

15 Years' Satellite Tracking of Raptors

Bernd-U. MEYBURG⁽¹⁾ & Christiane MEYBURG⁽²⁾

15 years' satellite tracking of raptors. Satellite telemetry has revolutionised the study of raptor migration and life histories, and will do so even more in the future. This is because the tracking systems can regularly estimate and record an individual's location worldwide over a period of several years.

To begin with we give a short overview of the development of the technical side of satellite telemetry and the present state of the art. This can be divided into three phases: the period during which only battery-powered transmitters with Doppler locating were available, the period during

which solar-powered transmitters with Doppler locating were used, and finally the period during which transmitters with GPS locating could be employed (TAB. I). The paper includes project planning tips for those putting this technical equipment to use. In addition, there is an overview of the questions for which the use of this technique can provide answers or has already done so (TAB. III). Finally we report on a few highlights of our own telemetry results, based on the monitoring of 146 individuals of 14 different species which we fitted with transmitters between 1992 and 2007 (TAB. II).

Key words: Raptors, Birds of prey, Satellite telemetry, Satellite tracking, GPS, Migration.

(1) Wangenheimstr. 32, D-14193 Berlin, Allemagne (BUMeyburg@aol.com).

(2) 31 Avenue du Maine, F-75015 Paris (Schwarzmilan@aol.com).

INTRODUCTION

The protection of migratory birds poses specific problems. The fact of migration makes study difficult, with classical ringing yielding only partial information regarding the migration routes and wintering area.

Satellite telemetry has revolutionised the study of raptor migration and behaviour and will develop this even further in the future (MEYBURG & FULLER, 2007). Methods of tracking animals by satellite can assemble and store their status worldwide for many years to come. This technique was first applied to birds in the 1980s but was still at an experimental stage until 1992, when sufficiently small and light transmitters making it possible to equip large species came on the market and we were able to pursue our studies in this field. Until recently this technique was based solely on the Hertzian signals of the ARGOS system.

The PTTs provided by GPS receivers are now made small enough to be used in ornithology. The locations obtained at present, of a precision within only a few dozen metres, make it possible to study territorial behaviour, use of the natural environment and feeding strategy (MEYBURG *et al.* 2006; MEYBURG &

FULLER, 2007). In many cases the GPS technique will replace others due to the quality of its terrestrial telemetry (VHF tracking).

The development of satellite telemetry (ST) covered three main phases. For the study of medium-sized species like the Osprey *Pandion haliaetus* these are summarised in Table 1.

METHODS OF TRACKING RAPTORS BY SATELLITE

The ARGOS system

For the study of raptors ST uses the ARGOS system. The birds have to be equipped with transmitters called PTTs or platforms weighing 5 g or more. This system provides estimations of the geographical position of the PTT as well as technical data provided by its receivers (e.g. voltage of the cells, activity, temperature, atmospheric pressure) everywhere in the world. The ARGOS users' handbook describes the way it operates in greater detail (<https://www.argos-system.org/manual/>) The three phases of the technical development of satellite telemetry: data shown is for the time period applicable to middle-sized species such as the Osprey.

TABLE I.– The three phases of the technical development of satellite telemetry: data shown is for the time period applicable to middle-sized species such as the Osprey

DATES	TYPE OF ARGOS TRANSMITTER	COMMENTS
1992-1995	Battery-powered PTTs with Doppler locations	Life expectancy of about one year when programmed to send for several hours every few days. Maximum of 100-150 locations per annum.
1995-2003	Solar-powered PTTs with Doppler locations	PTTs with a life expectancy of several years (one case of over 7 years) providing thousands of ARGOS locations per annum when sufficient light available, permitting study of migration.
Since 2004	Solar-powered PTTs with built-in GPS	Locations precise to within a few dozen metres, permitting analysis of behaviour in detail

Estimations of the PTTs position by ARGOS

The PTTs are located through the Doppler effect. ARGOS orbiting satellites are equipped with receivers. When the satellite is nearing the PTT, the frequency of reception increases beyond the nominal rate of transmission (401.650 MHz), whilst it diminishes as the satellite draws away. At the Doppler curve's point of inflection, when the frequencies of reception and transmission are equal, the satellite is vertically above the PTT. The system then calculates two possible positions for the PTT, symmetrically on either side of the satellite's ground track. ARGOS selects one of these as the most plausible, but the biologist must confirm its validity.

Researchers should meticulously examine the quality of the locations calculated by the system before using them for their analyses. Validation of the data depends on the bird's behavioural criteria (e.g. maximum speed, local or migratory movements) as well as the technical parameters provided by ARGOS (number of messages received during the satellite's passing, stability of the PTT's frequency). The locations provided are only estimations, the precision of which varies according to factors in large part unknown (MEYBURG & FULLER, 2007).

The raw data (coded messages) collected by the satellites are transmitted to the processing centres in France and the USA. The results obtained there, i.e. locations of the PTTs and qualified information on their precision, are available to PTT owners in different forms. The costs are based on the number of hours of each PTT's daily activity and the method of distribution of the data desired: automatic by mail, fax, direct access by users' Telnet or the ARGOS website, as well as monthly CDs. Users are able to access their data on their computers less than four hours after detection of the PTT by a satellite.

Locations by GPS

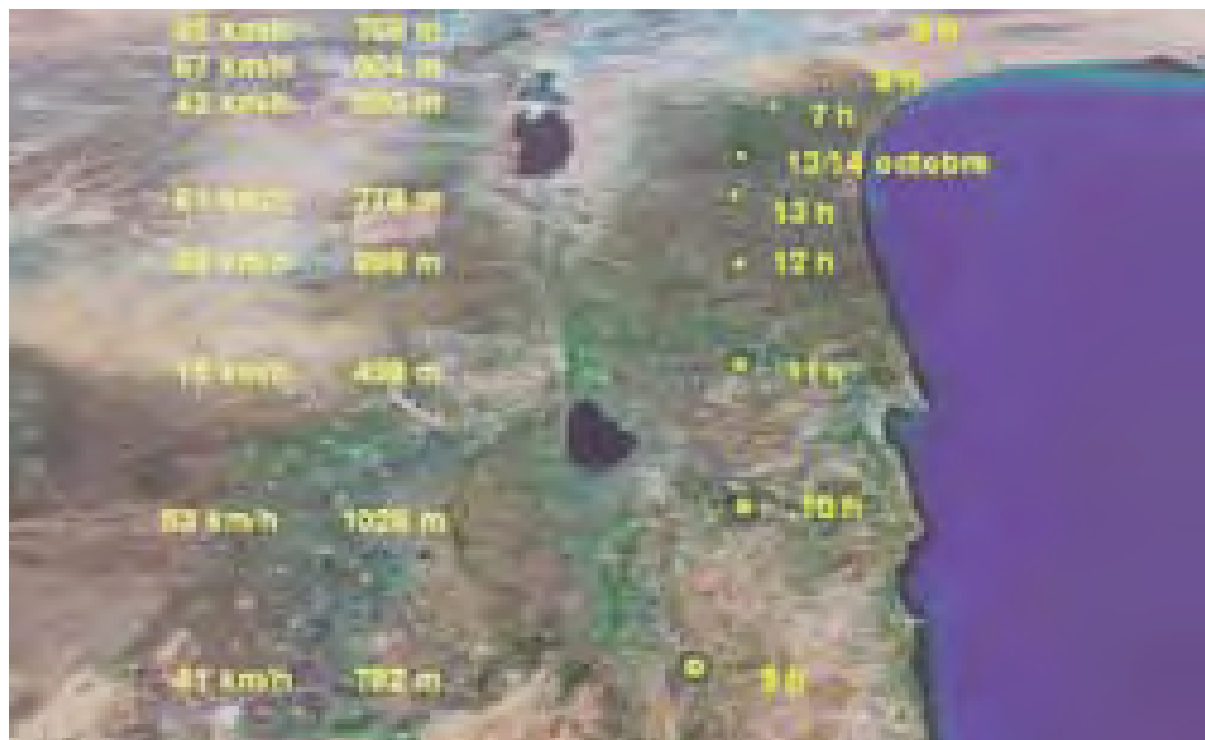
GPS (Global Positioning System) locates PTTs with a precision within the order of a few

dozen metres. A GPS receiver can be incorporated in an ARGOS transmitter. It receives transmissions from at least four satellites calculating the position of the PTT (in three dimensions for PTTs weighing 35 g or more). The GPS can be programmed to collect data at regular intervals; these are transmitted in coded messages to the users by the ARGOS system. The number of messages received varies depending on many factors (meteorological conditions, local Hertzian emissions, degree of openness of the areas frequented, electromagnetic fields). This permits the study of numerous parameters previously impossible to know (size of territory, use of the natural environment in the nest area) as well behaviour on migration, altitude, direction and speed of flight (FIG. 1). PTTs with built-in GPS consume a great deal of energy and there are considerable limitations as to their size, weight and longevity when batteries are used for avian PTTs. The lightest batteries obtaining GPS locations at present weigh 45 g. In our experience they barely last longer than a year if programmed to give one location per day. On the other hand, the weight of those using miniature photovoltaic cells absorbing solar energy has now been reduced to only 22 g (2007) and are able theoretically to provide a GPS position every hour.

Selection of the PTT

The choice of which type of PTT is governed by its effect on the bird's behaviour according to its size, weight and method of attachment. The energy needs of the ST for the transmission of data mean that the lower limit in weight for a solar-powered PTT giving Doppler locations is, at present, around 5 g. This, added to the physical effort involved in the bird's movements, the size of the accumulator and the space required by the solar cells, are factors determining the shape of the PTT. The whole appliance and its Teflon harness should not exceed a maximum of 3% of the bird's weight (MEYBURG & FULLER, 2007).

FIG. 1. Satellite photo of Israel (Mediterranean on right) showing an oblique view in flight direction of an adult male Lesser Spotted Eagle (with PT 23196) on passage on 13 and 14 October 2005. The marked points represent the GPS fixes made on the hour (in GMT), with the flight speed and height a.s.l. on the left. Also shown is the night roost on 13/14 October near Jerusalem.



