Steppe Eagle migration strategies – revealed by satellite telemetry

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Abstract Sixteen Steppe Eagles *Aquila nipalensis* were fitted with satellite transmitters during migration or on their wintering grounds (15 in Saudi Arabia, one in South Africa). From these 16 birds, a total of 3,734 location co-ordinates were received. Adult and immature Steppe Eagle migration strategies were markedly different in terms of timing (adults returned to breeding territories in southern Russia and Kazakhstan in late March and early April, whereas immatures arrived in mid May) but not in terms of route and wintering area. Immatures remained on the wintering grounds for substantially longer than adults, typically for about six months. An adult took almost eight weeks to cover 9,543 km from Botswana to Kazakhstan, averaging 177 km daily. The longest mean daily flight distance among all tracked individuals was approximately 355 km. In 1998, an adult male was recorded through a complete annual cycle; it spent 31.5% of the period in the wintering area in Ethiopia and Sudan, 41.9% in the breeding area in Kazakhstan, and 26.6% on migration.

The Steppe Eagle *Aquila nipalensis* is a long-distance migrant, breeding from southeast European Russia, east through the central Asian steppes to Manchuria in eastern China, and wintering in sub-Saharan Africa, the Arabian Peninsula, the Indian subcontinent and southwestern China. In Africa, Steppe Eagles winter across a huge area, extending from the eastern Sahel south to South Africa and Namibia. Brooke *et al.* (1972) suggested that adult and immature Steppe Eagles have different wintering grounds and Christensen & Sorensen (1989) found that adults predominate north of the equator while immatures and subadults are proportionately more common farther south, though with much overlap. Satellite-tracking data suggest that this is not the case, however (Meyburg *et al.* 2003).

In recent decades, major declines in the Steppe Eagle population have been reported; for example, Yosef & Fornasari (2004) found that the number passing through Israel has dropped by half since 1975, with the number of immatures having declined from 30% of the total in the 1980s to less than 2% in 2000. Whether these declines are real or simply the effect of changes in the species' wintering grounds and migration strategies is unclear. Throughout its range, potential threats to the Steppe Eagle include habitat loss, especially in steppe regions, human persecution, and electrocution on power lines (e.g. Davygora 1992, Karyakin & Novikova 2006). Currently categorised by BirdLife International as a species of 'Least Concern', the Steppe Eagle is under review to determine whether its status should be upgraded to 'Near Threatened' (Bird & Symes 2009).

The use of satellite telemetry has proved to be an innovative and appropriate method of recording the migration routes and dynamics of large and medium-sized birds (Meyburg *et al.* 2003, 2011; Meyburg & Fuller 2007). In this study, we examined the migration patterns of 16 Steppe Eagles to determine whether the strategy adopted differs between adults and immatures.

Study areas and methods

Since 1991, over 100 Steppe Eagles have been trapped at a site approximately 50 km ENE of Taif, Saudi Arabia (21°37'N 40°43'E) (Ostrowski *et al.* 2001; Meyburg *et al.* 2003). The birds' age was determined (retrospectively in some cases) by reference to Clark (1996), and sex by size and weight. In addition, a few individuals were trapped in October 1993 on the Red Sea coast of Saudi Arabia southeast of Mecca (20°03'N 40°25'E). For this study, 15 Steppe Eagles of varying ages trapped in Saudi Arabia (in October 1992, March and October 1993, October 1996 and October 1997) were fitted with a platform transmitter terminal (PTT). In addition, another bird (eagle E11) was fitted with a PTT in January 1995 in the Kruger National Park, South Africa.

Details of each Steppe Eagle and its transmitter are listed in table 1. Earlier PTTs were

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275. Steppe Eagle nest, Lower Volga River, Russia, June 2010.

Table 1. Details of 16 Steppe Eagles *Aquila nipalensis* fitted with a platform transmitter terminal (PTT). PTTs supplied by Microwave Telemetry, Columbia, MD, USA.

