Two complete migration cycles of an adult Hobby tracked by satellite

Bernd-Ulrich Meyburg, Paul W. Howey, Christiane Meyburg and Klaus Dietrich Fiuczynski

Abstract A prototype of the smallest satellite transmitter produced so far, weighing just 5 g, was fitted to an adult Hobby Falco subbuteo in Germany in August 2008. Two autumn and two spring migrations were recorded successfully from the unit carried by this particular Hobby. All four migration routes were to the west of a direct line between breeding site and wintering area. The migration route in spring 2010 was up to 2,150 km farther west than that in autumn 2009, effectively forming a 'migration loop'. This was much less pronounced in 2008/09. The direct distance from the breeding site to the southernmost point reached in Zimbabwe in 2008/09 was 10,065 km. The fastest flight speeds on migration were recorded in spring 2010 in Mali and Morocco, when 1,243 km was covered in two days. Also in spring 2010, during migration from Morocco to southern France (1,032 km in two days), the falcon migrated at night, when a fix was made over the Mediterranean in the vicinity of Gibraltar. Migration across the Sahara took 4-4.5 days on each migration. The West African equatorial rainforest appears to be a significant ecological barrier, and the significance of this is discussed. Migration was noticeably rapid there with distances of up to 580 km flown per day – also partly at night. During both wintering periods the falcon spent the majority of its time in the Angolan Miombo woodlands, but in winter it also travelled large distances: from 16th October 2008 to 7th April 2009, the bird covered a total distance of at least 9,025 km between identified night roosts. In 2009, the bird spent half the year in the wintering area, a third on the breeding grounds and the remaining 18% of the time on migration; i.e. 65% of its time in Africa and 35% in Europe.

he Hobby *Falco subbuteo* breeds across Europe and Asia and is a long-distance, trans-equatorial migrant. European (and probably Asian) birds winter in central and southern Africa (Brown *et al.* 1982; Pepler 1993; Mendelsohn 1997) and

the species' main wintering area is believed to be the Zambezi Basin between 10° and 20°S (Chapman 1999). According to Pinto (1983) and Dean (2000), the Hobby is an uncommon migrant in Angola from October until March, in Acacia and Miombo wood-

This paper is dedicated to Robin Chancellor, who contributed so much to raptor research and conservation by editing the Proceedings of all Birds of Prey World Conferences, and who died in October 2010 (see pp. 42–43).

lands from southern areas north across the central plateau to Bié.

Very little is known about the Hobby's migration. Only a small number of birds are observed at the well-known bottlenecks such as Gibraltar. A total of 5,720 Hobbies were ringed in ten European countries between 1909 and 1998 (including over 1,000 in Berlin and Brandenburg, Germany), of which 203 (3.5%) were subsequently recovered, although none south of the Sahara Desert (Chapman 2002). Since then, we know of only two ring-recoveries from Africa south of the Sahara. At present, mapping the wintering areas of long-distance migrants is based mainly on ring-recoveries, satellite telemetry, stable-isotope analysis of feathers or other tissues and through the use of genetic markers. Satellite tracking using the Argos system (Argos 1996) is now an accepted technique.

Study site and methods

The Hobby has been studied in Berlin and its environs for decades (Fiuczynski 1978, 1987, 2007; Fiuczynski & Nethersole-Thompson 1980). A nest-site in a disused Common Raven Corvus corax nest in pine trees northwest of Berlin (52°50'N/13°0'E) was in a territory occupied each year between 2005 and 2009, although young fledged from the site only in 2005 and 2008. On 9th August 2008, an adult female (weighing 265 g) was caught at this nest-site, using an adult White-tailed Eagle Haliaeetus albicilla as a decoy. The Hobby (which had raised two offspring) was fitted with a new type of satellite transmitter (Platform Transmitter Terminal, or PTT), which was at that time still in a development phase¹. The device was solar-powered and weighed 5 g (1.9% of the Hobby's body mass); it was attached as a 'backpack' using a harness with neck and body loops. The overall weight of the harness was approximately 1 g.

Satellite data were received through the Argos satellite-based positioning system.

These data were decoded and processed using software produced by Microwave Telemetry, Inc. (USA) and displayed via Google Earth Pro, ArcView GIS 3.2b (ESRI GIS and Mapping Software, USA), and Animal Movements Extension to ArcView GIS. To display migration routes, only location classes (LCs) 3, 2, 1 and 0 were used. LCs of inferior and poor quality (LC A, B and Z) were mostly excluded. The deviations 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. Unless stated otherwise, transmitter data are given in co-ordinated universal time. Only where important data points were missing were LCs of lesser quality used in our results.

We could not detect any effect of the transmitter on the Hobby's behaviour. The transmitter was programmed to operate on a duty cycle of 10 hours on/48 hours off. Ecological digital Google Earth maps were used to evaluate the data. They are based on original publications such as Olson *et al.* (2001) and DeFries *et al.* (2000).

Where possible, the falcon's night roosts were established in order to record habitat use and changes in location in the wintering area. As a rule, because of the transmitter's programming, it was possible to localise only every second roost (but most of them through several good fixes: LC 1–3). Other fixes made in daylight hours were disregarded. The distances between the individual night roosts were measured and the respective habitat determined by overlaying with digital maps.