When planning a study the choice between battery- and solar-powered transmitters must take priority. Battery-powered PTTs are generally very serviceable but have a relatively limited duration, making long-term studies (of over three years) impossible. We have received locations over 6 to 18 months using 30-90 g batteries, depending on the chosen frequency with which signals are received. Solar-powered PTTs can provide locations for many years but the regularity of transmissions depends on the intensity of the sunlight needed to recharge the accumulator sufficiently to allow the sending of radio signals. The incorporated GPS uses still more energy, which adds to the problems of receiving and collating data. It is most important to ensure that the bird's plumage does not risk covering the solar cells as insufficient light inhibits proper functioning. The same applies to birds living mainly under the forest canopy or nesting in cavities.

Before reaching a decision it is equally important to take account of the study's objective and any financial constraints. The price of a classic PTT was around US\$3,000 in 2007, that of the GPS version around US\$4,000. The costs of receiving locations can equal or even exceed the price of the PTT according to the programme chosen and the

use to be made of the ARGOS services. Reasons for the cessation of transmissions

The makers can so programme a PTT that it ceases to transmit after a fixed length of time but most researchers probably wish to receive locations for as long as possible. Battery-powered PTTs provide information on the voltage, making it possible to spot any drop in energy. It is, however, frequent for transmissions to cease sooner than planned and for no apparent reason. It is often very complex and difficult to determine the causes for the breaking-off of reception of signals.

Juvenile and immature birds often die from "natural causes" or are victims of persecution.

Adults too are heavily persecuted in many parts of the world or are killed by electrocution, collisions, etc. We have, however, been able to prove in many instances by direct observation of the birds, on re-trapping them or finding them dead long after the cessation of signals, that the solar-powered PTTs had ceased to be active while the birds were still alive. In certain cases neither we nor the maker could find the reason. Research programmes should allow for the mortality factors of birds fitted with PTTs as well as the probabilities of the transmitters breaking down. So far as solar-powered PTTs are concerned our record has been an adult female Greater Spotted Eagle

Aquila clanga fitted in July 1999 and still transmitting data today (August 2007). An adult male Lesser Spotted Eagle *Aquila pomarina* transmitted as far as its passage through Israel during its spring migration, returning to its nest site almost six years after its capture. It reached Germany a month later and we could see it still carrying its transmitter but without the antenna. One Osprey similarly lost or broke its antenna several months after being fitted. It is easier to determine the reasons for a PTT's breakdown when the adults return every year to their nest site.

ST is one of the many ways of tracking raptors. Before reaching a decision we advise persons wishing to use this technique to consider very carefully their objectives together with the potentially undesirable effects on the birds and the implications of their results. The literature provides numerous examples of research for which satellite telemetry has yielded exceptionally valuable information.

A FEW RESULTS FROM OUR STUDIES

It is naturally impossible to list here the results of our satellite tracking of close on 150 different birds of prey (cf. TAB II, Annexes). We will therefore confine ourselves to mentioning a few of them with aspects of particular interest. TABLE III (cf. annexes) presents a review, not exhaustive, of the various fields of raptor biology which should benefit from data procured through satellite telemetry.

Annual cycle, duration and speed of migration

One of our main objectives was to obtain as complete picture of the movements of adults throughout the year: the exact amount of time spent in the breeding sites, on migration and wintering (FIG. 7). This was achieved for the first time in 1994-1995 for an adult male Lesser Spotted Eagle tracked from northern Germany to its winter quarters in Zambia (MEYBURG *et al.*, 1995). This was the first detailed recording of this type for a European bird migrating to Africa. This eagle spent seven and a half weeks for each of its migrations over a distance of almost 9000 km. It flew a daily average of 166 km and its autumn and spring routes proved to be nearly identical. Its winter quarters in Zambia covered an area of 25,000 km². We have succeeded in documenting the movements of other eagle species for at least one whole year, such as Steppe Eagles *Aquila nipalensis*, Greater Spotted Eagles, Osprey, Honey Buzzard *Pernis apivorus*, Black and Red Kites *Milvus*

migrans and *M. milvus*. The results have only partly been published.

Thanks to solar-powered PTTs it has been possible to compare the routes and time spent on several consecutive years. Satellite tracking of a pair of Lesser Spotted Eagles nesting in the north-west of the species' breeding range yielded 3641 locations in all. Four autumn and two spring migrations were recorded in full between 1997 and 1999. The male took up its winter quarters in Zambia 9,300 km from its nest and the female 11,300 km in Zimbabwe, South Africa and Mozambique. She spent almost half the year on migration (47.6%) and only 9% wintering. The male devoted 35.1% of the year on migration and 21.1% wintering. The migrations lasted an average of 81 days (52 - 119 days), the autumn migrations being clearly longer (74-119 days) than those in spring (52-64 days). The speed of migration varied not only from year to year but also according to the regions crossed. The longest stages were recorded during the crossing of the Sahara (up to 521 km a day), with the highest speed reaching 66.8 km/h.

An adult female Black Kite furnished inverse results so far as the length of migration was concerned. This bird nesting in Thuringia in central Germany, fitted with a PTT on 16 June 2002, has to date (autumn 2007) yielded several thousand "Doppler" locations. Five winterings, mainly in southern Mauretania, and ten migration routes have been thoroughly documented. Each year it has migrated far more rapidly in autumn - the fastest taking only 17 days (averaging 332 km per day) - than in spring.

Migration routes and wintering zones hitherto unknown

Wahlberg's Eagle *Aquila wahlbergi* is a species frequently met with in many parts of Africa and yet there have been very few returns of rings and its migratory behaviour remains virtually a mystery. In Central Africa it disappears after the breeding season to a destination unknown.

The first satellite tracking of a Wahlberg's Eagle, between February and November 1994, gave proof of transequatorial migration within Africa. This adult female, after nesting in north Namibia, was tracked by satellite for a total distance of 8,816 km. At the end of the breeding season it flew northwards, visiting north Cameroon, north-east Nigeria and west Chad. The distance between its breeding territory and its sojourn outside the breeding season was 3,520 km. The northward migration took one month and the return southward took two weeks longer (MEYBURG *et al.*, 1995).

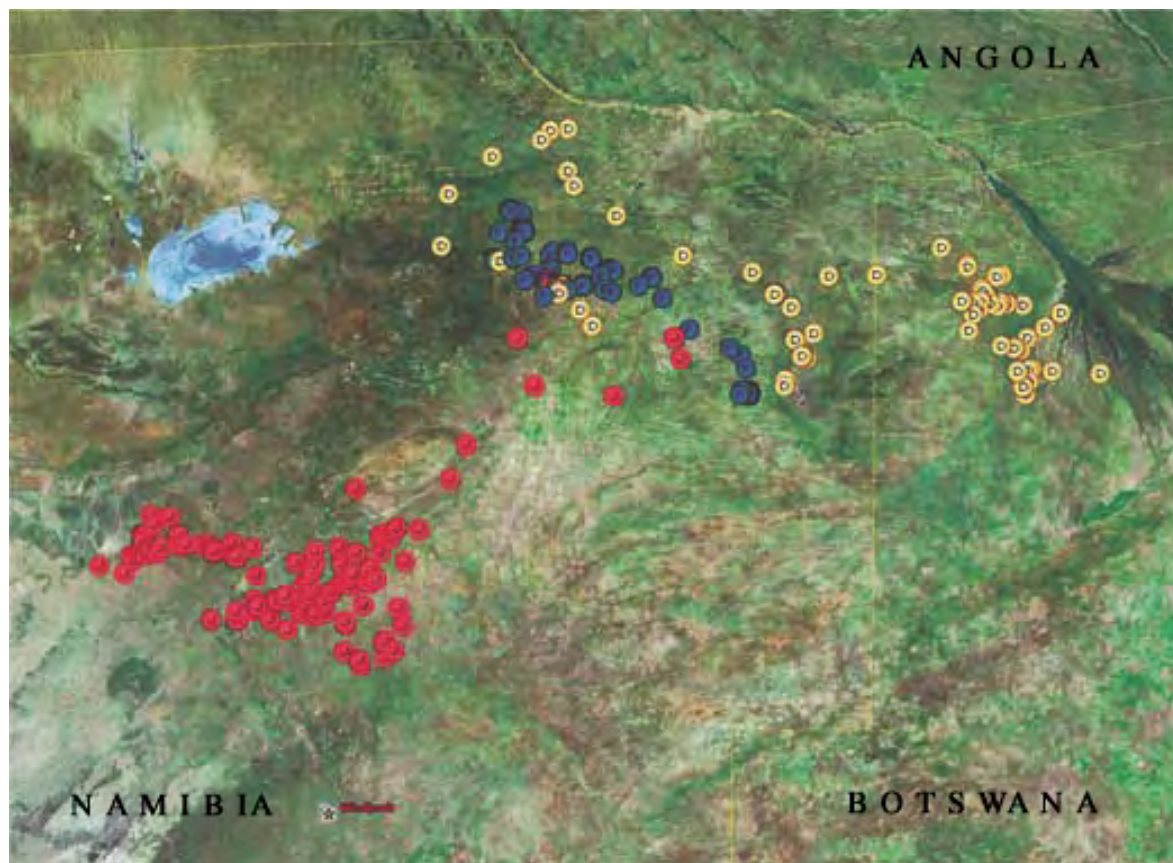
Since 1995 11 adult Greater Spotted Eagles from Poland have been tracked by satellite. They visited at least five countries where they had never, or hardly ever, been previously observed by ornithologists (Chad, Central African Republic, Tanzania, Zambia, Malawi). Two males overwintered in Zambia, around 1,500 km beyond the most southern wintering zones hitherto known for this species (Kenya and Uganda). The first male wintered in Zambia in 1996-97 and again in 1997-98, giving us proof that it spent these two consecutive winters in exactly the same region. During its first winter it remained there for two and a half months (26 December to 9 March 1997), in the north-east of the South Luangwa National Park, where it provided 114 locations. The following winter it returned to exactly the same winter quarters, where it was located 22 times. It remained in an area of only 22.75 km² (6.5 x 3.5 km). A second male overwintered in this same region and was accordingly included in the list of Zambian birds, probably the first time that a species has