Eagle no.	PTT no.	Age	Sex	Weight	Duty cycle (hours on/off)	Monitoring period	No. location co-ordinates received	Tracking period (days)	Total distance tracked (km)
E1	02912	adult	M	2,450 g	8 h/96 h	2nd Nov 92 to 10th Mar 93	77	129	1,754
E2	04168	juvenile	F	2,750 g	8 h/96 h	20th Oct 93 to 9th Dec 93	22	47	2,560
E3	04169	immature	?	?	8 h/96 h	17th Mar 93 to 10th Jun 93	33	86	4,146
E4	04170	adult	F	3,000 g	8 h/96 h	24th Oct 93 to 30th Jun 94 (2nd Jun 95) [a]	216	319	4,089
E5	20644	adult	F	2,950 g	8 h/96 h	24th Oct 93 to 24th Mar 94	79	152	17,129
E6	20645	juvenile	M	2,250 g	8 h/96 h	20th Oct 93 to 17th Mar 94	60	133	3,129
E7	20928	adult	F	3,050 g	8 h/96 h	24th Oct 93 to 15th Mar 94	58	145	3,813
E8	20929	juvenile	M	2,450 g	8 h/96 h	20th Oct 93 to 26th May 94	75	215	3,002
E9	20930	immature (c. 2 years)	F	2,800 g	8 h/56 h	20th Oct 93 to 27th Oct 94	192	370	11,129
E10	20931	adult	F	3,300 g	8 h/56 h	22nd Oct 93 to 3rd Sep 94 (18th Oct 94) [a]	394	361	9,220
E11	22693	adult	M	2,250 g	multi season [b]	2nd Jan 95 to 31st Mar 95	18	89	10,046
E12	27992	adult	F	3,200 g	12 h/120 h	27nd Oct 96 to 11th Aug 97	162	289	4,023
E13	27993	immature (c. 18 months)	F	3,250 g	12 h/120 h	23rd Oct 96 to 23rd Apr 97	96	183	7,716
E14	27994	immature (c. 3 years)	F	3,250 g	12 h/120 h	26th Oct 96 to 8th Dec 96	19	44	557
E15	27995	adult	F	3,450 g	12 h/120 h	27th Oct 96 to 7th Mar 97	65	132	1,895
E16	19627	adult	M	2,300 g	multi season [b]	21st Oct 97 to 13th Dec 98	2,168	419	16,572

[a] Date in parentheses is last date when a location was obtained. Either the transmitter had been lost or the bird had perished as no movement had been recorded since the previous date.
[b] Programmed with different cycles to conform to the expected migration periods.

battery-powered but the five transmitters fitted in 1996–97 were solar-powered, giving an extended life-cycle. The PTTs weighed 50–80 g. By prolonging battery life (through programming long off-hours into the duty cycles), individual eagles could be tracked for extended periods, in one case for over one year. Battery-powered PTTs were programmed to transmit for eight hours in each 64-hour period (in two cases), and eight hours in each 104-hour period (in eight cases). The transmitter fitted to E11 was programmed with different cycles to coincide with the eagle's expected movements during migration.

Data processing

Satellite data were received through the Argos satellite-based positioning system. These data were decoded and processed using software produced by Microwave Telemetry, Inc. and displayed via Google Earth Pro, ArcView GIS 3.2b (ESRI GIS and Mapping Software, Redlands, CA), and Animal Movements Extension to ArcView GIS. All location data were analysed individually and entered into databases.

To display migration routes, only location classes (LCs) 3, 2, 1 and 0 were used. LCs of inferior and poor quality (LCs A, B and Z) were mostly excluded. The error ranges indicated by Argos for class LC 3 (best quality) are 150 m, LC 2 up to 350 m, and LC 1 up to 1 km. Only where important data points were missing were LCs of lesser quality used in the results. Distances between wintering and summering areas, and between individual travel sectors, were calculated as the sum of the distances between all accepted neighbouring Argos locations.

Limitations on transmitter life and data

From the 11 birds equipped with battery-powered transmitters (E1–E11), a total of 1,219 location co-ordinates were obtained. The mean number of locations per eagle was 111 (range 18–394). Mean PTT life between fitting and the last location monitored was 224 days (range 47–370). In some cases, the transmitters continued to send signals after the birds had either perished or lost the transmitter. Excluding local movements, the total distance over which an individual was tracked reached 17,129 km (table 1). From the five birds with solar-powered PTTs (E12–E16), a total of 2,510 location co-ordinates were obtained (mean 502), and mean length of time active was 213 days (range 44–419).

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276. Steppe Eagle nest, Lower Volga River, Russia, June 2010. Note that the gape extends behind the eye, which distinguishes Steppe Eagle from similar *Aquila* eagles, especially Lesser Spotted *A. pomarina* and Greater Spotted Eagle *A. clanga*.

Of 15 Steppe Eagles trapped in the Arabian Peninsula, seven remained there throughout the winter; one was trapped on spring migration and continued its journey; one stopped transmitting before its final wintering area was established; and six crossed the Red Sea at the Bab-el-Mandeb Strait (between Yemen and Djibouti). Of those wintering in Africa, five remained in East Africa, in one case wintering north of Bab-el-Mandeb. One adult female travelled as far as southern Africa. Regardless of age, all six birds wintering in Africa conducted a loop migration around the Red Sea, arriving via Bab-el-Mandeb and departing via the northern end of the Red Sea (Suez) (Meyburg *et al.* 2003).

Loss of contact with PTTs occurred for various reasons. With some individuals (e.g. E5 and E9) the PTTs functioned until the batteries were depleted and the birds were evidently still alive. In other cases (e.g. E2 and E8) the batteries depleted prematurely. Contact was lost abruptly with some birds (e.g. E1, E3 and E7) long before the batteries would have become depleted. Possible causes include the loss of the PTT, a PTT defect or the death of the bird. A fourth group of birds eventually lost the PTT after a longer period, or were believed to have perished, indicated by the transmitter (e.g. PTT 04170 fitted to E4) continuing to transmit from the same location for an extended period.