The home ranges were determined with the help of fixed kernel techniques (Worton 1989) and the 'Minimum Convex Polygon' (MCP) method (Kenward 2001; Selkirk & Bishop 2002; Laver & Kelly 2008). The evaluation of the fixes was made using the homerange extension for ArcView from Rodgers & Carr (1998) as well as the home-range tools for ArcGis from Rodgers *et al.* (2007). Among other features, this computer program permits calculation of the MCP. The Floating

¹ Dimensions of the transmitter were $24 \times 14 \times 7.5$ mm – antenna hard nylon-coated flexible-stranded marine-grade stainless steel, 178 mm long, potted in high-grade epoxy resin – with sensors to measure temperature and its own battery voltage with each parameter relayed by Argos on each transmission. Micro-processor-controlled battery charging with a power output of 200mW and an operating frequency of 401.650 MHz +/- 36 kHz.

Amean method ('proximity to recalculated mean of selected fixes') was used to calculate the 95% and 80% MCPs. By this method, the arithmetical mean of all fixes is calculated, the point farthest away determined and deleted, and the arithmetical mean of all fixes recalculated. This procedure is repeated until only 95% or 80% of the fixes remain. Winter home ranges are calculated in surface area and presented here over a background of the global tree cover derived from remote sensing. Climate data from a large number of meteorological stations along the migration routes was obtained from the internet.

Results

The satellite transmitter fitted to the Hobby, the smallest and lightest unit available at the time, delivered astoundingly high numbers of good Argos Doppler fixes. The complete dataset comprised over 2,000 positions, of which 49% were high-quality locations (LC 1–3). There were fewer fixes in Europe (on average 65 per month) than in Africa (80 per



1. The female Hobby *Falco subbuteo* tracked in this paper, shown here after being fitted with the satellite tag at the nest-site, northwest of Berlin, in August 2008.

month), the lowest number being recorded in the Mediterranean region, which is explained by interference in this area (Gros & Malardé 2006). The percentage of high-quality fixes in Europe (22%) was much lower than that in Africa (72%). Signal transmission lasted for 21.5 months.

Altogether, two spring and two autumn migrations, as well as two wintering periods, were recorded (fig. 1). In 2009 the bird spent 49.3% of the year in the wintering area, 7.2% on spring migration, 32.3% in the breeding area and 11.2% on autumn migration (fig. 2).

Behaviour at the breeding site before departure on migration

After being fitted with the transmitter, the female behaved completely normally; it kept to its favoured lookout tree and remained close to the young birds. On 28th August 2008 the bird was located in the vicinity of its nest for the last time and on 30th August a fix was made in southern Germany, near Munich. The male parent remained in the

> breeding area and fed the young until 18th September. On 22nd September the male and the young had also departed on migration.

Behaviour on migration

All migration routes were clearly west of a direct line between the breeding site and the wintering area. The fixes recorded farthest from this line on migration (and the respective distances from it) were as follows: 10°30'N 4°40'E during the 2008 autumn migration in Nigeria (1,100 km); 14°20'N 10°5'E during the 2009 autumn migration, also in Nigeria (510 km); 29°30'N 1°33'E during the 2009 spring migration in Algeria (1,230 km); and 18°15'N 8°55'W during the 2010 spring migration in Mauritania (2,500 km).

The spring migration route in 2010 passed over the Strait of Gibraltar but all other migration routes crossed the central Mediterranean. North of the border between Nigeria and Cameroon (7°N 12°E), the four routes traced were fairly wide apart but were quite similar between 7°N and the wintering area (fig. 1). In Africa, the spring 2010 route was noticeably farther west than the other routes, being up to 2,150 km west of the autumn 2009 route and up to 1,500 km west of the spring 2009 route. This resulted in a 'migration loop' for 2009/10, which was not the case in 2008/09 (fig. 1).

The autumn migration in 2008 (8,525 km) took 49 days, that in 2009 (7,793 km) took 42 days. Spring migration in 2009 (7,640 km) took 35 days, while the much longer spring 2010 route (8,678 km as far as the German border) took 38 days. In spring 2010 the bird's migration speed slowed dramatically in southern Germany and no fixes were received after this time.

Autumn migration 2008

After departure on 28th/29th August, the route initially took a SSW direction and, after a short rest from 6th–13th September on the

island of Elba, off the west coast of Italy, continued in a SSE direction as far as North Africa. From Libya (20th September, 29°50'N 13°38'E) migration resumed again in a SSW direction, reaching its most westerly point (10°30'N 4°40'E) on 30th September in western Nigeria, near the border with Benin. After an initial 90° switch in direction to the southeast, from 8th October on the Nigeria-Cameroon border (7°N 12°E) the falcon took an almost southerly course. It held this course until arrival at its main wintering area in southern Angola on 17th October, after a total flight of some 8,525 km.

