areas over eight wintering seasons. The same core areas, particularly the Waterberg, Grootfontein (Namibia) and the eastern and western sides of the Okavango Delta (Botswana), were visited by two other eagles in 2012/2013, although not simultaneously. Such results potentially provide important information on areas where conservation activities might be focused to mitigate human degradation of habitat.

Dozens of species and millions of individual Palaearctic migrant birds are thought to wander over large ranges in pursuit of ephemeral food resources during their non-breeding visits to the southern hemisphere (Jones 1998, Dean 2004, Newton 2008). Many wintering strategies exist where traits such as mobility and philopatry vary according to species, population and environmental conditions
[AQ1] (Liminana et al. 2012a, Trierweiler et al. 2013). Irregular, long distance movements are particularly prevalent in semi-arid heterogeneous environments where food supplies are usually available on a spatially and temporally variable basis determined by variable rainfall (Jensen 1972, Jones 1998, Dean 2004, Meyburg et al. 2010). The lesser spotted eagle *Aquila pomarina* is one Palaeractic migrant which travels to forage in warmer African climates during the northern hemisphere winter. Much is known about the behaviour of these birds on their European breeding grounds (Meyburg 1973) and about their migratory routes, over both the Strait of Gibraltar, the eastern Mediterranean corridor (Onrubia et al. 2011) and over the Suez Channel and through eastern Africa (Meyburg et al. 1995, 2000, 2004). However, little is understood about how they spend their time while wintering in southern and eastern Africa (Meyburg et al. 2000, 2001, 2004, 2010, Kemp 2001). In particular, information on space utilisation by *A. pomarina* during their wintering visits has been limited to sporadic field observations, most notably of groups of birds arriving in localised places to feed opportunistically on emerging termite alates, young birds in breeding colonies and young frogs (Jensen 1972, Kemp 2001, Meyburg et al. 2010).

This paper reports on the use of satellite telemetry to gather information and develop an understanding of how individual lesser spotted eagles use space in their wintering habitat. Most current satellite transmitters, called Platform Terminal Transmitters (PTTs), use solar power and Global Positioning Systems (GPS) to record position fixes, altitude, speed and flight direction which are transmitted through the Argos Satellite system (Meyburg and Fuller 2007) and most recently Global System for Mobile Communications (GSM) enhanced transmitters (Meyburg and Meyburg 2013). Modern solar-powered PTTs are small and light enough to be used on medium-sized raptors (Meyburg and Meyburg 2009, 2013) and may generate tracking data over more than ten years. Spatial analyses of these data in geographical information systems can provide a detailed picture of the size, extent and temporal variation of summering and wintering ranges (Phipps et al. 2013).

Identifying safe wintering habitat for nomadic migrants has always posed a problem for conservation managers
(Newton 2008, Liminana et al. 2012a). So spatially explicit [AQ1]
information about where lesser spotted eagles move and concentrate their time during the non-breeding period can help to target conservation efforts to provide safe wintering habitat for this and other Palearctic migrants.

Material and methods

Study area

The study area covered the preferred wintering range of three adult *A. pomarina* individuals that were tracked using satellite telemetry (Fig. 1). These wintering ranges stretch across a belt of semi-arid savannah-woodland from northern Botswana and Namibia and into southern Angola (Gerkmann and Meyburg 2009, Meyburg et al. 2010).

Telemetry data

Tracking data from solar-powered GPS-enhanced PTTs (PTT no. 41861, 52030 and 52027) on the three eagles were received through the Argos satellite-based positioning system and decoded using Microwave Telemetry GPS Data Parser. The three transmitters provided several thousand fixes, each of which included a GPS location (only those fixes with an accuracy of 15 m or better were used), flight speed, and direction of movement, altitude above sea level and the date and time of the fix. Fixes were usually recorded each hour from 05:00 to 20:00 GMT + 2. Data were available for one bird (PTT no. 41861) for eight wintering phases from 2004/2005 to 2012/2013, while data from two other birds (PTT no. 52030 and 52027) were available for the 2012/2013 wintering phase.

The number of functional fixes recorded per year and per bird varied considerably (Table 1). As PTTs aged, increasing numbers of fixes become inaccurate and were discarded as battery life diminished. Within the 2004/2005 to 2012/2013 dataset for PTT no. 41861, the 2005/2006 wintering phase (November 2005 to January 2006) contained unusually few fixes due to low battery voltage during much of the season and was consequently excluded from the analysis. Low battery voltage can occasionally be a limiting factor for solar powered PTTs if incoming sunlight is low due to cloud coverage or if the solar panels are covered by feathers when the bird is little on the wing. In some instances whole days passed without a single accurate fix for these data. Data points with a 'low volt' label were deleted from the data set.

Analyses

To assess space use, locations were mapped at four different scales: a) the wintering range, which describes 95% of all data points (Gallerani Lawson and Rodgers 1997, Brothers et al. 1998), b) favoured activity zones (80% of points) where the birds spent much of their time, c) core areas (50% of points) where activity was extremely concentrated and which were visited repeatedly, both in the same and in different winters, and d) localised, possible intensive foraging clusters.