Migration

One of the most striking discoveries from this study was the loop migration around the Red Sea undertaken by all six of the Steppe Eagles that wintered in Africa (Meyburg *et al.* 2003). All six tracked birds crossed the southern Red Sea in autumn to enter Africa at Bab-el-Mandeb, while on spring migration they returned north to the west of the Red Sea and left Africa via the Gulf of Suez (Egypt) and Eilat (Israel). The movements of E13 led us to speculate that this bird was deterred from making the Red Sea crossing into Africa; it subsequently wintered in the Arabian Peninsula (see below). The easterly winds that predominate in February and March (Hellermann & Rosenstein 1983; Meyburg *et al.* 2003) presumably deter Steppe Eagles from crossing the Red Sea at the Bab-el-Mandeb and the detour via Suez extends the journey by approximately 1,250 km.

Speed and timing of migration

The daily distance travelled during migration varied between and within individuals. Various factors affect the distance travelled and time spent on migration, including weather conditions, the need to feed and the

Table 2. Period and duration of spring migration, total distance and mean daily flight distances travelled by selected Steppe Eagles monitored during this study.

Eagle no.	Wintering area	Departure date	Arrival date	Duration of migration (days)	Distance travelled (km)	Mean daily flight distance (km)
E11	South Africa	2nd Jan	31st Mar	50 [a]	9,738	195
E5	Botswana	29th Jan	24th Mar	54	9,543 [b]	177
E9	Chad, Sudan	12th Apr	18th May	37	5,877 (7,152) [c]	159
E10	Sudan	18th Feb	1st Apr	43	5,876 [d]	137
E4	Saudi Arabia	25th Feb	28th Mar	32	3,527 (4,089) [e]	110
E12	Saudi Arabia	1st Mar	2nd Apr	33	3,489 [f]	106
E13	Saudi Arabia	27th Mar	23rd Apr	28	2,801 (3,811) [g]	100
E16	Sudan, Ethiopia	24th Feb	9th Apr	45 [h]	7,315	193

Notes: [a] The migration was interrupted in the Sudan for 39 days but this is excluded from the above value. [b] From the point of departure. [c] 5,877 km from the point of departure of the spring migration but 7,152 km from the most distant wintering site in Chad. [d] From the Sudan. [e] 3,527 km from the point of departure of the spring migration, but 4,089 km from the southernmost point of its wintering site in Saudi Arabia. [f] From the last location in the winter home range. [g] From southwest Saudi Arabia, excluding a brief stopover in Yemen and 'pendulum swing' in northern Saudi Arabia. [h] The migration was interrupted for seven days but this is excluded from the calculation.

proximity of the destination – in simple terms, birds with farther to go are more anxious to press on. It became clear that birds that wintered farthest from their breeding area generally travelled greater daily distances and spent more time on their journey than the eagles wintering farther north. The mean daily flight distance was almost 200 km for those birds overwintering in southern Africa, but only slightly more than 100 km for those overwintering in Arabia (table 2).

For most eagles, the limited number of co-ordinates meant that it was not possible to record all overnight stops, which would have allowed us to determine individual daily flight distances precisely. We could measure only the average speed between two fixes, often more than 24 hours apart, and from this we calculated mean daily flight distances for different parts of the route. These daily distances travelled fluctuated considerably and showed a clear dependence on the weather (Meyburg *et al.* 1998).

Spaar & Bruderer (1996) used radar to measure the speed of migrating Steppe Eagles as they passed over Israel. Although they were able to track the eagles for short distances only, they calculated a mean speed of 44.6 km/h. Migrating Steppe Eagles spend about 50%–65% of daylight hours on migration, around six hours per day. A speed of 45 km/h maintained for six hours equates to 270 km/day, which is considerably greater than the mean distance recorded during this study.

Adults returned to the breeding areas at the end of March or in early April, whereas immatures arrived roughly six weeks later, in mid May (table 2). Only one immature (E13) arrived much earlier (23rd April). All the eagles tracked to their breeding areas spent the summer in southern Russia and western Kazakhstan, in the vicinity of the Aral Sea.

Birds wintering in Africa

On their arrival in Zimbabwe, Irwin (1981) suggested that most Steppe Eagles continue to the southwest and enter Botswana or Namibia. This pattern was confirmed by E5, which entered Botswana after leaving Zimbabwe. Irwin reported no return passage through Zimbabwe but the return route taken by E5 saw it move north through Zimbabwe from February onwards (fig. 1). Another bird (E11) overwintered in the Kruger National Park and migrated north along the eastern border of Zimbabwe. According to Ash & Atkins (2009) the only suggestion of a return passage through Ethiopia is provided by small numbers seen moving north at Langano (south of Addis Ababa) between mid March and mid April. It is noteworthy that E5 passed all the way through Ethiopia in the second half of February, and that E11 migrated along the Ethiopian/Sudanese border.