Spring migration 2009

Spring migration began some 27 km southeast of Quibala (10°50'S 15°11'E) and covered a distance of 259 km on that day. From northern Nigeria it flew progressively west of its route the previous autumn, covering daily flight distances of up to 380 km in the rain-

forest region and 395 km over the Sahara. At the beginning of May, after some 35 days of migration, the bird reached its breeding site (where a male had been observed during the last few days of April). In total, 7,640 km were covered at an average of 218 km/day. Some 5,169 km in 21 days (246 km/day) were covered as far as Algeria. During the Sahara crossing, 1,184 km were covered in just three days towards the end of April.

Autumn migration 2009

Departure from the breeding area took place on 29th or 30th August, the bird initially heading almost due south. After resting on the Mediterranean coast in the vicinity of the Tunisia–Algeria border from at least 7th to 14th September, no other rest stop was recorded. The bird's speed was quickest when crossing the Sahara and the equatorial rainforest, with 850 km being covered in Niger on 21st–22nd September and 913 km on 26th– 27th September in the rainforest region. In contrast, daily flight distances of only 70–220



2. The breeding site of the Hobby *Falco subbuteo* discussed in this paper, northwest of Berlin, August 2008.

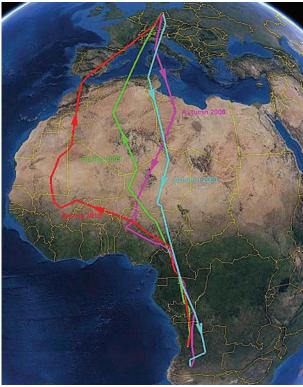


Fig. I. The autumn and spring migration routes of an adult Hobby *Falco subbuteo* between its breeding site in Germany and the wintering area in Angola, from autumn 2008 to spring 2010.

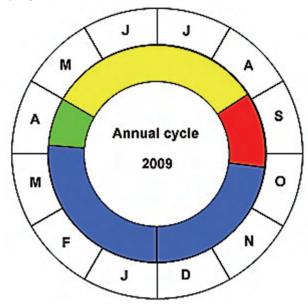


Fig. 2. The annual cycle of an adult Hobby *Falco subbuteo* as revealed by satellite telemetry. In 2009 the bird spent 49.3% of the year in the wintering area (blue), 7.2% on spring migration (green), 32.3% of the time in the breeding area (yellow) and 11.2% on autumn migration (red).

km were made in Nigeria and Angola. Around midday on 9th October, having covered a total of at least 7,795 km, it arrived in its wintering area in central Angola (13°41'S 15°52'E).

Spring migration 2010

Spring migration began on 31st March at 10°37'S 15°8'E. The bird rested in northern Angola on 2nd-4th April, before crossing the rainforest region on the equator where it made daily flight distances of up to 380 km. On 15th April the bird changed direction sharply to the northwest on the Cameroon–Nigeria border (7°N 12°E). It then flew in almost a straight line for 2,280 km to western Mali, including a stretch of 334 km along the River Niger on 22nd April. From Mali the bird headed almost directly north and reached the southern fringe of the Sahara on the evening of 24th April. It reached the Strait of Gibraltar on 30th April and made a night crossing. In Mali and Morocco it migrated 1,243 km on 28th-29th April; this average speed of 621 km/day is the fastest by this falcon on all the recorded migration routes. It also moved quickly from Gibraltar to the south of France, covering 1,032 km on 30th April and 1st May.

In contrast, the bird migrated very slowly from southern France (at an average of just 111 km/day) and did not reach the German-Swiss border at Schaffhausen until the evening of 7th May. Up to this point it had covered 8,678 km in 38 days (228 km/day). Some 9.5 days later the Hobby was located in southern Germany for the last time, in the vicinity of Nuremberg. It had flown just 191 km further and the distance to the nest-site was still 470 km. It remains unknown whether or not the female did reach the breeding



Fig. 3. The marked convergence of the migration routes against the background of the global tree cover (derived from remote sensing) during the crossing of the West African evergreen rainforest. The use of the narrowest part of the forest north of Kinshasa is clearly distinguishable.

area but then chose another site (which is certainly possible since no male occupied the original nest-site northwest of Berlin in 2010).

Migration speed

The transmitter was programmed so that it was generally possible to record the migration distance for a total of two or more consecutive days only. However, on ten occasions on spring migration the flight performance on a single day was recorded. The minimum daily flight distance was 95 km, the maximum 481 km and the average 248 km/day. However, the values of two or more days taken together indicate that on some days the falcon flew considerably further than 481 km, and must have covered at least 620 km. On days with short flight distances the bird presumably adopted a fly-and-forage migration strategy, especially between the southern fringe of the Sahara and the northern edge of the rainforest. This was also the case south of the rainforest, where the bird covered only about half the daily distance flown over the key barriers of the Sahara and the rainforest. On 7th October 2008 in Cameroon, for example, the bird had covered only 40 km by midday, and from then until evening it flew only a further 87 km.