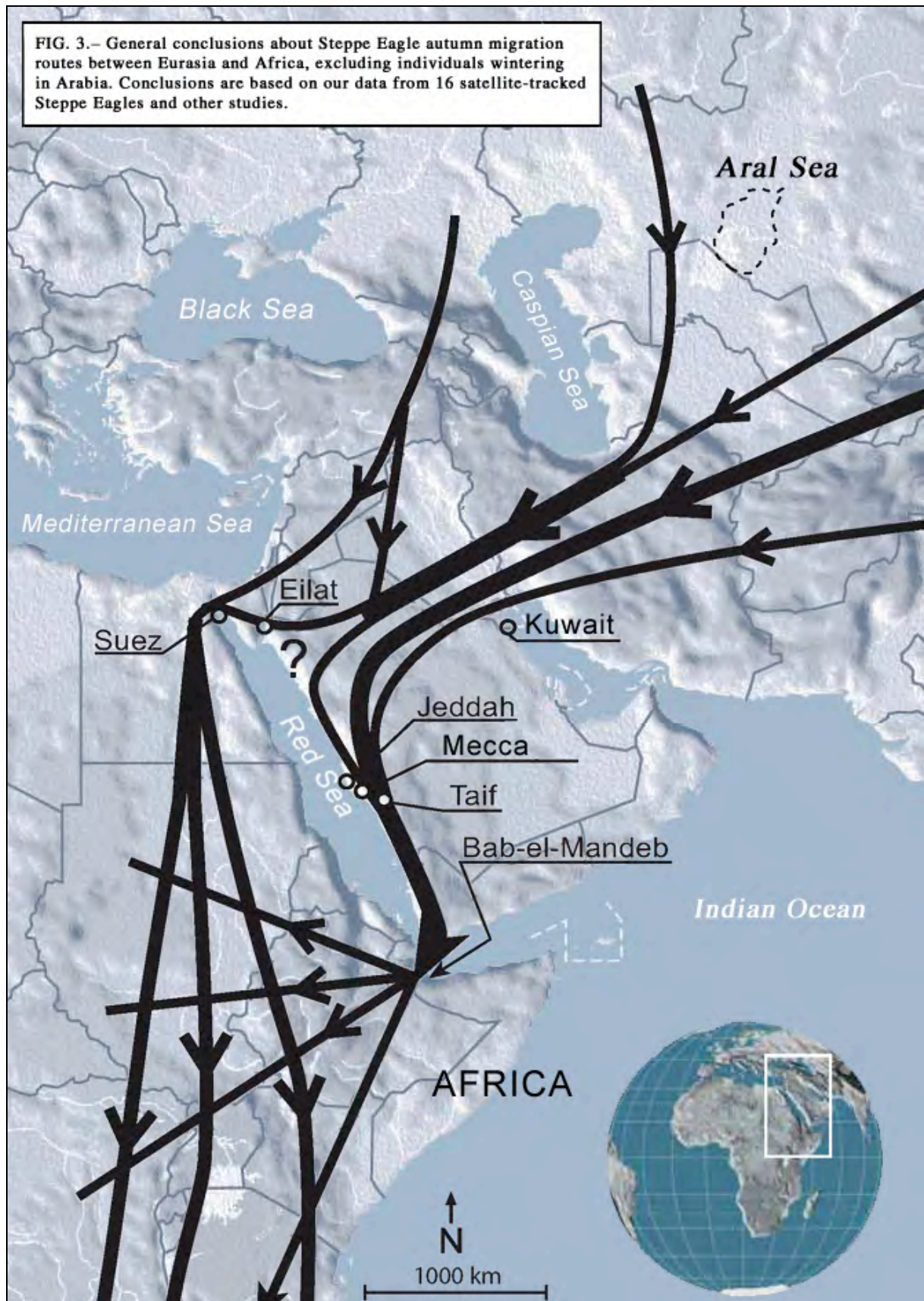
been accepted in this way without having in fact been observed. (MEYBURG *et al.*, 1998).

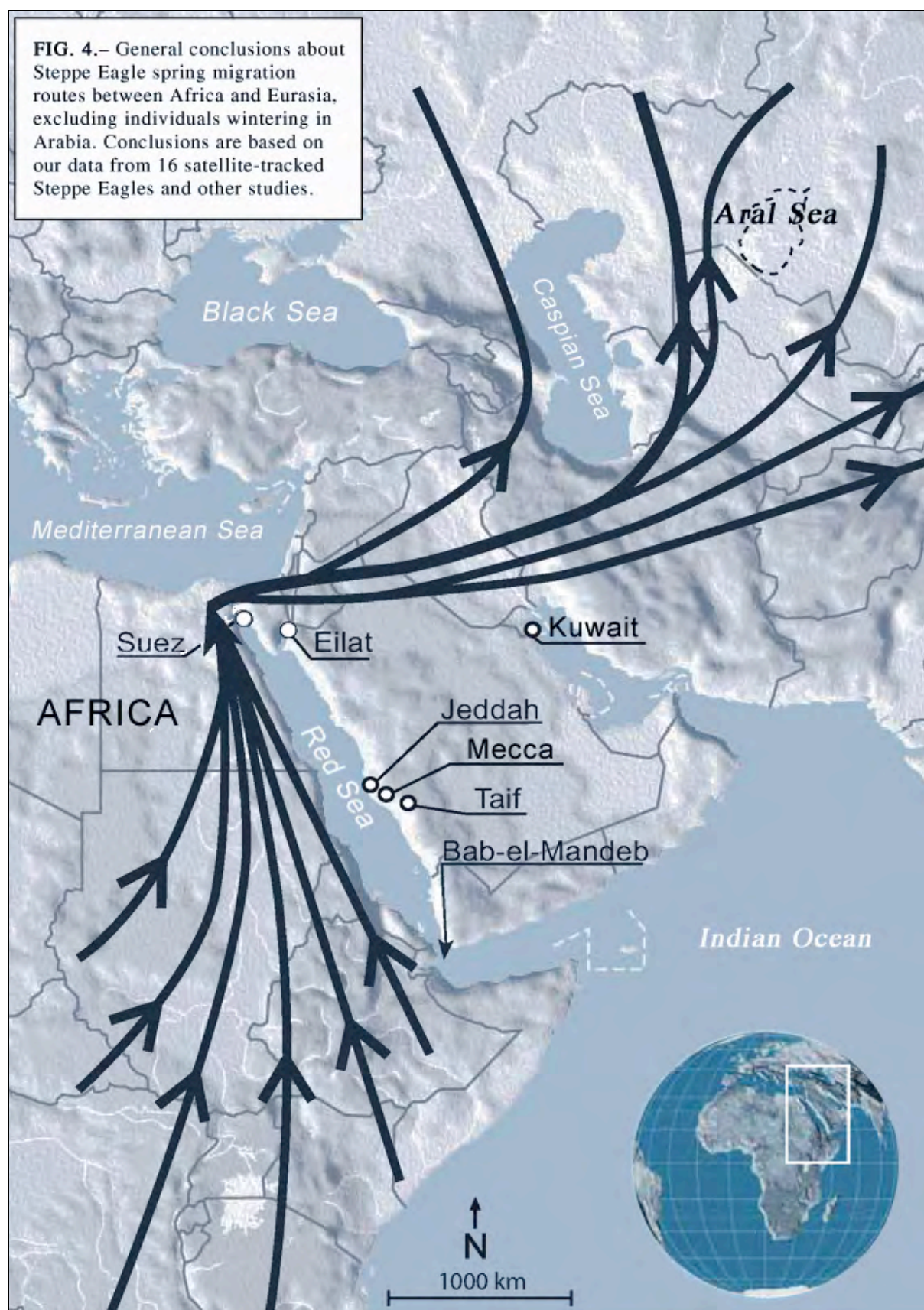
Fidelity to wintering grounds

Most birds of prey remain faithful to their nest sites and return there each year. Very little was known regarding this so far as wintering was concerned. For all the species tracked over a number of years (Lesser and Greater Spotted Eagles, Osprey, Steppe Eagles, Imperial Eagle *Aquila heliaca*, Black and Red Kites, Honey Buzzard) we established that the adults generally returned to the same winter quarters. This was proved in particular for an adult Greater Spotted Eagle tracked from 1999 on and still sending locations in August 2007. It wintered every year in the Goksu Delta in Turkey where in two years it was possible both to observe and to photograph it. Whereas the majority of species have winter quarters relatively limited in area, the Lesser Spotted Eagles behave nomadically and often wander several thousands of kilometres during their winter in Southern Africa. We could however confirm that they too always visit the same regions (MEYBURG *et al.* 2004) (FIG. 2).

FIG. 2.– Satellite photo with 963 GPS fixes (yellow = December, red = January, blue = February) of a female Lesser Spotted Eagle (with PT 41861) during its wintering from 9 December 2004 – 20 February 2005 in an area 76,000 km² in Namibia and Botswana between the Okavango Delta (on the right in the photo), the Etoscha Pan (top left) and Windhoek (bottom left).







One Black Kite spent several consecutive years in southern Mauretania and northern Mali but was also located one year in Senegal and even the Ivory Coast. A Red Kite, which also wintered in southern Spain for two years, spent the third winter in the north of Spain.

The question of Steppe Eagles' migration routes between Asia and Africa answered

The Steppe Eagle, weighing 2.4 and 3.9 kg, is, together with the White Stork *Ciconia ciconia*, the largest bird of the Palaearctic region regularly wintering in substantial numbers south of the equator in Africa.

During the past 35 years raptor migrations to the Near East have been studied in detail by making counts at concentration points and the migration of Steppe Eagles posed a few riddles. The counting of a greater number of migrating eagles at Eilat and Suez north of the Red Sea in spring than in autumn was a puzzling phenomenon. Indeed, one would have expected the opposite result in view of the increased mortality of young and immature birds as well as their longer-lasting stay in the wintering zones. This phenomenon was also observed with other species of raptor, particularly Steppe Buzzard *Buteo buteovulpineus*, Honey Buzzard and Black Kite, but also many other species of small-sized birds. Light was shed on this mystery thanks to ST (MEYBURG *et al.*, 2003).

Seven of the Steppe Eagles fitted with PTTs in autumn in Arabia flew to Africa via the Bab-el-Mandeb Straits in south Yemen, with others spending the winter on the Arabian peninsula.

Having wintered in Africa the spring migration of all these eagles led them to fly north of the Red Sea via Suez and Eilat, revealing the existence of a circular route round the Red Sea (FIG. 3 & 4). The existence of this route explains the differences noted by observers and answers the questions raised on this subject in the literature.