Eagle E5 (fig. 1)

During autumn migration, this adult female travelled from Saudi Arabia to Botswana, covering 5,882 km in 30 days (an average of 196 km/day). The mean daily flight distance that we measured ranged from 124 km to 266 km. The return migration, which began on 29th January 1994 and covered 9,543 km, was completed in 54 days, an average of 177

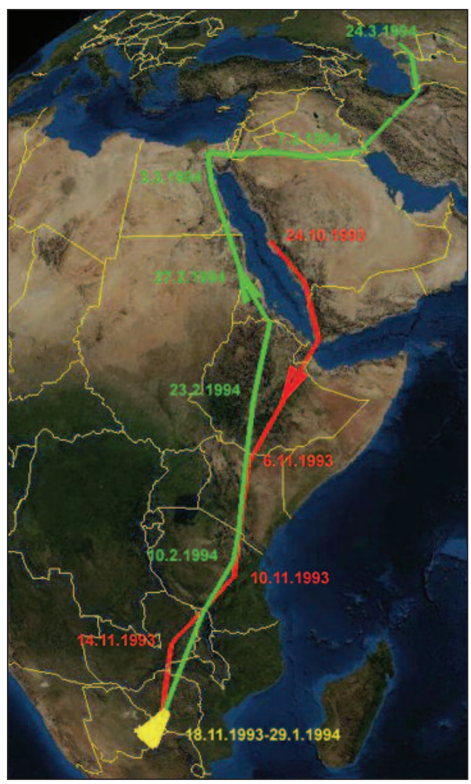

Fig. 1. Eagle E5. (Note: In figs. 1–5, red lines and dates denote autumn migration, yellow the wintering area, green the spring migration and blue the summering area.)

km/day. Along the Red Sea coast north to the vicinity of Suez, this bird covered a mean distance of 294 km/day. From here its speed decreased but picked up again from northern Saudi Arabia to Kazakhstan, where it averaged 238 km/day. Owing to the distance involved, this eagle took the greatest time to travel from the wintering grounds to the breeding area.

Of the 16 birds monitored in this study, E5 was tracked over the greatest distance (17,129 km). After taking into consideration the distance from breeding site to capture site, its total annual migration would have been in excess of 20,100 km, including 1,704 km travelled within the wintering grounds in Botswana, Zimbabwe and South Africa. The routes followed during the autumn and spring migration were remarkably similar south of the Kenya/Ethiopia border and the bird flew over the Ethiopian Highlands on both its south- and its northbound journeys. The location positions obtained failed to reveal whether this bird flew as far north as Suez, or whether it crossed the Gulf of Aqaba farther south.

Eagle E9 (fig. 2)

Having overwintered in Sudan, this immature female began its return migration on 12th April 1994 and travelled 5,877 km to reach the centre of the summering grounds in 37 days (mean 159 km/day), on 18th May (fig. 2). This period included stopovers lasting several days. Its route took it along the Red Sea coast, where it covered 1,641 km in five days (mean 328 km/day.

This bird was tracked for the second-longest period of any eagle in the study. Like the other birds wintering in Africa, it executed a loop migration of the Red Sea. Of particular interest is that it spent the winter in areas of Ethiopia, Sudan and southeastern Chad that are quite well separated. This is also the only Steppe Eagle monitored that migrated to the west of the Caspian Sea. The route followed during the early stage of its southward migration is noteworthy in that, between 5th and 18th September 1994, northwest of the Caspian Sea, it moved north again: only on 25th September was it located as far south as on 5th September. The last position location received, after the bird had been monitored for over one year, was from northwest Iraq, 1,750 km north of its place of capture. Adding that 1,750 km to the total distance tracked results in a year-round migration of 12,879 km.

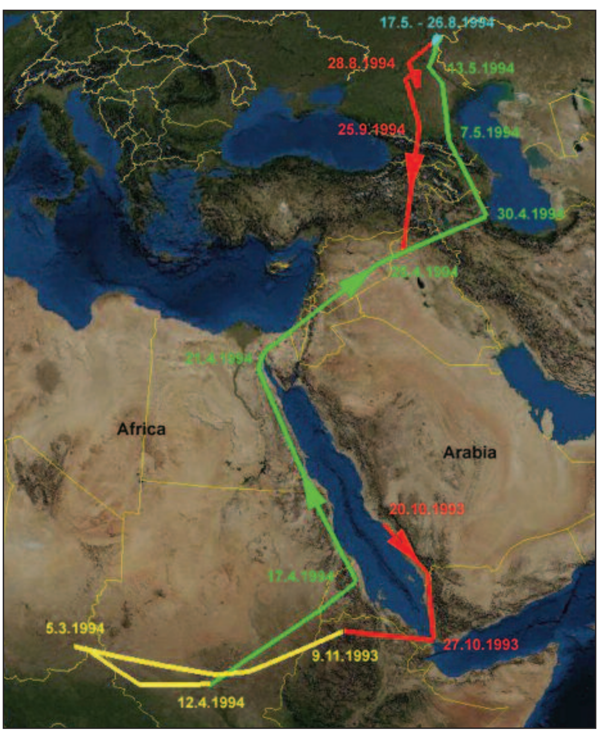

Fig. 2. Eagle E9.

Eagle E10 (fig. 3)

After being fitted with the transmitter in Saudi Arabia, this adult female travelled back and forth, reaching the Red Sea and returning inland again. Eventually it migrated south and crossed the Red Sea at the Bab-el-Mandeb to reach its wintering grounds in a relatively densely populated region of the Sudanese Sahel.