Kernel density estimation (KDE) was used to map the utilization distribution at the four levels. KDE is a geographic interpolation method that creates a probability surface from input locations. This contour-based method is often used for mapping home ranges and by design evaluates utilization distribution by generating high density centres based on the arrangement of points (Bowman 1985, Worton 1989, Hemson et al. 2005, Getz et al. 2007). The principle of kernel estimation is that a density estimate is evaluated from the input point dataset for each grid intersection across an area. The estimate is calculated by the kernel function that defines which locations from the input data are included and how they are weighted. The frequently used bivariate normal kernel method weights locations according to a bivariate Gaussian distribution that has its maximum at

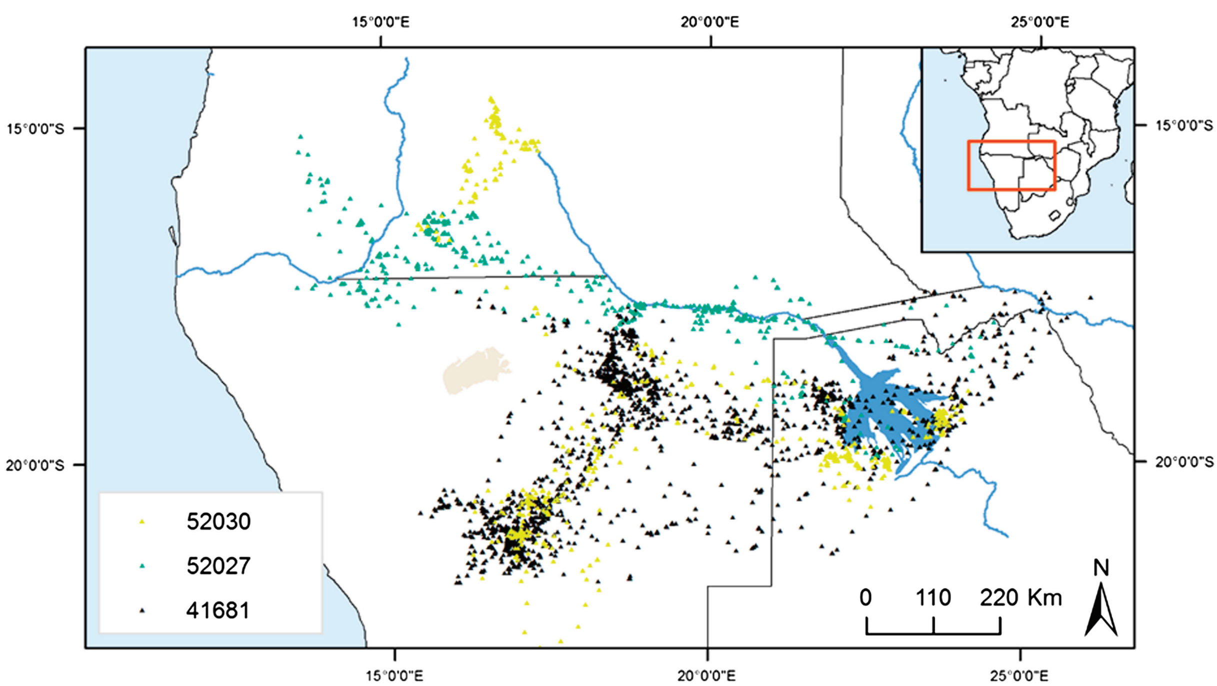

Figure 1. Distribution of lesser spotted eagle locational fixes for 41861 over eight wintering phases, from 2004/2005 to 2012/2013 (excluding 2005/2006), and for 52027 and 52030 over their wintering ranges in 2012/2013. The Okavango Delta and major perennial rivers are visible in blue and the Etosha Pan in Namibia in brown.

Table 1. Range estimates and utilization distribution from kernel estimation for different wintering phases for each lesser spotted eagle.

PTT no.	Wintering phase	PTT fixes	Entry into wintering range	Departure from wintering range	Wintering range (95%) (km^2)	Favoured activity zones (% of wintering range)	Core area (% of wintering range)
41861	2004–2005	1037	2/12/2004	22/1/2005	42 139		
	2006–2007	904	1/12/2006	9/2/2007	50 272		
	2007–2008	495	23/11/2007	29/1/2008	28 580		
	2008–2009	1029	24/11/2008	13/2/2009	56 059		
	2009–2010	707	30/11/2009	8/2/2010	40 568		
	2010–2011	632	23/11/2010	29/1/2011	47 332		
	2011–2012	456	22/12/2011	14/2/2012	49 863		
	2012–2013	395	17/12/2012	10/2/2013	31 194		
	2004–2013	5654			112 170	42.9%	14.3%
52030	2012–2013	2068	30/10/2012	28/2/2013	59 586	38.1%	10.9%
52027	2012–2013	1254	21/11/2012	31/1/2013	67 755	41.0%	12.5%

the grid point being processed, such that nearer points are weighted more heavily (Wood et al. 2000).

Positional fixes in the cleaned dataset were overlaid on a one square kilometre grid, which was selected to achieve a balance between spatial resolution and computer processing time. A one kilometre grid over the wintering ground (approximately 500 × 1000 km in most wintering phases) resulted in the processing of 50 000 grid cell intersections. A 5 km bandwidth was chosen. The resulting probability surface showed the weighted frequency of fixes within a five kilometre radius. A density of one at any point on the resulting raster means that one per cent of locations were observed within a five kilometre radius of that point, allowing results from different years and individuals to be compared.

Firstly, a KDE was used calculated on all cleaned positional fixes to map the utilization distribution showing **[AQ1]** the wintering range (95% contour sensu Liminana 2012a, b), favoured activity zones (80% contour) and core area **[AQ2]** (50% contour sensu Trierweiller et al. 2013) for each bird.

Secondly, in order to map small, localized clusters where the eagles probably foraged, locations were further filtered to include only points between 06:00 and 18:00 GMT + 2 as this is when these eagles are most likely to feed. Locations were also excluded if they were more likely to have been at roosting than feeding sites, for example when two or three locations were recorded immediately after dawn and just before the eagle moved elsewhere. A KDE was calculated on these points using a cell size of 50 m and search radius of 250 m. A total of 619 areas with a density of two or more points per square kilometre were thus identified as probable intensive foraging clusters.