Family break-up and emancipation of the young

It is relatively difficult to observe family ties after leaving the breeding site since the birds stray ever further from the nest towards the end of the emancipation of the young. Direct observation furnishes barely adequate information on the actual events. This is equally valid for wing-marking and terrestrial telemetry. In these cases it is very difficult to judge whether the parents and young leave together or separately. Only ST can provide such information with precision.

Thus, with this in view, we tracked a family of Greater Spotted Eagles (MEYBURG *et al.* 2005).

The two adults and their young were fitted with satellite transmitters in north-east Poland.

Family ties had broken up at the nest site with the departure of the female three or four days before the young bird. The male departed last on migration, a week after the female. The adults immediately set off in towards the Bosphorus, whilst the young headed too far south, probably dying in Albania at the end of October after having flown 1,687 km (FIG. 5, see next page).

For other species (Lesser Spotted Eagle, Osprey, Honey Buzzard) of which we have been able to equip both adults of certain pairs, the adults migrated separately in every case and wintered far apart from each other. In one instance alone did a pair of Ospreys spend the winter in the same region, which we take to be purely by chance since they migrated separately. To our knowledge all the males of every species returned to the same nest site, whereas certain Osprey and Lesser Spotted Eagle females settled and occasionally nested around 50 km distant from their nest of the preceding year.

Visits to neighbouring nests by Lesser Spotted Eagle

It has been generally accepted that nesting Lesser Spotted Eagles are strictly territorial and defend the area round their nests from intruders of the same species. It was thought that females looking after a young remained, like the parents of other species, within a perimeter of only a few kilometres round the nest until autumn. ST studies and DNA analyses have proved to us that this commonly accepted hypothesis has been wrong (MEYBURG *et al.*, 2007a). One female tracked by PTT-GPS on at least two occasions went over 50 km from the nest containing her young and also visited another active nest in the vicinity (FIG. 6). It was equally proved that at least two "foreign" females visited her own nest, one with a nest 57 km away, and spent quite a while there. Visits to the pair by strange females was also confirmed by direct observation.

These flights during the period of rearing the young and at a considerable distance from the nest came as a great surprise and, so far as we know, have not so far been observed in other raptor species. It is even more astonishing considering that the birds paying these visits stayed quite a long time without the occupants raising any objection, for we saw no particular signs of aggression on their part.

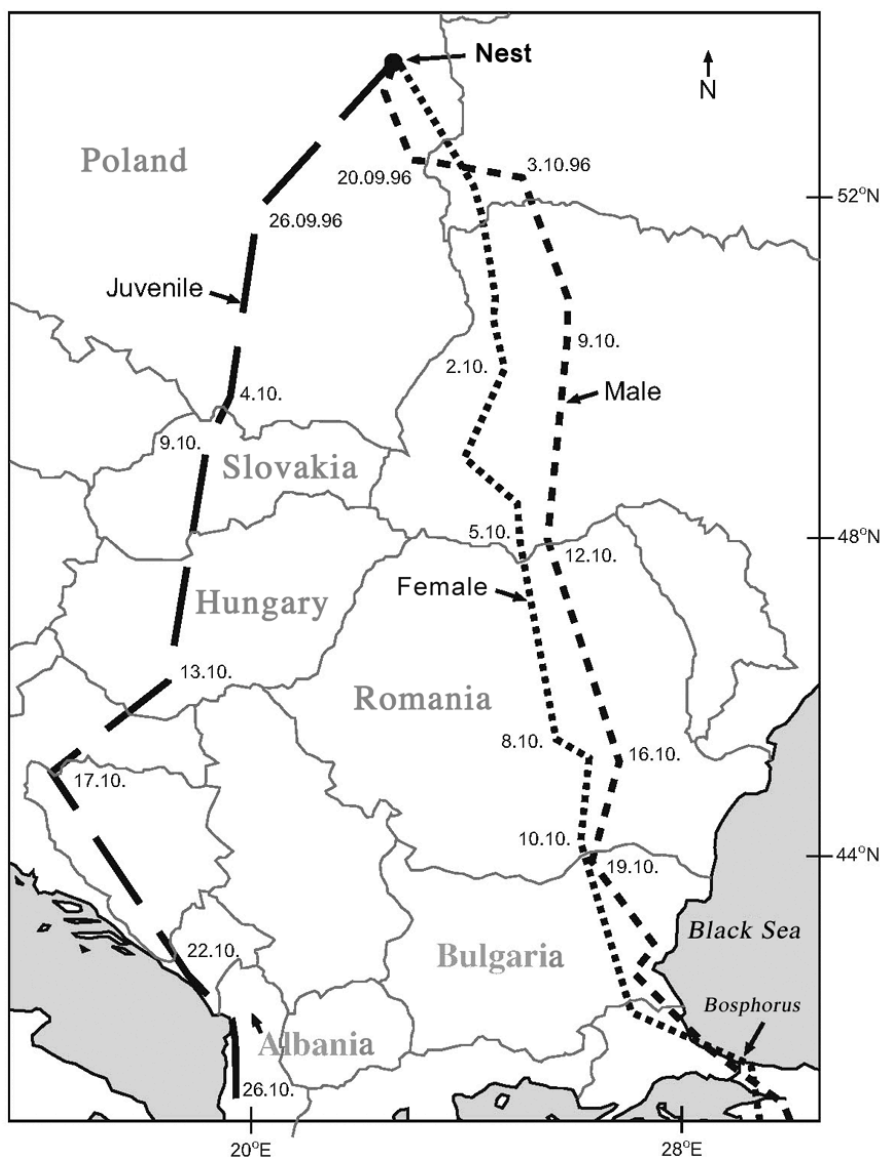


FIG. 5.— The autumn migration of the Greater Spotted Eagle family in Europe determined by satellite telemetry in 1996; dates of arrival at selected points on route are indicated.

We can only speculate as to the reasons for this behaviour. Lesser Spotted Eagles, even adults, being exposed to more than usually great dangers due to the great length of their migration to Africa and the risk of being shot in the Middle East, it can certainly happen that a female Lesser Spotted Eagle fails to find its partner at the previous year's nest site on its return in spring. If its partner is dead, it is an advantage for it to know the other nest sites both near and distant in order quickly to find a new partner. There are times when only a few days lie between the return from Africa and egg-laying, so that Lesser Spotted Eagles are under temporal pressure.

Breeding success can be influenced by the length of the migration

The date of the adults' arrival at the nest site seems to determine the ability or otherwise to breed of numerous species of migratory birds of prey. This is particularly evident when both partners arrive too late. An overdue return may inhibit egg-laying, as we have been able to observe in recent years with Lesser Spotted Eagle populations (FIG. 7). The most striking example of this was in 1997, during which most German pairs arrived abnormally late and only a third of them managed to breed. Most pairs even failed to lay. The same phenomenon took place in 2007 in Latvia where only 7% of the pairs laid.

It was generally but erroneously assumed that this delayed return from wintering was caused by bad weather conditions encountered during the spring migration, such as led in storks, for example, to catastrophic diminutions in breeding success.

Thanks to ST we were able to prove for the first time in 1997 that not only was the return to Europe overdue but also the departure in autumn 1996 had been delayed (MEYBURG *et al.*, 2007b). Responsibility for this delay was due to the bad weather conditions met with in Europe and the Near East between August and October. The four adults fitted with

transmitters progressed only very slowly, one of them crossing the Bosphorus on 5 and the other on 13 October. Passage through Israel only took place on 15 and 22 October, i.e. a delay of around two or three weeks compared with the visual observations conducted each year, giving the customary dates for the period of passage as 29 September to 5 October. Observations in Israel indicate that the dates of passage have generally appeared later in recent years. ST made it possible to give the precise dates of arrival in their winter quarters of three of these birds: 13 and 18 November and 23 December, thus equally late.

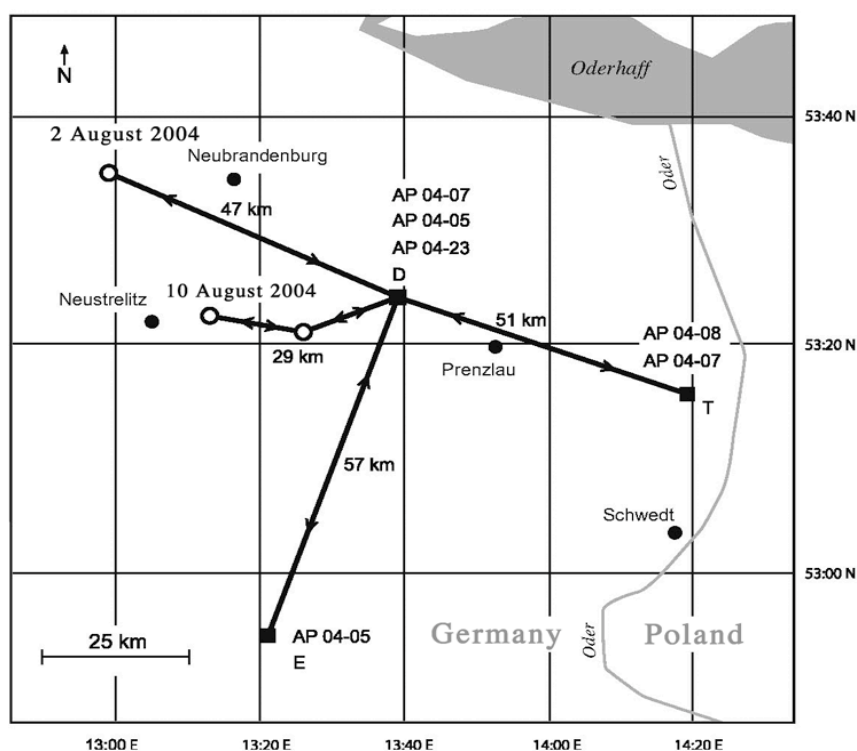


FIG. 6.— Three eyries of Lesser Spotted Eagles in Germany, D, E and T, (with distances) are shown, with the genetic code of the females whose moult feathers were found at the locations in 2004. Also shown, with dates, are the two northwesterly excursions of female AP 04-04 fitted with PTT 41861 belonging to nest D. These were determined by satellite telemetry GPS fixes.

In 1997 two of these eagles began their spring migrations on 14 and 16 March respectively, comparatively late according to the results from previous studies. The birds arrived two to three weeks late at their breeding sites. The eagle fitted with PTT 16865 crossed the Bosphorus on 17 April at a time when it would normally have reached its nest territory; it in fact arrived there on 4 May. On 12 April the bird with PTT 16867 was near Konya in Turkey, 430 km from the Bosphorus,

whereas by this date many eagles have generally arrived north of Berlin.