Crossing the Sahara

Crossing the Sahara took some 4-4.5 days on each occasion. In spring 2009, the bird crossed some 2,100 km of the Sahara in Niger and Algeria between the morning of 22nd April and midday on 26th. On 23rd-25th April the average daily distance covered in Algeria was 400 km. In spring 2010, the Sahara was crossed during 25th-29th April, mainly in Mauritania (and to a lesser extent in Mali and Morocco), a total distance of 1,670 km. On five days the bird covered an average distance of 440 km, including the desert fringes. The exact daily flight distance was recorded on three days - 25th April (481 km), 26th April (212 km), and 27th April (326 km) - followed by the remaining 1,240 km on 28th-29th. At 08.18 hrs on 25th, the bird had already flown 123 km from its night roost, while between 10.00 and 11.00 hrs it flew only a few kilometres. On 27th, the bird started migrating as early as 04.00 hrs (some two hours before sunrise) but rested from at least 06.30 to 11.00 hrs. In three cases, average flight speeds of 25, 30 and 42.5 kph over several hours of flight were calculated.

Migration across the rainforest

The West African equatorial rainforest appears to be a significant ecological barrier. All four routes across the rainforest (from approx. 5°45'N 12°33'E to 0°15'S 14°20'E) were very close to one another, and from the Nigeria-Cameroon border to Angola there was hardly any deviation. The routes passed through a large, roughly north-south corridor (or 'peninsula') of more open habitats dominated by farmland, degraded woodland and moist savannah (fig. 3). This corridor is some 370 km long and 200 km wide and stretches north from Kinshasa, DR Congo, to about 0°15'S 14°20'E. This significantly shortens the distance to be flown over continuous rainforest, to some 450-600 km.

In autumn 2008, the lowland forest in Congo was crossed in a 680-km-long stretch. Here the falcon travelled at a rate of about 580 km/day, one of the highest daily distances recorded. In autumn 2009 the distance flown over the rainforest was c. 695 km, covered at a rate of about 450 km/day. In spring 2009, a stretch of 730 km was flown over the rainforest between the afternoon of 12th April and c. 01.00 hrs on 15th April at an average of 380 km/day. In spring 2010, daily distance covered over the rainforest and adjacent areas was c. 400 km.

Migration during twilight and at night

Migration at night was recorded repeatedly while crossing the Sahara and rainforest areas, but also in the Mediterranean. For example, in order to reach the northern perimeter of the rainforest in Cameroon, the bird flew an additional 260 km after sunset on 14th April 2009, and arrived at its night roost, clear of the rainforest, after midnight. On one part of the route, 57 km in length, it flew at an average speed of 34 km/h. In spring 2010 the Hobby also covered part of the route in darkness until reaching the northern fringe of the rainforest. During the early morning of 9th April, before sunrise, it covered over 250 km; thereafter, until midday, it flew only 90 km. The fixes did not permit us to establish whether it migrated throughout the night.

The bird migrated in the dark in at least the early morning hours while crossing the Sahara in 2010 (see above). Furthermore, on 30th April 2010, the Hobby was located over the Mediterranean near Gibraltar at 02.54 hrs, some 2.5 hours before sunrise. From its surmised night roost in Morocco it had at this time already covered 122 km and so must have been on the move for at least three hours.

Wintering

On both occasions, the Hobby wintered mainly in the same regions (Cunene, Huila and Cuando Cubango) of south and central Angola and, to a lesser extent, in the far northeast of Namibia, where it visited the same areas in both winter periods. The 'home range' in winter was very large with the actual size dependent on the method of calculation. In 2008/09 it comprised 406,000 km² and in 2009/10 it covered 461,000 km² (Kernel 80%). Calculations based on the MCP method arrived at the following values. In 2008/09, MCP 95% equalled 280,000 km²

 Table 1. Habitat use in the wintering area calculated on the basis of identified night roosts, and taking account of the excursion into Zambia 2008/09.

	No. of night roosts 2008/09	%	No. of night roosts 2009/10	%	
Angolan Miombo woodlands	38	50	45	58	
Zambezian Baikiaea woodlands	28	37	19	24	
Southern Miombo woodlands	3	4	-	-	
Kalahari Acacia-Baikiaea woodlands	3	4	12	15	
Angolan montane forest-grassland mosaic	1	1	1	1	
Angolan Mompane woodlands	1	1	1	1	
Western Zambezian grasslands	1	1	-	-	
Southern African bushveld	1	1	-	-	

and MCP 80% was 226,000 km². In 2009/2010, MCP 95% equalled 278,000 km² and MCP 80% was 248,000 km². An excursion to Zimbabwe in 2008/09 (see below) was not included in these calculations.

The bird spent about half its time in winter (50% in 2008/09, 58% in 2009/10) in the Angolan Miombo woodlands (fig. 4 and table 1), a habitat made up of alternating moist, large-leaved savannah and woods 5–10 m high interspersed with grassland, at an altitude mainly 1,000– 1,500 m above sea level. The Miombo is characterised by several unique ecological factors, including an abundance of termites, which are an important food source for the Hobby. The second most important habitat was the Zambezian Baikiaea woodlands.