To understand how time was spent in intensive foraging clusters, points inside clusters were classified as perched or flying based on the recorded instantaneous flight speeds, (rather than time over distance between successive locations) (sensu Safi et al. 2013). Locations with instantaneous flight speeds of less than 10km/hour were defined as perched and those of greater than 10 km h^{-1} as flying.

Results and discussion

Timing of movements

The eagles usually arrived in their wintering range in the belt of semi-arid savannah-woodland in November, with 30 October being the earliest arrival recorded (Table 1). The timing of their arrival in southern Africa coincided with the southward shift of the Intertropical Convergence Zone (ITCZ) and consequent onset of warm tropical rains and ephemeral food resources (Jones 1998, Simmons et al. 1999, Gerkmann and Meyburg 2009).

The birds then spent an average of 100 d (maximum of 120 d in 2013 by bird 52030) in their wintering range before departing north, usually in the last week of January or the first fortnight of February (latest departure was on 28 February, Table 1).

For bird 41681, seven of its eight wintering phases began with an entry into its wintering range east of the Okavango Delta, where the eagle spent variable lengths (one or two days in some years but up to a 11 consecutive days [10 to 21 December, 2004/2005] – and a month intermittently [30 November to 26 December, 2007/2008]) before moving westwards into Namibia (Fig. 2a). This is probably due to the fact that the warm tropical rain generated by the ITCZ starts in the east and usually only reaches Namibia in the west of the study area slightly later in the wintering season. In 2013, one other bird (52027, Fig. 2b) also spent several days around the delta immediately after its southward migration. Close inspection of the places visited by the eagles suggested that they did not forage in and around the delta's permanent swamps. However, dry alluvial sediments around the delta are relatively nutrient-rich (Mendelsohn et al. 2010) and the eagles may have been attracted to food sources associated with these more productive soils.

Utilization distribution

The satellite telemetry positional data in Fig. 1 show the distribution of locations of the three individuals during the wintering phase. The average size of the wintering range of bird 41861 was 43 250 km^2 over eight winter sojourns, but the range varied between 28 580 km^2 in 2007/2008 and 56 059 km^2 in 2008/2009, the smallest ranges being in those years when relatively few locations were recorded (Table 1). The total wintering range, calculated from all positional data from 2004 to 2013, was estimated to be 112 170 (Table 1) for 41861. The wintering ranges of the other two eagles covered 59 586 (Table 1 for bird 52023) and 67 755 km^2 (Table 1 for bird 52027) in the single winter they were tracked.