This delay did not solely concern birds carrying transmitters; practically all eagles arrived with a similar delay in 1997, not only in Germany but also in Latvia. We presume that in many cases, as with the birds tracked by satellite, their departure on migration began too late the previous autumn and it was not the bad weather conditions during the spring migration which caused the nesting failure for many pairs in 1997.

The reason why the eagles leave their wintering grounds too late has not yet been explained. It is possible that the birds are "programmed" to stay there a certain time to build up sufficient reserves of energy, so that a late arrival in autumn would in consequence lead to a late departure in spring. Another possible explanation could be the serious drought prevailing since 1970 in the region where the birds winter in Southern Africa. This is the result of climatic changes caused by the

El Nino phenomenon, first recognised in 1726 but still not fully explained and probably aggravated by global warming. The diminution of rainfall in this zone probably reduces the density of prey for the Lesser Spotted Eagles so that they may be compelled to stay longer to gain strength for the return migration to Europe. The tracking of two of the eagles wintering in Namibia proved that they were seeking zones with the heaviest rainfall (MEYBURG *et al.*, 2001).

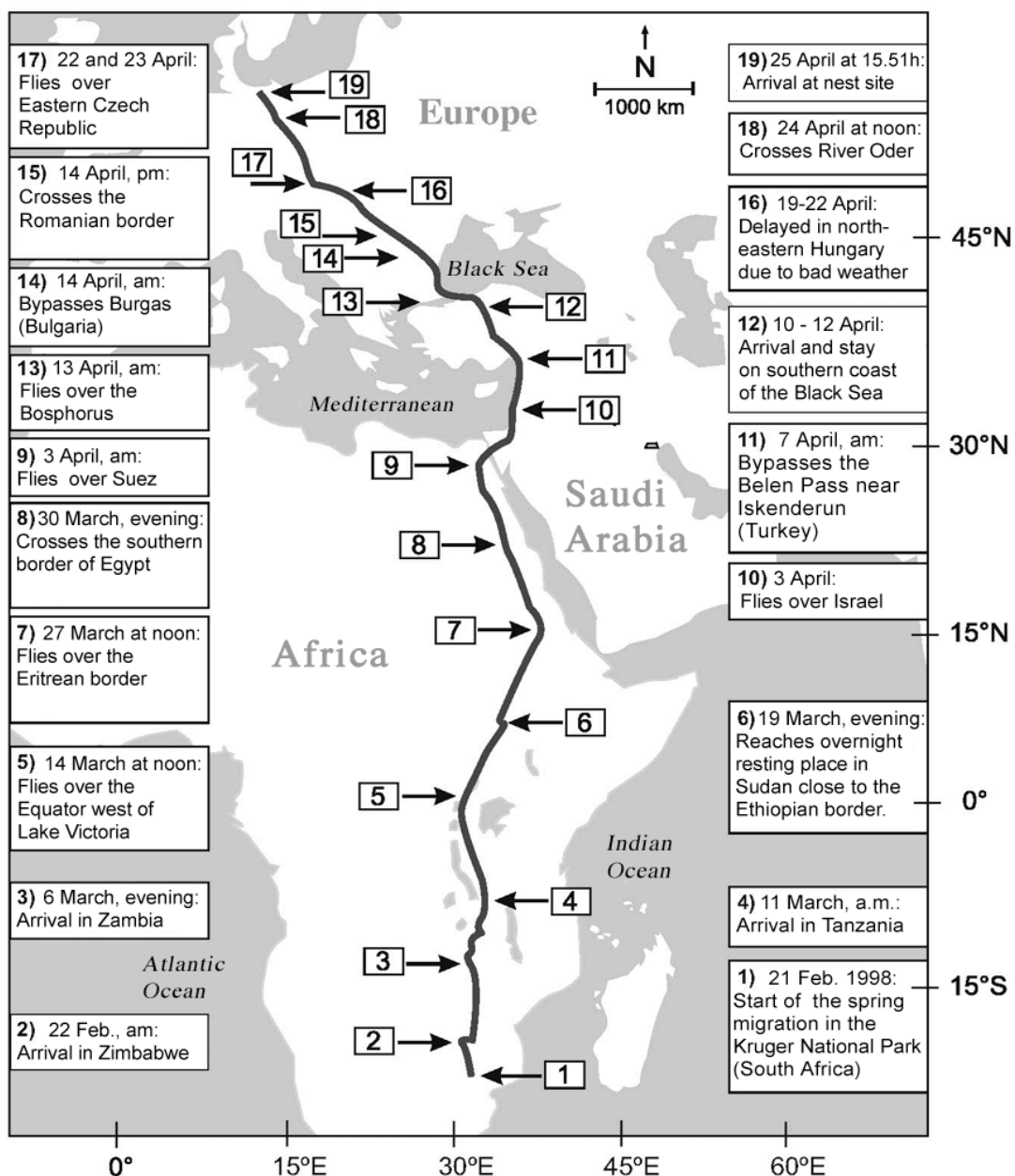


FIG. 7.– The migration route of the adult Lesser Spotted Eagle female fitted with transmitter 27999 from winter quarters in South Africa to breeding site in Germany with details of some of the passage points. Among the satellite fixes were all night roosts along the 10,753 km long migration route.

The overwintering of Lesser Spotted Eagles in Zambia takes place during the hot and humid season from December to April. The marked decrease in rainfall led, for example, to a modification in the vegetation of the Kafue plain between 1984 and 1994, transforming it into steppe. Other regions are equally undergoing change brought about by deforestation and replacement of the natural vegetation by either cultivated or arid areas less suited to furnish food for the Lesser Spotted Eagle.

Many authors hold climatic changes, and global warming in particular, to be responsible for this modification in migratory behaviour but they rarely seek any explanation other than coincidence.

The Lesser Spotted Eagle seems to be one of the very few species for which a later arrival in Europe is known. Closer study of this phenomenon of delayed return needs to be made by reason of its impact on breeding success. ST has revealed a relation between the phenomenon of migration and breeding

and shown the extent to which study of migration and overwintering is vital for understanding the biology of long-distance migrants.

Young raptors spending their first years in Africa

Many large-sized species of European raptor (Osprey, Egyptian Vulture *Neophron percnopterus*, Lesser Spotted Eagle) do not all return to their place of birth during their first years. Their behaviour during this period of their lives remains unknown.

We accordingly followed the movements of three young Egyptian Vultures from France (Luberon) and Bulgaria (MEYBURG *et al.*, 2004.) Over 4300 locations have been collected from these birds, tracing their migration routes and movements in Africa. The two French birds left at almost the same time and overwintered in the Sahel, south of Mauretania (FIG. 8) after a migration of 3,750 km. The Bulgarian bird flew 5,340 km and stayed mainly south-east of Chad.

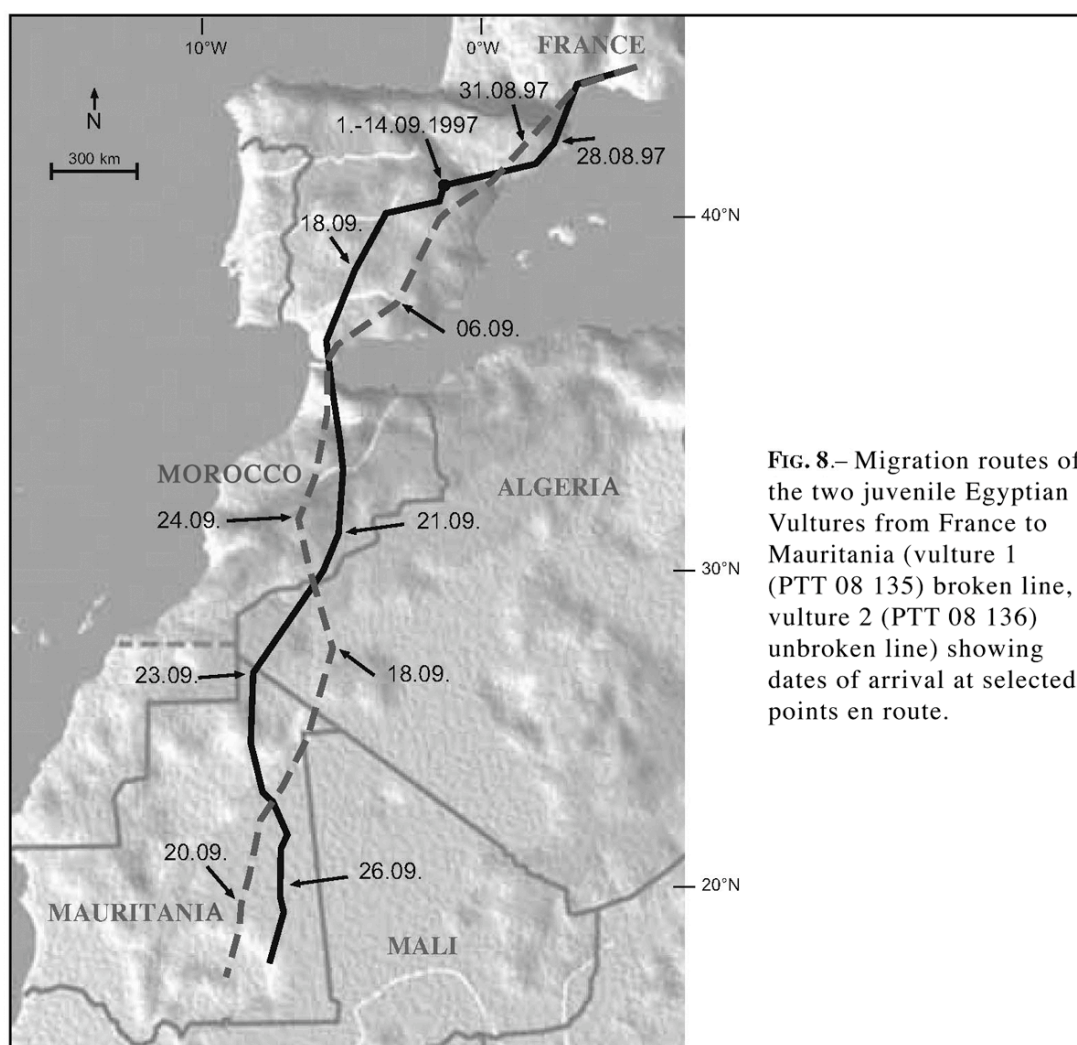


FIG. 8.– Migration routes of the two juvenile Egyptian Vultures from France to Mauritania (vulture 1 (PTT 08 135) broken line, vulture 2 (PTT 08 136) unbroken line) showing dates of arrival at selected points en route.