After spending the winter in Sudan, it returned to the breeding grounds on 1st April 1994, travelling 5,876 km in 43 days (mean 137 km/day; fig. 3). During the two and a half days it took to travel across Iran, it travelled at a mean speed of 355 km/day, the longest mean daily flight distance recorded in this study.

The breeding site of this bird was visited in late July 1994

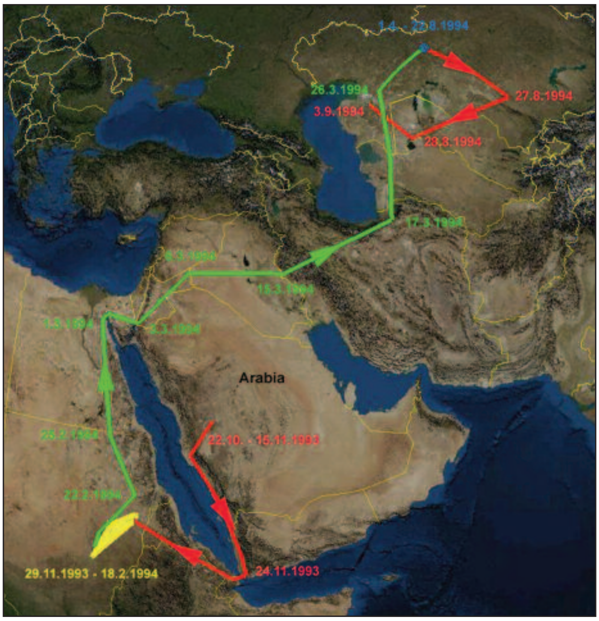

Fig. 3. Eagle E10.

(49°18'N 60°35'E), where the bird was observed and photographed. The nest had been built on the ground and contained two fully feathered young. Despite having bred successfully, it left the breeding site unexpectedly early, being last recorded there on 22nd August. (Perhaps some female Steppe Eagles leave before their offspring and male partners, which is the case in some Lesser Spotted *Aquila pomarina* and Greater Spotted Eagles *A. clanga*; Meyburg *et al.* unpubl.) By 27th August it was already 368 km to the southeast, and a series of good location positions revealed an astonishing 2,073-km loop migration around the Aral Sea. From 3rd September, the transmitter sent a series of signals from the same location (44°58'N 54°01'E), far west of the Aral Sea, indicating that the eagle had either perished or lost the transmitter.

Eagle E11

On northward migration, this adult male covered the 9,738 km from South Africa to Kazakhstan in 50 days, travelling on average 195 km/day. Northward migration began on 2nd January and continued until 24th January, at which point it spent 39 days in Sudan, remaining there until 4th March when migration recommenced. It reached the breeding site on 31st March. The greatest speed recorded occurred as it travelled 1,438 km across Tanzania and Kenya, averaging 274 km/day, but it also reached 247.4 km/day as it flew along the Caspian Sea.

Eagle 16 (fig. 4)

This bird was tracked for the longest period of any bird in this study – almost 14 months – and its transmitter provided the most data (2,168 position locations). After being fitted with the transmitter in Saudi Arabia, it migrated via the Bab-el-Mandeb to its wintering area in eastern Sudan, close to the border of Ethiopia, which it reached on 8th November 1997. Here it remained until 24th February 1998, although it travelled 550 km SSW, roughly along the border between Sudan and Ethiopia, during 13th–17th December. Spring migration began in earnest on 25th February and the bird followed the

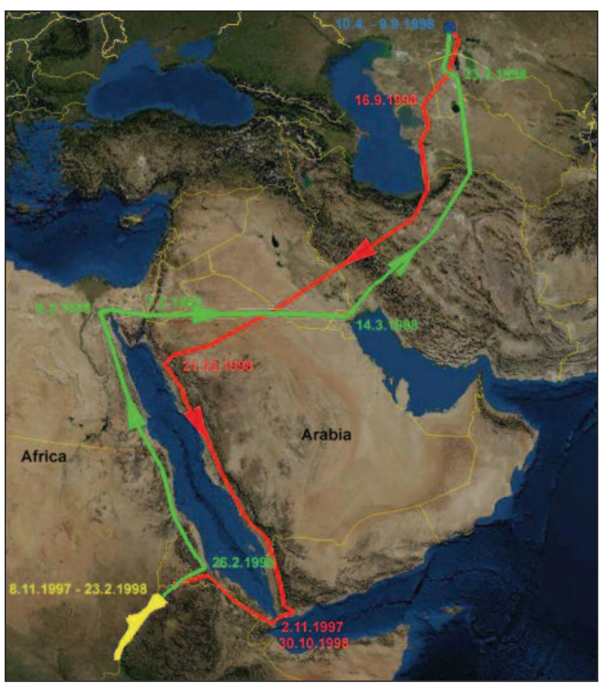

Fig. 4. Eagle E16.

western coastline of the Red Sea to Suez, then east via Eilat to Kuwait on the Persian Gulf coast. From here, it flew to the southeast corner of the Caspian Sea, then north between the Caspian and Aral Seas until it reached its likely breeding site in Kazakhstan, (47°32’N 58°49’E), some 200 km north of the Aral Sea in the hilly uplands to the southeast of the Mugodzhary Mountains. Steppe Eagles are common there, with up to 300 pairs breeding at a density of approximately 1.51 pairs/100 km² (Karyakin *et al.* 2007). Autumn migration began on 10th September and it reached the Bab-el-Mandeb on 26th October. On 5th November 1998, it returned to the previous year’s wintering area.