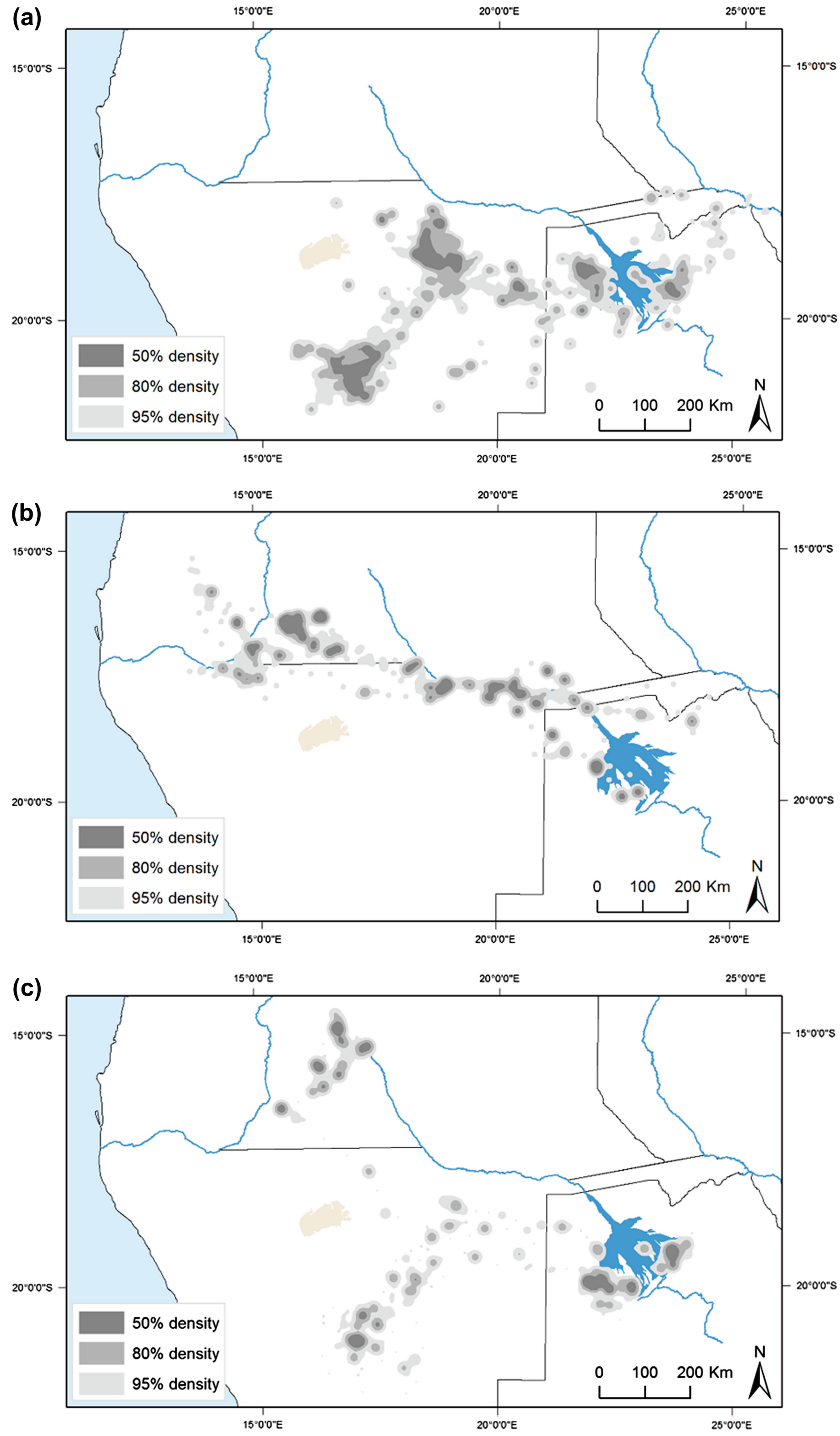

Figure 2. Kernel density estimation surfaces for lesser spotted eagles using 5 km bandwidth and 95% (pale grey), 80% (medium grey) and 50% (dark grey) contours for (a) 41861 over eight wintering phases, from 2004/2005 to 2012/2013 (excluding 2005/2006), (b) 52027 and (c) 52030 over the wintering range 2012/2013. The Okavango Delta and perennial rivers are visible in blue and the Etosha in Namibia in brown.

Table 2. The number of PTT fixes for lesser spotted eagle 41861 per wintering phase for each of the core areas (50% contour). Of particular note are sites 9, 11, 12, 13 and 14 at Tsumkwe Pans, Okavango Delta East, Okavango Delta West, Grootfontien and Waterberg, respectively (shown on the map in Fig. 3).

50% site ID	Area (km)	Number of PTT fixes per wintering phase 2004/2005	2006/2007	2007/2008	2008/2009	2009/2010	2010/2011	2011/2012	2012/2013	Total	No. of visits
1	14						2			2	1
2	40	34								34	1
3	76								39	39	1
4	143						50			50	1
5	37			19	15					34	2
6	49				14			17		31	2
7	58	37				30				67	2
8	217	2			2			22	1	27	4
9	490	25	30		49				1	105	4
10	476	1	61			30	13	7		112	5
11	757	33		77	16	19	18		2	165	6
12	1268	105	37	41	63	2		15	17	280	7
13	4666	208	181	123	264	101	78	29	61	1045	8
14	5663	150	184	92	267	299	198	159	126	1475	8

KDE contour plots represent both the number of locations and the proximity of locations in an area. Areas where the largest concentrations of locations occurred show portions of the wintering range that exceeded an equal-use pattern and may be due to frequent visits by the eagles or localised aggregations of locations when the eagle remains within a limited area for some time (Fig. 2).

The use of the landscape within the wintering ranges was extremely uneven. Between 38.1 and 42.9% of each eagle's wintering range fell within the contours that encompassed 80% of activity, or favoured activity zones, while between 10.9 and 14.3% of each wintering range fell within the 50% KDE contour, or core areas (Table 2). Half of the eagles' activity thus occurred within just over 10% of their ranges, and large areas in the wintering range were unused or only traversed to reach favoured activity zones and core areas. Some favoured activity zones were visited intensively by 41861 in only one of the eight wintering phases (Fig. 2).

Core areas contained many locations from different wintering periods and were thus used repeatedly by bird 41861. Six core areas were identified as being used by 46181 in different years, and four of the core areas were also used by the other two birds (52027 and 52023) during the single winter they were tracked. Core areas made up 35.5% (39 837 km^2) of the total wintering range of 41861 and overlapped 82.9% of the favoured activity zones of this bird.

Bird 41861 returned to core areas around Grootfontein and Waterberg (sites 13 and 14 in Fig. 3) most frequently in the eight wintering seasons, but it spent little time in the space separating the two core areas. In most years, the largest portion of the wintering phase was spent in the Waterberg area. The eastern and western sides of the Okavango Delta (sites 11 and 12, Fig. 3) were visited in six and seven of the wintering phases, respectively (Table 2) and all of these visits occurred at the beginning of the wintering phase.

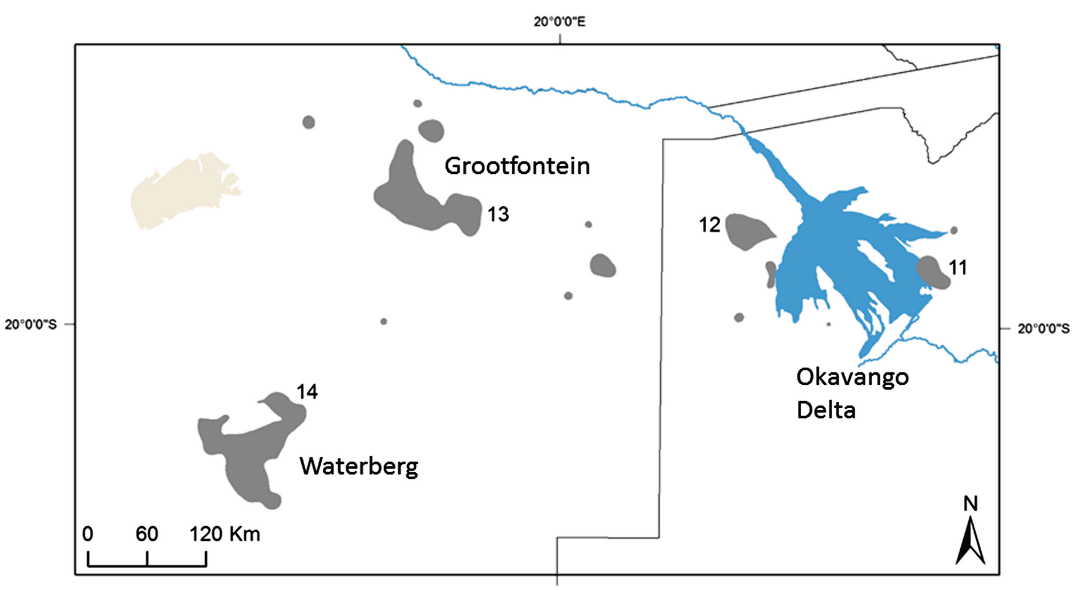

Figure 3. Core areas of concentrated activity for 41861 over eight wintering phases for lesser spotted eagle, with the most frequently visited sites, highlighted namely Tsumkwe (9), Okavango Delta East (11), Okavango Delta West (12), Grootfontein (13) and Waterberg (14).