Winter 2008/09

From 17th October to 7th April there were 543 fixes in the wintering area, of which 392 were in the classes LC 1-3 (fig. 5). Over two months after arriving in southern Angola it moved further in a southeasterly direction and arrived in Zimbabwe on 29th December. On 1st January 2009 it reached the southernmost point of this winter movement (19°45'S 29°45'E), between the cities of Bulawayo and Harare in central Zimbabwe (fig. 6). The distance migrated from the breeding site, not including regional movement in Angola, was 10,065 km up to this point. The Hobby did not linger in Zimbabwe and retreated almost immediately to its wintering area in Angola/Namibia. The total distance of this excursion from 25th December 2008 to 12th January 2009 was some 2,785 km, at an average of 174 km/day. A total of 76 night roosts were identified, of which 66 (87%) were in Angola, three each in Namibia, Zimbabwe and Zambia, and one in Botswana.

In its main wintering area the Hobby showed a propensity for travel, illustrated by the recording of no

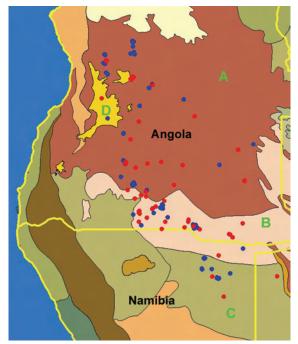


Fig. 4. Roost-site locations during both wintering periods (2008/09 red, 2009/10 blue) in different habitats (A = Angolan Miombo woodlands, B = Zambezian Baikiaea woodlands, C = Kalahari Acacia-Baikiaea woodlands, D = Angolan montane forest-grassland mosaic).

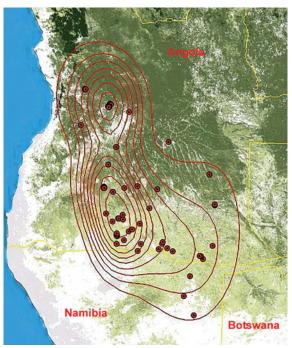


Fig. 5. The Kernel home range in winter 2008/09 based on 69 night roosts in Angola and Namibia (plotted against the background of the global tree cover, derived from remote sensing).



3. Hobby Falco subbuteo, Tammisaari, Finland, July 2005.

fewer than 543 different tracking fixes. From 16th October 2008 to 7th April 2009, the bird never spent as long as a week in the same place and covered a total distance of at least 9,025 km. This calculation is based on the distance between the 76 precise night-roost fixes, which amounted to somewhat less than half of all overnight stops. Within Angola, these fixes, usually recorded at an interval of 48 hours, were sometimes more than 300 km apart. This means that the actual distance covered by the bird during this winter period was significantly greater.

Winter 2009/10

The Hobby remained in the same wintering area from 9th October 2009 to 31st March 2010 without any long-distance excursion in this winter (fig. 7). Some 77 night roosts were located, 11 in northwest Namibia (1st–25th

January) and the remainder in Angola. The consecutive distances from roost to roost totalled 6,432 km (fig. 8); as in the previous winter, the real distance covered during winter must have been considerably greater. The same areas were visited repeatedly, some of them the same as in the previous winter period.

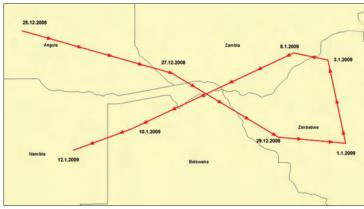


Fig. 6. The 2,785 km-long excursion to Zimbabwe during winter 2008/09.

Discussion

With the advance of satellitetelemetry technology, information on the ecology and life history of raptors has been greatly increased compared with what could possibly have been gathered during decades of conventional telemetry and ringing. However, when using telemetry as a study method, the weight of the transmitter (and its harness) should not exceed 3% of the body mass of the study subject, in order not to affect the bird's behaviour and thus bias the study results (Meyburg & Fuller 2007). This limitation has not been respected in several recent falcon studies. The 3% rule still excludes 85% of all bird species from satellite telemetry studies and, of nearly 10,000 species of birds alive today, only about 1,500 are large enough to carry even the smallest, 5-g transmitters. The prototype of what is currently the smallest transmitter, weighing just 5 g, was first used successfully by us on the adult female Hobby described in this paper.

Early departure of the female on migration

In both years the female departed at the same time (28th/29th August), irrespective of whether or not there were young to be cared for. This early departure from the breeding territory of the female Hobby, long suspected to be the case with females (Fiuczynski 1987), was confirmed in this study. In the first few weeks after the young fledge, the female plays an important role in territorial defence and in the receipt and distribution of prey (chiefly birds) brought back by the male. As the flight skills of the young improve, they reach the returning male before the female, so that she increasingly takes a lesser role in rearing the young (Fiuczynski

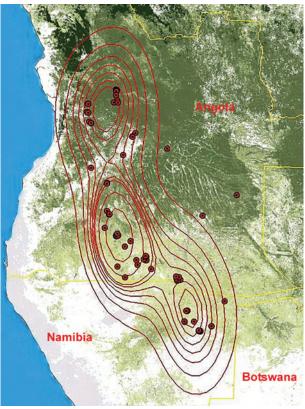


Fig. 7. The Kernel home range in winter 2009/10, based on 77 night roosts (plotted against the background of the global tree cover, derived from remote sensing).



Fig. 8. Changes in location between the 77 night roosts during winter 2009/10.