Birds wintering in the Arabian Peninsula

The birds that overwintered in Saudi Arabia completed the journey from wintering areas to the breeding grounds in the shortest times but their migration speed was slower than that of the birds wintering in Africa. Among the adult birds, E4 took the shortest time to reach the breeding grounds. Spring migration commenced on 25th February and was complete on 28th March: 3,527 km in 32 days, a mean speed of 110 km/day, although the daily distances covered varied considerably. During the two-week period that E12 took to cover the major part of its route to the northwestern shore of the Aral Sea, it covered a relatively high mean daily flight distance of 178 km/day. The greatest distances travelled, up to 194 km/day, were at the start of the migration in Saudi Arabia and Kuwait, during 1st–5th March. Thereafter its pace slowed and on later sectors along the migration route, the speed dropped to a mean of 182 km/day, and then 157 km/day. During 17th–22nd March, E12 paused to the northwest of the Aral Sea, covering only 79 km. From here, to cover the relatively short distance to the breeding site, it travelled at an average of 51 km/day.

Eagle E13 (fig. 5)

This immature female was estimated to be approximately 18 months old when fitted with a transmitter in Saudi Arabia on 23rd October 1996. From there, it flew 1,029 km SSE, parallel with the Red Sea coast to a point 82 km east of Bab-el-Mandeb on the night of 2nd/3rd November. From there, we expected that it would cross the Red Sea into Africa the following day, but instead it travelled north along a route approximately parallel to its southerly journey, reaching the Yemen–Saudi Arabia border on 8th November, and spending the rest of the winter in Saudi Arabia, almost reaching the border with Iraq at one point and travelling a total of 5,537 km.

It left its wintering range on 27th March 1997 and flew at a mean speed of just 100 km/day on its 2,801-km homeward journey, reaching the breeding area (halfway between the northern shores of the Caspian and Aral Seas) on 23rd April, some 2,801 km after leaving Saudi Arabia on 1st April. In the central part of its journey, between Isfahan in Iran and the southwestern shore of the Aral Sea, it reached a mean speed of 204 km/day. By wintering so far north, this individual reached the breeding area in just four weeks, the shortest time in this study.

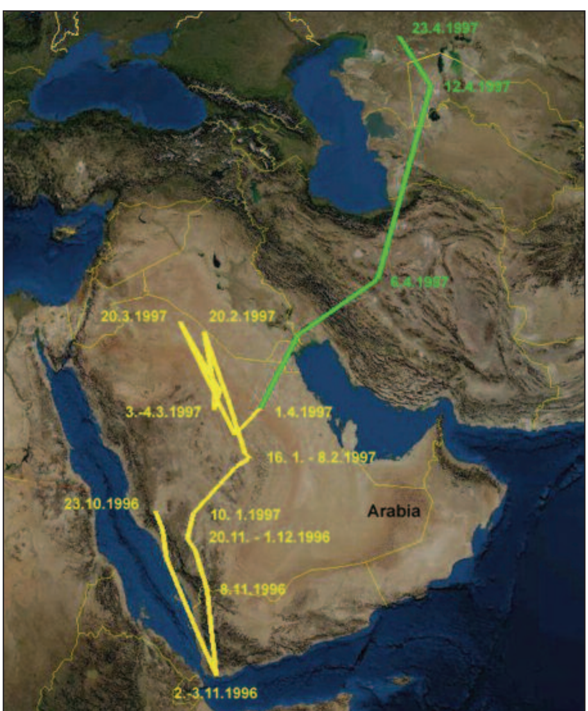

Fig. 5. Eagle E13.

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277. Juvenile Steppe Eagles, Salalah, Oman, November 2011.

Timing of passage and route followed at migration bottlenecks

Passage of Steppe Eagles over Suez and Eilat begins in early to mid February and continues to late April and early May, peaking in late February and early March (Christensen & Sorensen 1989); though note that Zduniak *et al.* (2010) found that the arrival of the first birds during 1994–2008 was becoming significantly earlier. This corresponds well with the dates that adult eagles E5, E10 and E11 reached this bottleneck area. Immature female E9 passed through this region on 22nd April, close to the end of the migration period. The timing of passage over Bab-el-Mandeb in late October and early November also corresponded well with observations by Welch & Welch (1989); only E10 passed rather late.

Our satellite-tracking data do not confirm the suggestion from ground-based observations that adults and immatures may favour different routes at the northern end of the Red Sea – with adults preferring to cross the southern Golf of Suez while immatures continue north to Suez (Shirihai *et al.* 2000). Furthermore, our data do not support the assumption that birds migrating over Suez subsequently pass through northern Sinai and thence into Israel, rather than via Eilat (Shirihai *et al.* 2000). For example, E5, E10 and E16 all passed through both Suez and Eilat on their way north in spring (figs. 1, 3 & 4).