Table 3. Diagrammatic portrayals of periods when bird 41861 concentrated its activity in four main favoured activity zones (80% kernel areas) around the four numbered core areas shown in Fig. 3. The table should be read from right to left to follow directions of movement from zone 11 in the east, west to zone 12 and then zones 13 and 14. Dates on which the bird entered and the number of days spent in each zone are shown. The bird was elsewhere at times falling outside those entry dates and periods of days. The total number of days spent in each zone are shown in the last line of the table.

Wintering	Zone 14		Zone 13		Zone 12		Zone 11	
Phase	entry	days	entry	days	entry	days	entry	days
2004/2005							03-Dec	5
					09-Dec	13		
			29-Dec	3				
	01-Jan	12						
	17-Jan	14						
			30-Jan	16				
			17-Feb	0.5				
					21-Feb	0.5		
2006/2007					05-Dec	6		
			11-Dec	9				
	21-Dec	12						
			02-Jan	16				
	27-Jan	9						
					07-Feb	1		
2007/2008							25-Nov	15
					(includes 12 d when transmitter failed)			
					23-Dec	7		
			31-Dec	15				
	17-Jan	8						
			26-Jan	4				
2008/2009							24-Nov	4
					28-Nov	1		
							06-Dec	2
					08-Dec	0.5		
							08-Dec	0.5
					09-Dec	5		
	14-Dec	6						
			22-Dec	19				
	12-Jan	1						
			13-Jan	0.5				
	13-Jan	0.5						
			14-Jan	5				
	19-Jan	21						
					10-Feb	2		
2009–2010							30-Nov	4
					04-Dec	1		
			05-Dec	17				
	22-Dec	39						
			31-Jan	4				
2010–2011							28-Nov	2
	01-Dec	5						
			06-Dec	3				
			17-Dec	14				
	01-Jan	18						
							27-Jan	2
							22-Dec	2
					26-Dec	4		
			31-Dec	1				
	01-Jan	2						
			03-Jan	12				
	14-Jan	23						
2012–2013							17-Dec	1
					21-Dec	3		
			25-Dec	3				
	28-Dec	12						
	14-Jan	6						
			22-Jan	9				
Total days		**188.5**		**151**		**44**		**37.5**

Movements by one individual over eight wintering phases

For bird 41861, seven of its eight wintering phases began with an entry into its wintering range east of the Okavango Delta, where the eagle generally spent short periods of time (Table 3) before moving westwards into Namibia as shown in Fig. 4a and b which provide examples of how the bird moved between favoured activity zones during two seasons.

Bird 41861 spent varying lengths of time in different favoured activity zones during seven wintering phases (Table 3). The longest periods were spent in the Grootfontein and Waterberg areas, while shorter visits were made to the two areas in the east (Table 3). In 2004–2005 bird 41861 made relatively few trips between favoured activity zones and its movement from east to west and rotation between zones was similar to that recorded in most other years (Fig. 2a and Table 3). By contrast, many more trips between Grootfontein and Waterberg were made in 2008–2009 (Fig. 2b and Table 3), suggesting that resource availability in these areas varied between wintering phases.

It is likely that movement between areas was either driven by a lack of resources in the area from which the bird moved or by food becoming available in an area to which the bird moved. Many ornithologists have speculated that *A. pomarina* capitalizes on the emergence of ephemeral food sources by following rain fronts (Jensen 1972, Simmons 1997, Simmons et al. 1999, Meyburg et al. 2004, Gerkmann and Meyburg 2009).

Fine-scaled space utilization

Intensive foraging clusters provided information on how space was used on a fine scale, and how much foraging probably occurred at localised, short-lived food sources. Of all locations recorded for each eagle between 06:00 and 18:00, 58.9, 61.2 and 52.1% respectively were inside Intensive foraging clusters (Table 4). Since the locations were limited to daylight hours, it is probable that the birds were therefore at sources of food for half or more of each day on average. Other co-ordinates outside the clusters made up