4. Hobby Falco subbuteo, Tammisaari, Finland, July 2005.

1987). The provision of small birds as food for the young is clearly an important precondition for the long-distance migration flight that begins in September, and this, as well as territorial defence, is reliably carried out by the male as the young improve their flying skills.

Migration routes

For most long-distance migrants, ring-recoveries from Africa are far too few to properly explain the patterns and strategies associated with migration. We are aware of just two such ring-recoveries for the Hobby south of the Sahara. A Dutch bird, ringed as nestling on the Wadden Sea Island of Texel on 26th July 1982 (53°03'N 4°43'E), was found dead on 26th November 1992 near Kabwe, Zambia (14°26'S 28°27'E), a recovery distance of 7,820 km (Dowsett et al. 2008); while a nestling ringed in Pälkäne, southern Finland, on 19th July 2006 was found electrocuted on 7th March 2007 in South Africa, a recovery distance of 9,650 km (Finnish Ringing Centre, www.luomus.fi/english/zoology/ ringing/index.htm). In addition, Strandberg et al. (2009a,b) published results obtained from the satellite tracking of four Hobbies between their breeding grounds in Sweden and their wintering areas in southern Africa (although they were not able to follow the birds in winter or on their subsequent spring migration).

Our satellite-tracked Hobby showed no clear preference for the shortest sea crossing when traversing the Mediterranean. Frequent sea crossings by the smaller falcons have been reported by earlier radar studies at the south coast of Spain, in both spring and autumn (Meyer *et al.* 2000, 2003).

The four flight paths plotted were far apart across much of Africa, the maximum east–west separation being 2,150 km, a distance that far exceeds the expected normal range of vision. This suggests that the Hobby did not navigate by following familiar landmarks but that it could find its target regions after extensive deviation, presumably by 'map-based' navigation and possibly in combination with path integration. The four routes showed several distinctly non-random features, however. In particular, there was an overall westerly bias to the routes, compared with a direct line between the breeding and wintering areas. The westerly deviation from a straight-line route was particularly pronounced over and to the north of Nigeria during spring migration, especially in 2010. Furthermore, there was a striking convergence of the four routes over an inland area close to the equator, well north of the bird's final winter destination in Angola, which closely matches the findings of Strandberg et al. (2009b). Such convergence of migration routes is generally thought to occur in response to distinctive topography (for example the bottlenecks of large soaring birds at places such as Gibraltar and the Bosporus) and/or reflect a species' navigation to a particular target area, such as a welldefined winter range.

The most challenging aspects of our findings to explain are the extensive migration loop, in particular the extreme westerly course, of the spring 2010 migration route; the convergence near the equator; and the vast distances that the bird covered in its wintering area. In particular, we have no convincing explanation for the 2010 spring migration route, especially given that most species usually migrate more to the east in spring than in autumn (Newton 2008). Analysis of the data on wind direction and precipitation from all meteorological stations along the migration routes provided us with no further clues, although Strandberg et al. (2009b) suggested that the westward shift of routes they observed over the Sahara was in response to drift in easterly crosswinds. Interestingly, two adult Eleonora's Falcons F. eleonorae also migrated much farther to the west in spring than in autumn (Gschweng et al. 2008). One contributory factor to the bird's route could be the migration tracks of Barn Swallows Hirundo rustica, House Martins Delichon urbicum, Common Swifts Apus apus and other important prey species (hirundines and swifts make up 55% of the avian prey species of the Hobby around Berlin; Fiuczynski et al. 2009). Barn Swallows in particular have similar migration routes and wintering areas to the Hobby, and departure and arrival times in Europe are also very similar to those of the Hobby (e.g. Sparks & Braslavská 2001). In France in recent years (2008-10), there has been a close similarity in terms of the passage periods in both

British Birds 104 • January 2011 • 2-15

spring and autumn of these two species (see www.hirondelle.oiseaux.net/migration.html), but the exact migration routes of hirundines and swifts within Africa are unknown. In spring, experienced Barn Swallows may be able to return north in about five weeks at a speed of about 300 km/day (Mead 1970); this again is similar to the performance of the Hobby, which may exploit the swallows as a convenient prey species. This is also supported by observations in Zambia (see below).

The convergence of the Hobby's routes near the equator fit neatly with the hypothesis that the bird aimed to take advantage of the narrowest crossing of the equatorial rainforest, and this suggests that this habitat is avoided by northern migrants not only for wintering but also during migration. The rainforest may be a barrier not only because the habitat structure of the forest is unfavourable for hunting, but also because of the weather conditions, with high rainfall. Our results thus support Strandberg et al. (2009b) that the continuous evergreen rainforest constitutes an important barrier that affects the major flyways and stopover strategies by which Hobbies, and perhaps other migratory landbirds, travel to and from their winter quarters in southern Africa. It is most important that we understand the role of the rainforest as an ecological barrier of possibly continental-scale significance for the evolution and future of the Palearctic-African bird migration systems.