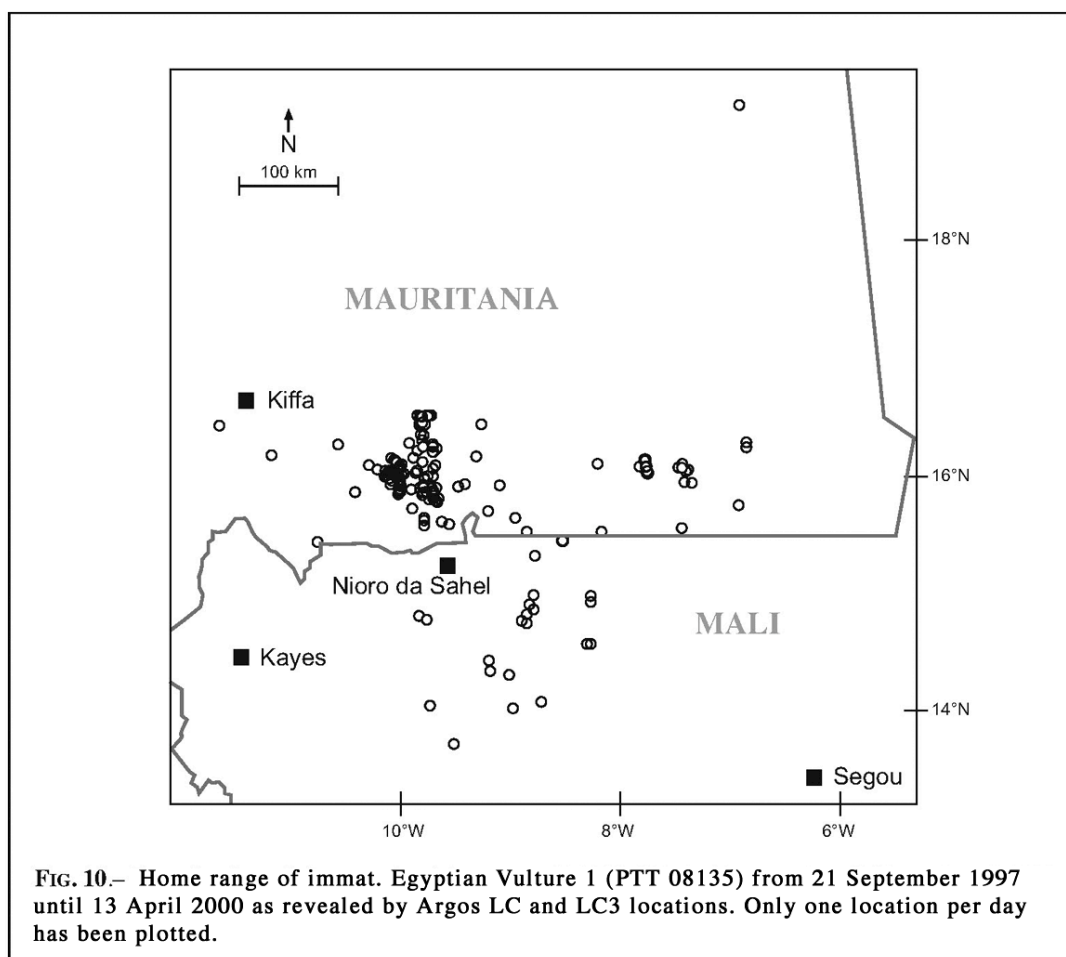
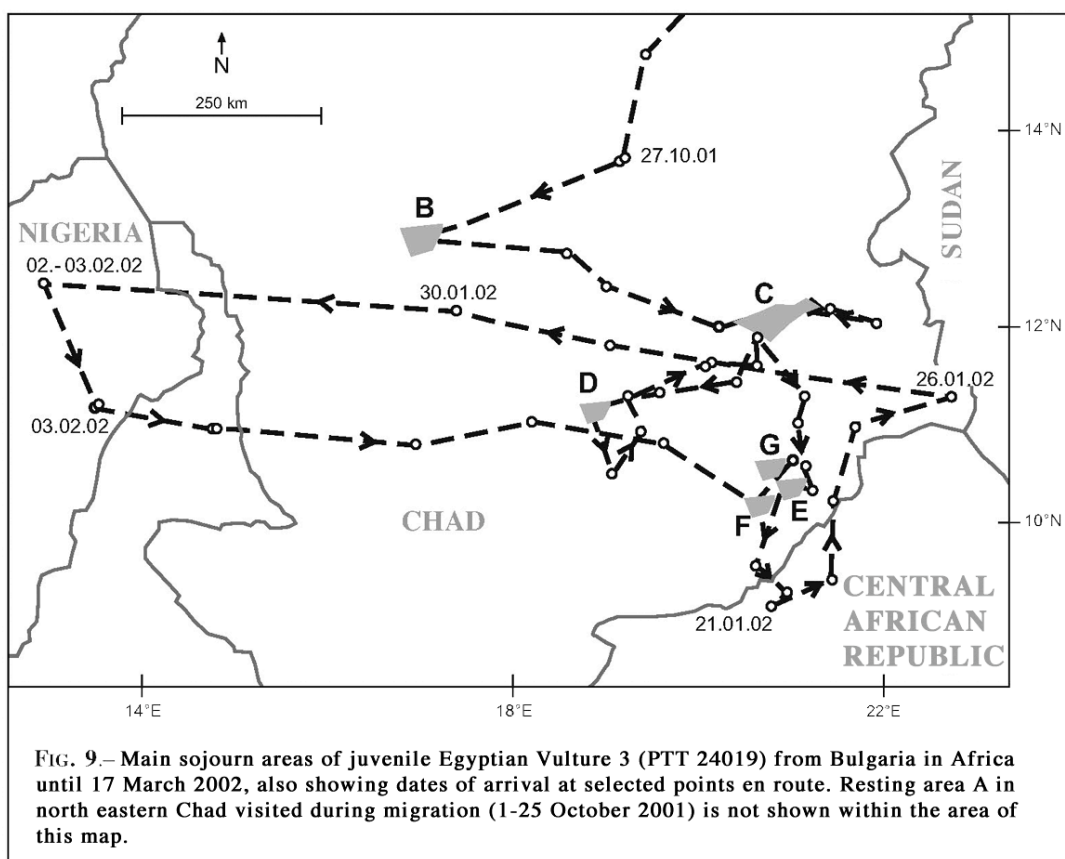


FIG. 11.–Satellite image with the home range of a male S (with PTT 23 196, marked in red) and female Lesser Spotted Eagle W (blue) and their eyries in 2005. This is at the northwest edge of the species' distribution in Germany.

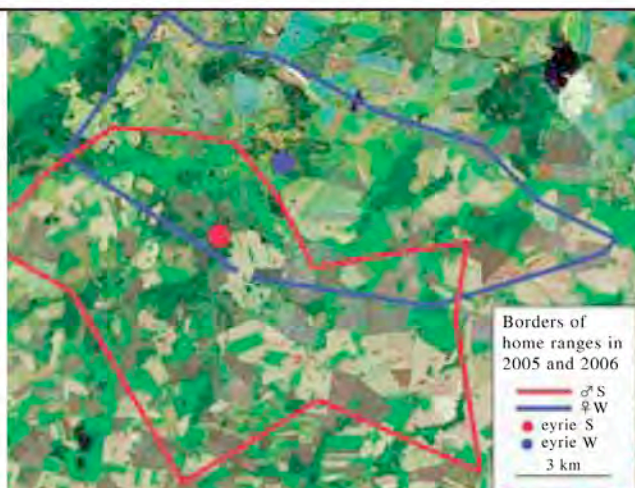


FIG. 12.– The borders of the home ranges of male Lesser Spotted Eagle S in 2005 (red) and 2006 (green). The eyrie, used in both years, is marked with a red dot and that of the neighbouring pair of unsuccessful breeders, eyrie W, with a blue dot. After the failure of brood W, male S extended its home range considerably into the territory of the neighbouring pair.

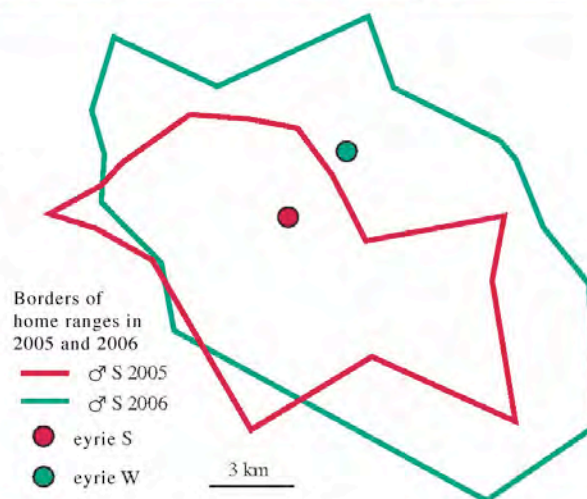
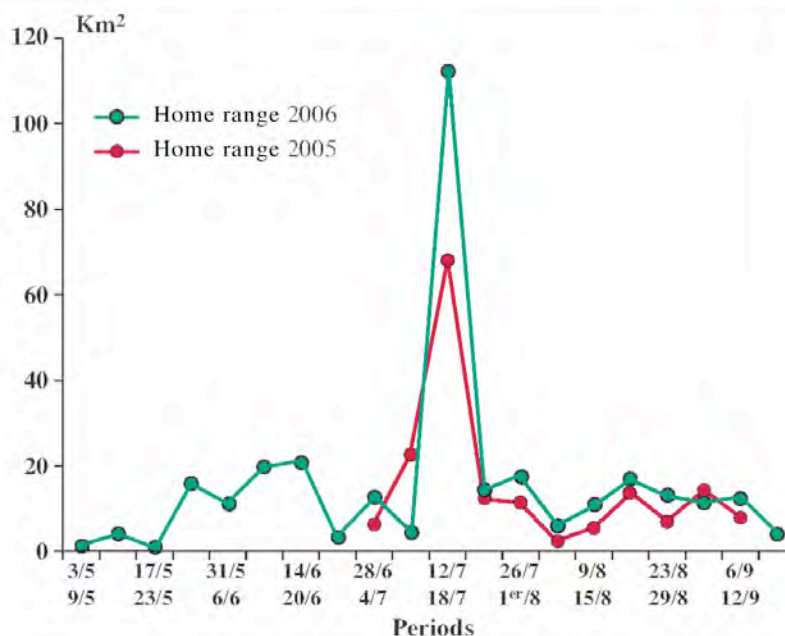


FIG. 13.– Weekly home range sizes of male Lesser Spotted Eagle S in 2005 (red) and 2006 (green).