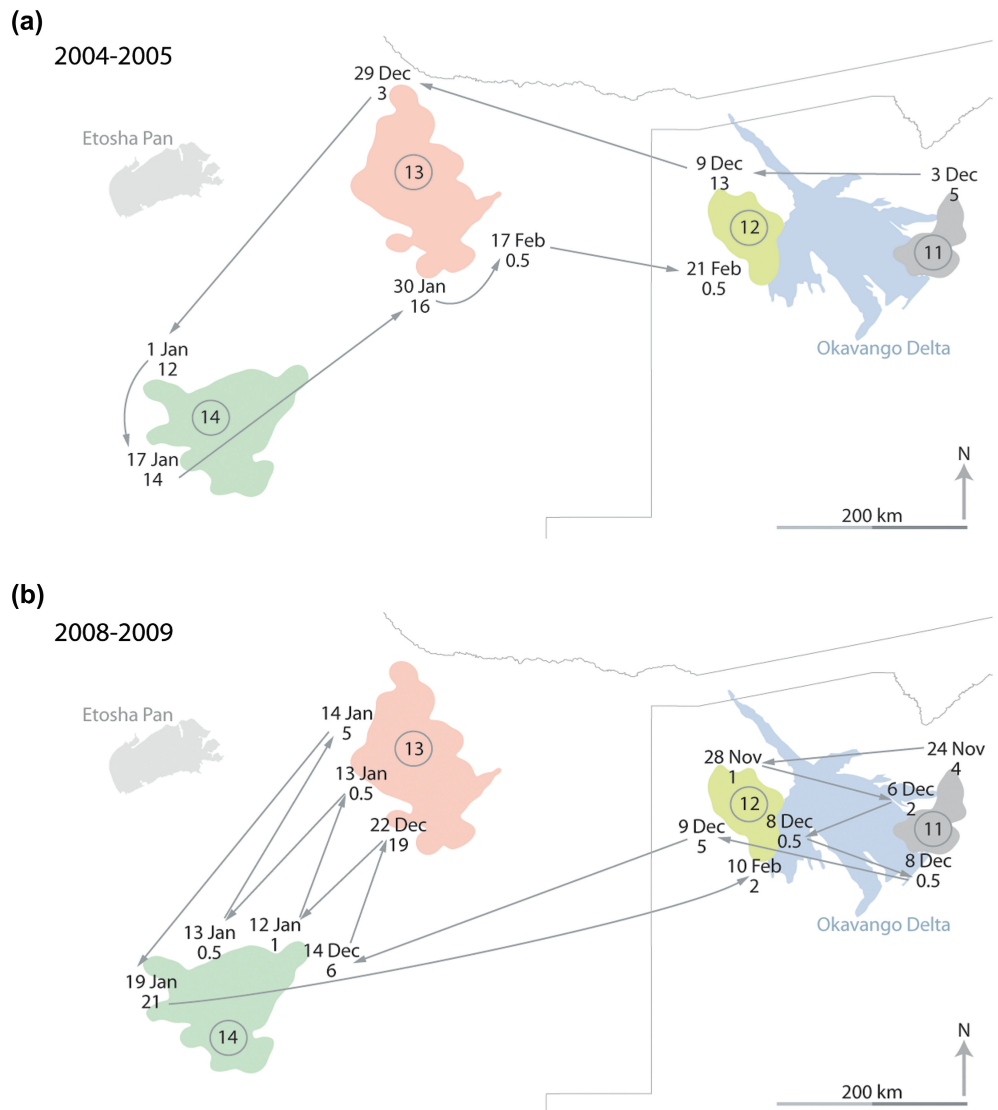

Figure 4. Periods when bird 41861 concentrated its activity in the four main favored activity zones (80% kernel areas) around the four core zones 11–14 (Fig. 2a) in 2005–2005 (a) and 2008–2009 (b). Dates on which the bird entered and the number of days spent in each zone are shown. The bird was elsewhere at times falling outside those entry dates and periods of days.

Table 4. Numbers and percentage of locations recorded for lesser spotted eagles during daylight hours; inside and outside intensive foraging clusters; and flying inside and outside intensive foraging clusters. Locations were treated as ‘flying’ when the GPS speed was recorded as 10 km h–1 or higher.

	PTT 52030		PTT 52037		PTT 41861	
	No.	%	No.	%	No.	%
Total points	1257		777		3807	
Number clusters	119		79		421	
Inside clusters	769	61.2	405	52.1	2241	58.9
Outside clusters	488	38.8	372	47.9	1566	41.1
Flying inside clusters	15	2.0	6	1.5	21	0.9
Flying outside clusters	325	66.6	308	82.8	781	49.9

between 38.8 and 47.9% of all locations (Table 4), and the eagles then apparently spent much of their time moving since 49.8 to 66.6% of locations were recorded outside of clusters with where classified as flying. By contrast, only 0.9 and 2.0% of the locations inside clusters had flight speeds of more than 10 km h–1 indicating that the birds were normally perched while inside clusters (Table 4).

While the longest a bird remained in a cluster was about six days, the eagles normally spent only several hours in a cluster before moving on. Clusters were also seldom visited more than once. For example, of the 421 clusters identified for eagle 41861 over its eight wintering seasons, only 15 (3.5%) were visited more than once in the same or subsequent seasons.

Eagle 41861 probably visited substantially more clusters during those eight seasons than recorded since its PTT did not function all the time (Table 1). Thus, 80, 62 and 68 clusters were identified in the three seasons in which more than 600 locations were recorded between 06:00 and 18:00, but only 34, 37, 40, 45 and 54 clusters in the five seasons when far fewer locations were received (Table 1). Eagle 52030 visited 119 clusters during 2012–2013 when 1257 day-time locations were logged, while 79 clusters were identified for eagle 52027 when 777 co-ordinates were recorded during the day in its 2012–2013 wintering season. The average number of clusters visited per season was 82 based on the number of clusters for these two eagles and those identified in the three seasons when more than 900 locations were recorded for eagle 41861.

Figure 5 gives an example of how one eagle moved around between clusters over a period of 18 consecutive days. Twenty-two clusters were visited during this period, the maximum being three clusters in a day. On one day the bird did not settle in a cluster. The eagle flew at least 3400 km during these 18 d, as measured along direct lines between successive GPS locations.