Migration speed

The flight speed of the Hobby tracked in our study during outward migration was significantly faster (8,525 km in 49 days or 7,793 km in 42 days, 174 and 185 km/day respectively) than the somewhat longer migrations of the Swedish Hobbies tracked by Strandberg et al. (2009a), which needed on average 61 days for a mean distance of 9,223 km (151 km/day). To date there are no other data for us to compare with the spring migration routes described here. The differences that we found in migration speed during the Sahara and rainforest crossings, compared with other parts of the route, were also recorded for the Swedish Hobbies. The daily rains associated with the rainforest may limit the

foraging possibilities for this species and this may be one explanation of the increased speed over and close to the forest.

In terms of other species, North American Peregrine Falcons *F. peregrinus* flew at similar speeds in autumn (172 km/day) over a route of similar length (8,624 km on average) (Fuller *et al.* 1998). Two Eleonora's Falcons also covered somewhat similar daily distances (192 and 219 km) (López-López *et al.* 2009). The night flight of the Hobby is surprising, however, as this has so far been established for very few species of raptor (Bildstein 2006).

Wintering

In Zambia, the first Hobbies to arrive from the north often appear in early October (mean date 15th October over 30 years), while departure is in mid March (mean last date is 30th March for a 28-year sample); extreme dates are 22nd September and 23rd April (Dowsett *et al.* 2008). The main passage south seems to be influenced by the arrival of heavy rains, when the largest numbers of this species are associated with flocks of Barn Swallows.

The long distances covered by this individual Hobby in the wintering area are surprising, as are the vast home ranges. The total distance travelled in winter was probably more than that travelled in autumn or spring on migration, at least in winter 2008/09. It was not possible to establish the cause of these extensive flights. A great deal of the falcon's diet probably consisted of energyrich termites, which are particularly common in the rainy season in the areas of Angola visited by the bird. We are not aware of comparative data for other falcons. However, a Black Kite Milvus migrans tracked by GPS transmitter covered at least 14,000 km in its wintering area in West Africa (Meyburg & Meyburg 2009). That bird had three different home ranges of up to 88,000 km² in consecutive years.

Acknowledgments

Our thanks go the responsible authorities for permission to trap the falcon and deploy the transmitters. Rouven Polep and Holm Benning enabled us to test transmitter fastenings for long periods on Hobbies in captivity. Paul Sömmer ran checks on the breeding site and erected an artificial nest platform.

References

- Argos. 1996. User's Manual. CLS/Service Argos, Toulouse. (www.argos-system.org/manual).
- Bildstein, K. L. 2006. Migrating Raptors of the World: their ecology and conservation. Cornell University Press, London.
- Brown, L. H., Urban, E. K., & Newman, K. 1982. The Birds of Africa. Vol. I. Academic Press, London.
- Chapman, A. 1999. *The Hobby*. Arlequin Press, Chelmsford.
- 2002. Eurasian Hobby. In: Wernham, C. V., Toms, M. P., Marchant, J. H., Clark, J. A., Siriwardena, G. M., & Baillie, S. R. (eds.), The Migration Atlas: movements of the birds of Britain and Ireland, pp. 253–255. Poyser, London.
- Dean, W. J. R. 2000. The Birds of Angola. BOU, Tring.
- DeFries, R. S., Hansen, M. C., Townshend, J. R. G., Janetos, A. C., & Loveland, T. R. 2000. A new global I-km data set of percentage tree cover derived from remote sensing. *Global Change Biol.* 6: 247–254.
- Dowsett, R. J., Aspinwall, D. R., & Dowsett-Lemaire, F. 2008. The Birds of Zambia. Tauraco Press and Aves, Liège.
- Fiuczynski, D. 1978. Zur Populationsökologie des Baumfalken (*Falco subbuteo* L., 1758). *Zool. Jahrb. Systematik* 105: 193–257.
- 1987. Der Baumfalke Falco subbuteo. Neue Brehm-Bücherei No. 575. Ziemsen Verlag, Wittenberg.
- 2007. Populationsdynamik des Baumfalken (Falco subbuteo) in den letzten 50 Jahren in Berlin mit Anmerkungen über die anderen Greifvögel. Sitzungsber. Ges. Naturforschender Freunde Berlin (N.F.) 46: 47–57.
- & Nethersole-Thompson, D. 1980. Hobby studies in England and Germany. Brit. Birds 73: 275–295.
- Hastädt, V., & Sömmer, P. 2009. Der Baumfalke (Falco subbuteo) im Berliner Raum: Populationsentwicklung, Reproduktion, Habitatveränderung und Schutzmaßnahmen. Populationsökologie Greifvogel- und Eulenarten 6: 327–340.
- Fuller, M. R., Segaar, W. S., & Schueck, L. S. 1998. Routes and travel rates of migrating Peregrine Falcons Falco peregrinus and Swainson's Hawks Buteo swainsoni in the western hemisphere. J. Avian Biol. 29: 433–440.
- Gros, P., & Malardé, J-P. 2006. Argos performance in Europe. *Tracker News* 7: 8.
- Gschweng, M., Kalko, E. K.V., Querner, U., Fiedler, W., & Berthold, P. 2008. All across Africa: highly individual migration routes of Eleonora's Falcon. *Proc. Roy. Soc.* B. 275: 2887–2896.
- Kenward, R. E. 2001. A Manual for Wildlife Radio-tagging. Academic Press, London.
- Laver, P. N., & Kelly, M. J. 2008. A critical review of home range studies. J. Wildl. Mgmt. 72: 290–298.
- López-López, P., Liminana, L., Mellone, U., & Urios, V. 2009. Autumn Migration of Eleonora's Falcon Falco eleonorae tracked by satellite telemetry. Zool. Studies 48: 485–491.
- Mead, C. J. 1970. The winter quarters of British Swallows. *Bird Study* 17: 229–240.
- Mendelsohn, J. M. 1997. Hobby Falcon. In: Harrison, J. A., Allan, D. G., Underhill, L. G., Herremans, M., Tree, A. J., Parker, V., & Brown, C. J. (eds.), The Atlas of South African Birds, Vol. 1 Non-passerines, pp. 252–253. BirdLife South Africa and Avian