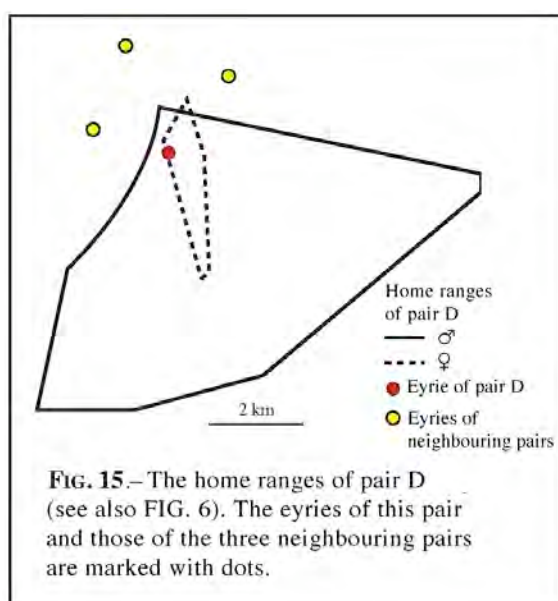
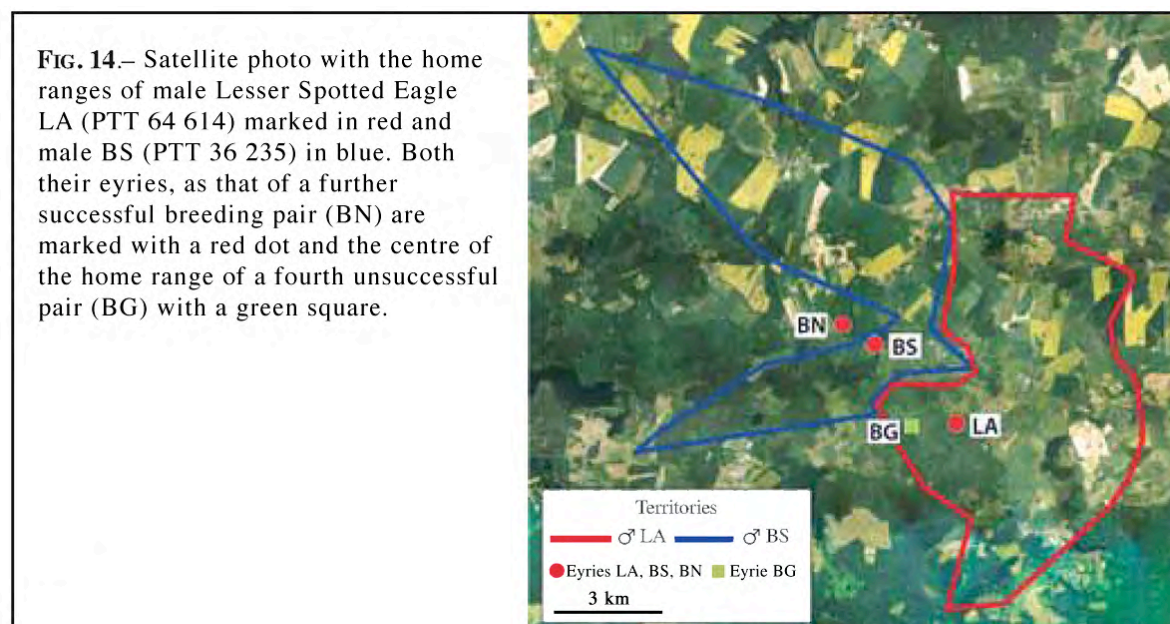
After its arrival it undertook a further migration within Africa in January and February, flying 2,600 km as far as north-east Nigeris and then returning (FIG. 9). The two French birds remained in the the same winter quarters in Mauretania throughout their sojourn in Africa. The total area of the zone visited was respectively 69,000 and 50,000 km², recorded by numerous locations of excellent quality.

One of the French vultures was tracked without a break and continued to stay in the area of its choice for two and a half years, from its arrival in the evening of 21 September 1997 to its departure on 13 April 2000 (FIG. 10). This area extended 80 km north/south and 50 km

east/west, its centre being at 16°2,N/9°52,W. Within this perimeter the bird moved only short daily distances; on 12 April 1998, however, it covered 63 km and on 3 November 1998 78 km between two consecutive nights. At the end of March 1998 it flew 500 km eastward and took up other winter quarters for two and a half months (28 March-12 June) before returning to its previous locality.

It only left this region of Africa when three years old (probably in its fourth plumage) (FIG. 10).

The second French vulture was observed near its birthplace in the South of France when aged about three.



GPS locations permit precise study of territory size and habitat use

Between 2004 and 2006 we were able to analyse territorial behaviour, the size of areas of activity and habitat use by seven adult Lesser Spotted Eagles (five male and two female) fitted with GPS PTTs in Germany, several of which are still being tracked. This study is the outcome of analysis of 2,976 GPS locations and visual observations on the site. The territory area of four males followed during one breeding season was a minimum if 32.78 km². The fifth male (S), which was tracked for two years, used territories of 93.78 km² in 2005 and 172.29 in 2006. The average size of these six territories was 72.29 km². The areas of activity of the two females differed greatly in size (Female D: 1.56 km² and Female W 82.3 km² -cf. FIGS. 11 and 15), although both bred successfully. Female D (PTT 41861) left her nest for several dozen

kilometres on at least three occasions, as has already been indicated above.

These major excursions were not taken into account when calculating the extent of her domain.

Having bred successfully the males remained strictly limited with clearly distinct territories. The females were not repulsed when they visited their neighbours' territories (cf. FIG. 11) and even spent quite some time at other nests. After the breeding failure of some pairs their territories were in part occupied by nearby pairs (cf. FIGS. 12 and 14). The three males (D, BT and LA) never ventured further than a maximum of 6 to 7 kilometres from their nest, the female W and male BS around 11 km and male S, which provided the largest number of GPS locations, over 13.

Territory size and the distances to which the eagles ventured varied depending on the stage reached in the breeding cycle. Male S strayed increasingly from the nest after its arrival in spring. It was in mid-July of the two years it was tracked up to this point that it flew the furthest and had the greatest area of activity. The dimensions of its territory subsequently shrank until its departure in autumn. The use of territory was intensive to a greater or smaller degree: 84% of the 677 locations of male S in 2005 were recorded in an area of only 14.24 km². In 2006 this same bird provided 989 GPS locations of which 71.4% lay within an area of 15.43 km².

In the spring of that year (2007) male BS several times visited the nest of its neighbour, which had not yet returned from migration, and also other parts of its territory. This never again recurred following the arrival of the lawful occupant a few days later.

ACKNOWLEDGEMENTS

We extend our thanks to the administrations of the different countries where we have fitted birds with PTTs for granting us the necessary permits. We are grateful to the DFG (Deutsche Forschungsgemeinschaft) among others for their financial support. Rostock and Poznan Zoos allowed us to use their birds (White-tailed Eagle and Eagle Owl), the Berlin-Friedrichsfelde Tierpark even made us a present of a live adult White-tailed Eagle to act as a decoy, the ornithological park "Le Marais aux Oiseaux" on the island of Oleron (France), lent us a European Eagle Owl to help in the capturing of eagles. We thank in particular Dr. Paul Howey and his colleagues at Microwaved Telemetry Inc. (USA), supplier

of most of the transmitters, for their support and help over the years, together with the ARGOS team at Toulouse. The German Embassies in several countries (Kuwait, Ethiopia, Mali among others) allowed us to retrieve several PTTs from birds shot or exhausted. These studies could not have been carried out without the participation of numerous ornithologists in the countries where we trapped and fitted raptors (France, Germany, Slovakia, Hungary, Bulgaria, Poland, Latvia, Belarus, Russia, Greece, Israel, Saudi Arabia, Namibia, Zambia, South Africa) and we thank them all most gratefully for their collaboration, support and observations, their number being too extensive for us to be able to mention them individually.

REFERENCES

- ALERSTAM, (T.), HAKE (M.), & KJELLÉN (N.) 2006.— Temporal and spatial patterns of repeated migratory journeys by Ospreys. *Anim. Behav.*, 71:555-566.
- BRODEUR (S.), DÉCARIE (R.), BIRD (D.M.) & FULLER (M.) 1996.— Complete migration cycle of Golden Eagles breeding in northern Quebec. *Condor*, 98 : 293-299.
- ELLIS (D.H.), MOON (S.L.) & ROBINSON (J.W.) 2001.— Annual movements of a Steppe Eagle (*Aquila nipalensis*) summering in Mongolia and wintering in Tibet. *Bombay Nat. Hist. Soc.*, 98: 335-340.
- FULLER (M.R.), SEEGAR (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.
- HAINES (A.M.), MCGRADY (M.J.), MARTELL (M.S.), DAYTON (B.J.), HENKE (M.B.) & SEEGAR (W.S.) 2003.— Migration routes and wintering locations of Broad-winged Hawks tracked by satellite telemetry. *Wilson Bull.*, 115 : 166-169.
- HIGUCHI (H.), SHIU (H.), NAKAMURA (H.), UEMATSU (A.), KUNO (K.), SAEKI (M.), HOTTA (M.), TOKITA (K.), MORIYA (E.), MORISHITA (E.) & TAMURA (M.) 2005.— Migration of Honey Buzzards *Pernis apivorus* based on satellite tracking. *Ornithol. Science*, 4:109-115.
- MARTELL (M.S.), HENNY (C.J.), NYE (P.E.) & SOLENSKY (M.J.) 2001.— Fall migration routes, timing, and wintering sites of North American Ospreys as determined by satellite telemetry. *Condor*, 103: 715-724
- McGRADY (M.J.), MAECHTLE (T.L.), VARGAS (J.J.), SEEGAR (W.S.) & PORRAS PEÑA (M.C.) 2002.— Migration and ranging of Peregrine Falcons wintering on the Gulf of Mexico coast, Tamaulipas, Mexico. *Condor*, 104 : 39-48.