Activity in the clusters was focussed on extremely small areas since locations within each cluster were usually close to each other. For example, the average nearest neighbour distance between points for 41861 within clusters was 18.4 m, fractionally more than the maximum resolution of 15 m of the GPS co-ordinates. We suggest that movements

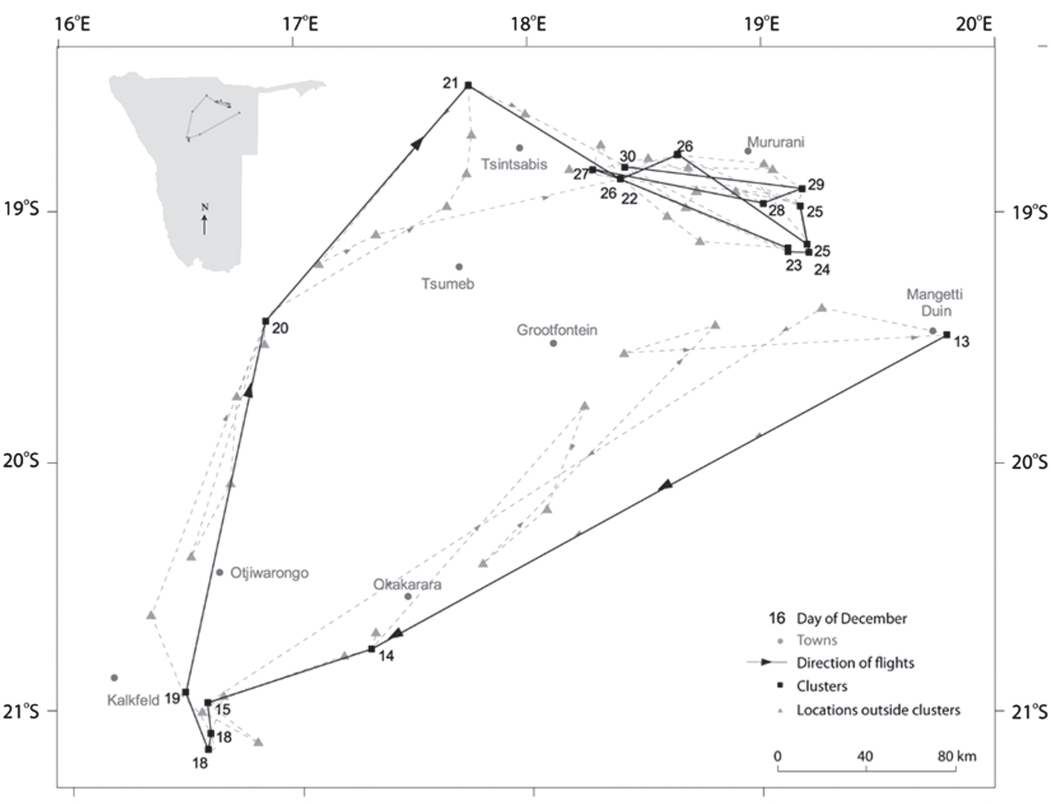

Figure 5. Movements by eagle 41861 between 13 and 30 December 2008 in central northern Namibia (see inset). Numbers are the day of the month and the arrows show directions from one cluster and the next. The bird however seldom flew directly from one cluster to another, and often wandered over other areas. Locations where the bird were recorded on such wandering flights outside the clusters are shown as triangles.

to these highly localised clusters are eagles following short-lived ephemeral food source emergences such as termite emergences (typically lasting a few hours) or tadpole and froglet emergences at ephemeral wetlands (typically for a few days or weeks) (J. Mendelsohn unpubl.).

Conclusions

To our knowledge, this is the first study to have demonstrated that the lesser spotted eagle, a presumed nomadic migrant concentrates and rotates its time and foraging activity in certain core areas. The return of bird 41861 to core areas during different winters further suggests that the use of particular selected areas is a strong trait and indicated philopatry of this bird in its wintering range.

Newton (2008) discusses the need for accurate knowledge of areas used by wintering migrants for conservation action. In the western Sahel migratory raptors face pressures from land use change and their populations have declined severely in recent years (Thiollay 2006). Land uses are changing in Namibia and Botswana where indirect, or non-target, poisoning may be a further threat to lesser spotted eagles, for example when locusts and quelea colonies are sprayed.

The core areas used by lesser spotted eagles may have particular conservation value, and follow up work should investigate how many of these eagles and other species and individuals make use of the areas. More information on the pattern and timing of use of core areas could also help further planning. The same is true for information on the use of flight paths, such as that used by 41861 in arriving each year near the Okavango Delta.

The dispersion of clusters and behaviour of the eagles suggest that the very small intensive foraging clusters may have provided ephemeral sources of food, most likely of short-lived emergences of termites. This result is supported by field observations of birds congregating at ephemeral sources of concentrated prey (Jensen 1972, Simmons et al. 1999, Kemp 2001, Meyburg et al. 2010, unpubl.). The average of 82 clusters identified each year probably provides an indication of the number of separate ephemeral food sources found and used by individual lesser spotted eagles during the wintering sojourns in southern Africa.