Demography Unit, Johannesburg.

- Meyburg, B-U., & Fuller, M. R. 2007. Satellite tracking. In: Bird, D. M., & Bildstein, K. L. (eds.), *Raptor Research and Management Techniques*, pp. 242–248. Hancock House Publishers, Surrey, Canada.
- & Meyburg, C. 2009. G^PS-Satelliten-Telemetrie bei einem adulten Schwarzmilan Milvus migrans: Aufenthaltsraum während der Brutzeit, Zug und Überwinterung. Populationsökologie Greifvogel- und Eulenarten 6: 311–352.
- Meyer, S. K., Sparr, R., & Bruderer, B. 2000. To cross the sea or to follow the coast? Flight directions and behaviour of migrating raptors approaching the Mediterranean Sea in autumn. *Behaviour* 137: 379–399.
- —, —, & 2003. Sea crossing behaviour of falcons and harriers at the southern Mediterranean coast of Spain. Avian Sci. 3: 153–162.
- Newton, I. 2008. The Migration Ecology of Birds. Academic Press, London.
- Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, V., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P. & Kassem, K. R. 2001. Terrestrial Ecoregions of the World: A New Map of Life on Earth. *BioScience* 51: 933–938.
- Pepler, D. 1993. Diet and hunting behaviour of the European Hobby (*Falco subbuteo*) in Africa. In: Nicholls, M. K., & Clarke, R. (eds.), *Biology and Conservation of Small Falcons*, pp. 163–170.

The Hawk and Owl Trust, London.

- Pinto, A. A. da Rosa. 1983. Ornitologia de Angola. Vol. I. Instituto de Investigacao Científica Tropical, Lisbon.
- Rodgers, A. R., & Carr, A. P. 1998. HRE: *The Home Range Extension for ArcView*. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario.
- —, —, Beyer, H. L., Smith, L., & Kie, J. G. 2007. *HRT: Home Range Tools for ArcGIS*. Version 1.1. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario.
- Selkirk, S. W., & Bishop, I. D. 2002. Improving and extending home range and habitat analysis by integration with a Geographic Information System. *Transactions in GIS* 6: 151–159.
- Sparks, T. H., & Braslavská, O. 2001. The effects of temperature, altitude and latitude on the arrival and departure dates of the Swallow *Hirundo rustica* in the Slovak Republic. *Int. J. Biometeorol.* 45: 212–216.
- Strandberg, R., Klaassen, R. H. G., Olofsson, P., & Alerstam, T. 2009a. Daily travel schedules of adult Eurasian Hobbies *Falco subbuteo* — variability in flight hours and migration speed along the route. *Ardea* 97: 287–295.
- —, —, Hake, M., Olofsson, P., & Alerstam, T. 2009b. Converging migration routes of Eurasian Hobbies *Falco subbuteo* crossing the African equatorial rain forest. *Proc. Roy. Soc.* B 276: 727–733.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164–168.
- Prof. Dr Bernd-Ulrich Meyburg, Wangenheimstr. 32, 14193 Berlin, Germany; e-mail BUMeyburg@aol.com

Dr Paul W. Howey, Microwave Telemetry, Inc., 8835 Columbia 100 Parkway, Suites K & L, Columbia, MD 21045, USA; e-mail Paul@microwavetelemetry.com

Christiane Meyburg, 31, Avenue du maine, 75015 Paris, France; e-mail Schwarzmilan@aol.com Dr Klaus Dietrich Fiuczynski, Westfalenring 26, 12207 Berlin, Germany; e-mail klaus fiuczynski@yahoo.de

A

Bernd-Ulrich Meyburg is chairman of the World Working Group on Birds of Prey (WWGBP). He has carried out research on no fewer than 16 raptor species since 1992 using satellite telemetry. **Paul Howey** is president and owner of Microwave Telemetry, Inc. (USA), and a pioneer in producing satellite-tracking devices for birds. He built the first 5 g satellite transmitters. **Christiane Meyburg** worked as a researcher at the National Institute of Statistics and Economic Studies (INSEE) in Paris. Since 1992 she has helped her husband analyse the satellite-tracking data from his projects. **Klaus Dietrich Fiuczynski** worked as a teacher, completed a PhD on the Hobby and has written a major monograph on this species (a new edition of which is almost complete).