Movements on the wintering grounds

During winter, the number and size of home ranges used differed widely among individuals. Furthermore, some travelled long distances during the winter, making it difficult to define home ranges. Owing to the relatively high number of good position locations received (c. 30 in each case), the winter ranges of three birds are particularly well documented.

Eagle E4

The winter movements of E4 formed the best dataset in our study. From 24th October 1993 to 20th February 1994, it occupied two distinct home ranges, within an overall 'wintering area' that stretched 560 km between the northwest and southeast extremities. The first home range, used from 24th October until 12th November 1993 and extending over an area of 91 km^2, centred on the road from Taif to Riyadh, in Saudi Arabia, where roadside animal corpses may have provided a

Table 3. Winter home-range location and size, and duration of stay in the wintering area for selected Steppe Eagles in this study.

Eagle no.	Duration of stay	Location of winter home range	Co-ordinates	Home range (km^2)
E1	30th Nov 92 to 26th Feb 93	Saudi Arabia (50 km NE Taif)	21.37°N 40.43°E	317
E4	24th Oct to 12th Nov 93	Saudi Arabia (150 km NE Taif)	22.13°N 41.26°E	91
	16th Nov 93 to 19th Jan 94	Saudi Arabia (120 km NE Abha)	18.46°N 44.17°E	4,540
	31st Jan to 20th Feb 94	Saudi Arabia (130 km NE Taif)	21.43°N 41.23°E	1,960
E9	9th Nov to 2nd Dec 93	NW Ethiopia (95 km W Aksum)	14.08°N 37.50°E	4,740
	3rd–7th Dec 93	South Sudan (65 km SE Kadugli)	10.38°N 30.12°E	56
	12th Feb to 5th Mar 94	Southeast Chad (60 km E Am Timan)	10.59°N 20.51°E	140
	7th–14th Mar 94	Southeast Chad (45 km SE Dourdoura)	11.05°N 21.44°E	5
	18th Mar to 12th Apr 94	South Sudan (120 km S Kadugli)	09.54°N 29.54°E	28
E10	29th Nov 93 to 28th Jan 94	Sudan (260 km E Khartoum)	15.53°N 35.22°E	18,000
	30th Jan to 18th Feb 94	Sudan (220 km S Khartoum)	13.42°N 32.58°E	172
E7	27th Oct 93 to 11th Feb 94	Saudi Arabia (220 km E Medina)	24.34°N 41.47°E	18,500
E5	13th Dec 93 to 20th Jan 94	Eastern Botswana (235 km N Gaborone)	22.32°S 26.02°E	4,150
E12	2nd Nov 96 to 1st Mar 97	Saudi Arabia (220 km E Medina)	24.34°N 41.47°E	65,000
E13	1st Dec 96 to 5th Jan 97	Saudi Arabia (260 km SE Taif)	20.01°N 42.30°E	5
	22nd Jan to 9th Feb 97	Saudi Arabia (112 km WSW Riyadh)	24.15°N 45.42°E	30
E15	8th Nov 96 to 27th Feb 97	Saudi Arabia (178 km WNW Riyadh)	25.17°N 45.08°E	621
E16	8th Nov 97 to 24th Feb 98	Sudan (60 km E Ad-Damazin)	11.39°N 34.56°E	12,810

food source. The second home range, the centre of which was 485 km from the first, was at Gabal al-Wagid and occupied between 16th November 1993 and 19th January 1994. Although it ranged over 4,540 km^2, E4 spent much of its time along a small section of the only road in the region, again suggesting that roadside corpses were scavenged. E4 then returned to the first home range for the rest of the winter, but the area it roamed was now substantially larger, covering 1,960 km^2 (table 3).

Eagle E5

E5 overwintered in Botswana (fig. 1), reaching the southernmost location in South Africa on 23rd November. From here, it flew 545 km to the vicinity of Bulawayo, Zimbabwe, and returned to Botswana in a direction almost parallel to its original route, where it finally established a winter home range. Here it remained from 13th December 1993 to 20th January 1994, covering an area of 4,150 km^2 (table 3).

Eagle E9

E9 spent parts of winter 1993/94 in no fewer than five areas, situated in Ethiopia, Sudan and Chad (fig. 2). The home range in Ethiopia was 917 km from the two neighbouring ranges in Sudan, which in turn were 1,100 km away from the wintering site in Chad.

Time spent on the wintering grounds and departure dates

Since most adults return to the breeding grounds in late March and early April, those birds wintering farther north are able to maintain a winter home range for a longer period. This has many advantages, since an individual can identify the optimum places to forage and feed regularly at such sites, whereas migrating birds depend on feeding opportunistically en route. Adult birds wintering in the Arabian Peninsula can remain in their winter home range longer than those wintering in Africa, typically for over four months and almost twice as long as those wintering in southern Africa (table 3). Immatures are not under the same pressure to reach the breeding grounds quickly and some may spend up to six months on the wintering grounds. Some juvenile birds may spend their first summer on the wintering grounds (although this is yet to be confirmed by satellite tracking), but older immatures usually return north.