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References

Bowman, A. W. 1985. A comparative study of some kernel-based nonparametric density estimators. – J. Stat. Comp. Sim. 21: 313–327.
Brothers, N., Gales, R., Hedd, A. and Robertson, G. 1998. Foraging movements of the Shy Albatross *Diomedea cauta* breeding in Australia; implications for interactions with longline fisheries. – Ibis 140: 446–457.
Dean, W. R. J. 2004. Nomadic desert birds. – Springer.
Gallerani Lawson, E. J. and Rodgers, A. R. 1997. Differences in home-range size computed by commonly used software programs. – Wildl. Soc. Bull. 25: 721–729.
Gerkmann, B. and Meyburg, B. 2009. Habitats used by lesser spotted eagles (*Aquila pomarina*) during migration and wintering as revealed by Satellite tracking and remote sensing. – Populationsökol. Greifvogel Eulenarten 6: 87–102.
Getz, W. M., Fortmann-roe, S., Cross, P. C., Lyons, A. J., Ryan, S. J. and Wilmers, C. C. 2007. LoCoH: nonparameteric Kernel methods for constructing home ranges and utilization distributions. – PLoS One 2: e207.
Hemson, G., Johnson, P., South, A., Kenward, R., Ripley, R. and Macdonald, D. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home- range analyses with least-squares cross-validation. – J. Anim. Ecol. 74: 455–463.
Jensen, R. A. C. 1972. The steppe eagle *Aquila nipalensis* and other termite-eating raptors in south west Africa. – Madoqua 1: 73–76.
Jones, P. 1998. Community dynamics of arboreal insectivorous birds in African savannas in relation to seasonal rainfall patterns and habitat change. – In: Newberry, D. M., Prins, H. H. T. and Brown, N. D. (eds), Dynamics of tropical communities. Cambridge Univ. Press, pp. 421–477.
Kemp, A. 2001. Concentration of non-breeding lesser spotted eagles *Aquila pomarina* at abundant food: a breeding colony of red-billed quelea, *Quelea quelea*, in the Kruger National Park, South Africa. – Acta Ornithoecol. 4: 325–329.
Liminana, R., Romero, M., Mellone, U and Urios, V. 2012. Mapping the migratory routes and wintering areas of lesser kestrels *Falco naumanni*: new insights from satellite telemetry. – Ibis 154: 389–399.
Liminana, R., Soutullo, A., Arroyo, B. and Urios, V. 2012b. Protected areas do not fulfil the wintering habitat needs of the trans-Saharan migratory Montagu's harrier. – Biol. Conserv. 145: 62–69.
Mendelsohn, J. M., vanderPost, C., Ramberg, L., Murray-Hudson, M., Wolski, P. and Mosepele, K. 2010. Okavango Delta: floods of life. – RAISON, Namibia.
Meyburg, B.-U. 1973. Studies of less familiar birds 172 lesser spotted eagle. – Br. Birds 66: 439–447.
Meyburg, B.-U. and Fuller, M. R. 2007. Satellite tracking. – In: Bird, D. M. and Bildstein, K. L. (eds), Raptor research and management techniques. Hancock House Publishers, pp. 242–248.
Meyburg, B.-U. and Meyburg, C. 2009. Wanderung mit Rucksack: Satellitentelemetrie bei Vögeln. – Falke 56: 256–263.
Meyburg, B.-U. and Meyburg, C. 2013. Telemetrie in der Greifvogelforschung. – Greifvögel Falknerei 2013: 26–60.
Meyburg, B.-U., Scheller, W. and Meyburg, C. 1995. Zug und Überwinterung des Schreiadlers aquila pomarina: Satellitentelemetrische Untersuchungen. – J. Ornithol. 136: 401–402.
Meyburg, B.-U., Schelle, W. and Meyburg, C. 2000. Migration and wintering of the lesser spotted eagle *Aquila pomarina*: a study by means of satellite telemetry. – Global Environ. Res. 4: 183–193.
Meyburg, B.-U., Ellis, D. H., Meyburg, C., Mendelsohn, J. M. and Scheller, W. 2001. Satellite tracking of two lesser spotted

eagles, *Aquila pomarina*, migrating from Namibia. – Ostrich 72: 35–40.

Meyburg, B.-U., Meyburg, C., Bělka, T., Šreibr, O. and Vrana, J. 2004. Migration, wintering and breeding of a lesser spotted eagle (*Aquila pomarina*) from Slovakia tracked by satellite. – J. Ornithol. 145: 1–7.

Meyburg, B.-U., Matthes, J. and Meyburg, C. 2010. Überwinterungsökologie: Schreiadler und Blutschnabelweber. – Falke 57: 236–243.

Newton, I. 2008. The ecology of bird migration. – Academic Press.

Onrubia, A., Muñoz, A. R., Arroyo, G. M., Ramírez, J., De La Cruz, A., Barrios, L., Meyburg, B.-U., Meyburg, C. and Langgemach, T. 2011. Autumn migration of lesser spotted eagle *Aquila pomarina* in the Strait of Gibraltar: accidental or regular? – Ardea 99: 113–116.

Phipps, W. L., Willis, S. G., Wolter, K. and Naidoo, V. 2013. Foraging ranges of immature African white-backed vultures (*Gyps africanus*) and their use of protected areas in southern Africa. – PLoS One 8: e52813.

Safi, K., Kranstauber, B, Weinzierl, R., Griffin, L., Rees, E. C., Cabot, D., Cruz, S., Proaño, C., Takekawa, J. Y., Newman, S. H., Waldenström, J., Bengtsson, D., Kays, R., Wikelski, M. and Bohrer, G. 2013. Flying with the wind: scale dependency of speed and direction measurements in modelling wind support in avian flight. – BMC Movement Ecol. 1: 1–11.

Simmons, R. E. 1997. Lesser spotted eagle. – In: Harrison, J. A. and Cherry, M. (eds), The atlas of southern African birds, vol. 1: non-passerines. BirdLife South Africa, p. 181.

Simmons, R. E., Barnard, P. and Jamieson, I. G. 1999. What precipitates influxes of wetland birds to ephemeral pans in arid landscapes? Observations from Namibia. – Ostrich 70: 145–148.

Thiollay, J.-M. 2006. The decline of raptors in west Africa: long-term assessment and the role of protected areas. – Ibis 148: 240–254.

Trierweiler, C., Mullie, W. C., Drent, R. H., Exo, K.-M., Komdeur, **[AQ2]** J., Bairlein, F., Harouna, A., de Bakker, M. and Koks, B. J. 2013. A Palaearctic migratory raptor species tracks shifting prey availability within its wintering range in the Sahel. – J. Anim. Ecol. 82: 107–120.

Wood, A. G., Naef-Daenzer, B., Prince, P. A. and Croxall, J. P. 2000. Quantifying habitat use in satellite-tracked pelagic seabirds: application of kernel estimation to albatross locations. – J. Avian Biol. 31: 278–286.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home ranges. – Ecology 70: 164–168.