Discussion

Many sources have described the passage of Steppe Eagles and other raptors at migration bottlenecks, (e.g. Shirihai 1982, Fleming 1983, Welch & Welch 1988, 1991, Shirihai & Christie 1992, Shirihai *et al.* 2000, DeCandido *et al.* 2001, Den Besten 2004), but the patterns and strategies associated with migration, in particular of the complete annual cycle, have not been determined fully. Since ring-recoveries are few and, apart from this study, only a single Steppe Eagle has been tracked by satellite (Ellis *et al.* 2001), little is known about the speed and timing of migration of this species on a large scale.

To date, the complete annual cycle of just one Steppe Eagle (E16, an adult male) has been mapped. In 1998 this individual spent 31.5% of the year (115 days) in the wintering area, in Ethiopia and Sudan; 41.9% (153 days) in the breeding area, in Kazakhstan; and 26.6% migrating, of which 12.1% (45 days) was during spring and 14.5% (53 days) in autumn. It returned to the wintering area on almost the same day in two successive years: 8th November 1997 and 5th November 1998.

The findings of this study do not support the theory that adult and immature Steppe Eagles spend the winter in different regions of Africa. Our field observations in Kenya, Tanzania, Zambia, Namibia and South Africa were consistent with the data acquired from the eagles we tracked. Relatively few individuals flew to southern Africa, irrespective of age, but many more wintered in eastern Africa. In Tanzania, we observed the species in large concentrations in December and January, including adults, juveniles and immatures.

Ongoing migration studies of other species, including Ospreys *Pandion haliaetus*, Lesser Spotted and Greater Spotted Eagles, using solar-powered PTTs that transmit a signal constantly, have shown that distances in excess of 400 km/day (and exceptionally over 500 km/day) may be covered (Meyburg *et al.* unpublished data). It is possible that Steppe Eagles cover similar distances, but this could not be verified in this study owing to the constraints of the PTTs used. It is also possible that, because of their higher wing loading, larger species cannot travel as far in a single day as smaller species.

Studies of Lesser Spotted and Greater Spotted Eagles suggest that these species can do little to increase their flight speed during migration. Individuals must wait for the air to warm and thermals to develop before migration can begin. As the air cools in the afternoon, the heat energy given off by the ground is insufficient to form thermals, and at this point active migration ceases for the day. To a ground-based observer, this pattern is reflected in morning and late afternoon activity peaks. Rapidly rising thermals may carry soaring raptors to altitudes beyond the visual acuity of the human eye; migration appears to tail off by late morning but increase again later as raptors descend and search for a safe roosting site. Thermals allow a maximum of 7–8 hours travelling time per day, depending on location. Since flight speed cannot be significantly altered, birds that have further to travel must initiate their migration sooner and use a greater proportion of the daily 'thermal allowance' for travelling rather than resting or hunting.

Migration and the human impact

The fact that a substantial proportion of the Steppe Eagle population now overwinters in the Arabian Peninsula may reflect an improved food supply. In recent years, the number of herds of domestic ungulates has increased dramatically as a result of artificial feeding; a plentiful supply of food is at hand for the eagles, which systematically seek areas where animal carcases have been left lying. At such locations, where the Steppe Eagle is by far the most numerous raptor, it is now not unusual to see 50–100 birds together. This 'new' food supply may have resulted in fewer birds migrating as far as eastern Africa and especially southern Africa. The ecological advantage for a few individuals to continue to migrate to southern Africa is unclear.

By wintering over such a huge geographical region of Africa and southern Asia, it seems that the Steppe Eagle may have minimised the risks associated with persecution, disease, lack of food and habitat destruction at a population level. Populations using the same breeding area but different migratory tracks and wintering areas are exposed to varying levels of environmental and anthropic pressures such as drought, habitat destruction or illegal hunting. Widely separated wintering ranges have the potential to buffer populations against temporarily adverse conditions in one part of the range, but more permanent differences between alternative migration routes or wintering areas have the potential to create source or sink subpopulations.

By the same token, conservation strategies for such species are harder to design and implement. To inform global conservation planning for the Steppe Eagle, it is important for future research to determine (i) the proportion of the global population wintering in the Indian subcontinent and Africa, and in the different areas within Africa; (ii) specific threats associated with different migratory pathways and wintering areas using a combination of satellite data and field studies; and (iii) the genetic structure of and exchanges between subpopulations that show different migration and wintering strategies.

Some questions have been clarified by the use of satellite telemetry but further research is needed to better understand winter habitat use and foraging ecology of Steppe Eagles. Since the introduction of global positioning satellite technology, questions regarding habitat use, home-range size, migration flight speed and height have been more precisely studied in some other species, but not yet in the Steppe Eagle. It remains unclear if and where a migration divide exists, and to what extent the breeding areas of birds wintering in southern Asia, Arabia and Africa overlap.

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278. Nest of Steppe Eagle with young chicks in typical breeding habitat, in the Mugodzhary Mountains, just north of the Aral Sea, Kazakhstan, May 2006.

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