- MCGRADY (M.J.), UETA (M.), POTAPOV (E.R.), UTEKHINA (I.), MASTEROV (V.), LADYGUINE (A.), ZYKOV (V.), CIBOR (J.), FULLER (M.) & SEEGAR (W.S.) 2003.– Movements by juvenile and immature Steller's Sea Eagles *Haliaeetus pelagicus* tracked by satellite. *Ibis*, 145 : 318-328.
- MEYBURG (B.-U.) & FULLER (M. R.) 2007.– *Satellite Telemetry*. In BIRD (D.) & BILDSTEIN (K.) Raptor Research and Management Techniques, Hancock House, Blaine, Canada, pp. 242-248.
- MEYBURG (B.-U.) & LOBKOV (E. G.) 1994.– Satellite tracking of a juvenile Steller's Sea Eagle *Haliaeetus pelagicus*. *Ibis*, 136: 105-106.
- MEYBURG (B.-U.) & MEYBURG (C.) 2005.– Tracking the Endangered Greater Spotted Eagle. *Tracker News*, 6: 4.
- MEYBURG (B.-U.), MEYBURG (C.) 2007.– Postfledging behavior and outward migration of a hybrid Greater x Lesser Spotted Eagle (*Aquila clanga* x *A. pomarina*). *J. Raptor Res.*, 41: 165-170.
- MEYBURG (B.-U.), SCHELLER (W.) & MEYBURG (C.) 1993.– Satelliten-Telemetrie bei einem juvenilen Schreiadler *Aquila pomarina* auf dem Herbstzug. *Journal für Ornithologie*, 134: 173-179.
- MEYBURG (B.-U.), BLOHM (T.), MEYBURG (C.), BÖRNER (I.) & SÖMMER (P.) 1994.– Satelliten- und Bodentelemetrie bei einem jungen Seeadler *Haliaeetus albicilla* in der Uckermark: Wiedereingliederung in den Familienverband, Bettelflug, Familienauflösung, Dispersion und Überwinterung. *VOGELWELT*, 115: 115-120.
- MEYBURG (B.-U.), SCHELLER (W.) & MEYBURG (C.) 1995a.– Zug und Überwinterung des Schreiadlers *Aquila pomarina*: Satellitentelemetrische Untersuchungen. *Journal für Ornithologie*, 136: 401-422.
- MEYBURG (B.-U.), EICHAKER (X.), MEYBURG (C.) & PAILLAT (P.) 1995b.– Migrations of an adult Spotted Eagle tracked by satellite. *British Birds*, 88: 357-361.
- MEYBURG (B.-U.), MENDELSON (J. M.), ELLIS (D. H.), SMITH (D. G.), MEYBURG (C.) & KEMP (A. C.) 1995c.– Year-round movements of a Wahlbergs Eagle *Aquila wahlbergi* tracked by satellite. *Ostrich*, 66: 135-140.
- MEYBURG (B.-U.), HARASZTHY (L.), MEYBURG (C.) & VISZLO (I.) 1995d.– Satelliten- und Bodentelemetrie bei einem jungen Kaiseradler *Aquila heliaca* : Familienauflösung und Dispersion. *Vogelwelt*, 116: 153-157.
- MEYBURG (B.-U.), MEYBURG (C.) & PACTEAU (C.) 1996.– Migration automnale d'un Circaète Jean-Le-Blanc *Circaetus gallicus* suivi par satellite. *Alauda*, 64 : 339-344.
- MEYBURG (B.-U.), MEYBURG (C.) & BARBRAUD (J.-C.) 1998a.– Migration strategies of an adult Short-toed Eagle *Circaetus gallicus* tracked by satellite. *Alauda*, 66: 39-48.
- MEYBURG (B.-U.), MEYBURG (C.), MIZERA (T.), MACIOROWSKI (G.) & KOWALSKI (J.) 1998b.– Greater Spotted Eagle wintering in Zambia. *Africa. Birds & Birding*, 3: 62-68.
- MEYBURG (B.-U.), ELLIS (D.H.), MEYBURG (C.), MENDELSON (J.M.) & SCHELLER (W.) 2001.– Satellite tracking of two Lesser Spotted Eagles, *Aquila pomarina*, migrating from Namibia. *Ostrich*, 72: 35-40.
- MEYBURG (B.-U.), MATTHES (J.) & MEYBURG (C.) 2002.– Satellitetracked Lesser Spotted Eagle avoids crossing water at the Gulf of Suez. *British Birds*, 95: 372- 376.
- MEYBURG (B.-U.), PAILLAT (P.) & MEYBURG (C.) 2003.– Migration routes of Steppe Eagles between Asia and Africa: A study by means of satellite telemetry. *Condor*, 105: 219- 227.
- MEYBURG (B.-U.), MEYBURG (C.), BELKA (T.), SREIBER (O.) & VRANA (J.) 2004a.– Migration, wintering and breeding of a Lesser Spotted Eagle (*Aquila pomarina*) from Slovakia tracked by Satellite. *Journal of Ornithology*, 145: 1-7.
- MEYBURG (B.-U.), GALLARDO (M.), MEYBURG (C.) & DIMITROVA (E.) 2004b.– Migrations and sojourn in Africa of Egyptian Vultures (*Neophron percnopterus*) tracked by satellite. *Journal of Ornithology*, 145: 273-280.
- MEYBURG (B.-U.), MEYBURG (C.), MIZERA (T.), MACIOROWSKI (G.) & KOWALSKI (J.) 2005.– Family break up, departure, and autumn migration in Europe of a family of Greater Spotted Eagles (*Aquila clanga*) as reported by satellite telemetry. *J. of Raptor Res.*, 39: 462-466.
- MEYBURG (B.-U.), MEYBURG (C.), MATTHES (J.) & MATTHES (H.) 2006.– GPS-Satelliten-Telemetrie beim Schreiadler (*Aquila pomarina*): Aktionsraum und Territorialverhalten. *Vogelwelt* 127: 127-144.
- MEYBURG (B.-U.), MEYBURG (C.), FRANCK-NEUMANN, (F.) 2007a.– Why do female Lesser Spotted Eagles (*Aquila pomarina*) visit strange nests remote from their own ? *Journal of Ornithology*, 148: 157-166.
- MEYBURG (B.-U.), MEYBURG (C.), MATTHES (J.) & MATTHES (H.) 2007b.– Heimzug, verspätete Frühjahrsankunft, vorübergehender Partnerwechsel und Bruterfolg beim Schreiadler *Aquila pomarina*. *Vogelwelt*, 128: 21-31.
- RAFANOMEZANTSOA (S.), WATSON (R.T.) & THORSTROM (R.) 2002.– Juvenile dispersal of Madagascar Fish-eagles tracked by satellite telemetry. *J. Raptor Res.*, 36: 309-314.
- STEENHOF (K.), FULLER (M. R.), KOCHERT (M. N.) & BATES (K. K.) 2005.– Long-range movements and breeding dispersal of Prairie Falcons from southwest Idaho. *Condor*, 107 :481-496.
- THORUP (K.), ALERSTAM (T.), HAKE (M.) & KJELLÉN (N.) 2003a.– Can vector summation describe the orientation system of juvenile Ospreys and Honey Buzzards? An analysis of ring recoveries and satellite tracking. *Oikos*, 103 :350-359.

- THORUP (K.), ALERSTAM (T.), HAKE (M.) & KJELLÉN (N.) 2003b.– Bird orientation: compensation for wind drift in migrating raptors is age dependent. *Proceedings of the Royal Society of London*, B 270:S8-S11.
- THORUP (K.), ALERSTAM (T.), HAKE (M.), & KJELLÉN (N.) 2006.– Travelling or stopping of migrating birds in relation to wind: an illustration for the Osprey. *Behav. Ecol.*, 17 : 497-502.
- UETA (M.), SATO (F.), NAKAGAWA (J.) & MITA (N.) 2000.– Migration routes and differences of migration schedule between adult and young Steller's Sea Eagles *Haliaeetus pelagicus*. *Ibis*, 142: 35-39.
- UETA (M.) & HIGUCHI (H.) 2002.– Difference in migration pattern between adult and immature birds using satellites. *Auk*, 119: 832-835.

ZUSAMMENFASSUNG

15 Jahre satellitentelemetrische Untersuchungen an Greifvögeln. Die Satelliten-Telemetrie (ST) hat die Erforschung der Biologie der Greifvögel revolutioniert, insbesondere die Untersuchung ihres Zuges, und bereits viele neue Erkenntnisse zutage gefördert.

Sie wird dies in zunehmendem Masse auch in der Zukunft tun. Wir geben hier zunächst einen kurzen Überblick über die Entwicklung der Technik der ST sowie den derzeitigen Stand. Dabei lassen sich drei Zeitphasen unterscheiden, der Zeitraum in dem lediglich Sender mit Batteriebetrieb und Doppler-Ortung zur Verfügung standen, die Phase in der es Sender mit Solarbetrieb und Doppler-Ortung gab, und schließlich die letzte Phase, in der Sender mit GPS-Ortung eingesetzt werden können (TAB. I). Es werden Hinweise zur Planung von Projekten gegeben, bei denen diese Technik zum Einsatz kommen soll. Ferner findet sich in TAB. III eine Übersicht zu den Fragen, die sich mittels dieser Technik untersuchen lassen bzw. die bereits untersucht wurden.

Wir berichten schließlich über einige Highlights eigener Telemetrie-Ergebnisse, die bei der Markierung von 146 Individuen zwischen 1992 und 2007 gewonnen werden konnten, die 14 Arten angehören (TAB. II).

ANNEXES

TABLE II.– Overview of the 146 raptors fitted with PTTs between 1992 and 2007 within the framework of our Argos program1 126.

Species	Number	Country where fitted with PTTs & remarks	References and comments
Lesser Spotted Eagle	43	Almost exclusively adults, the majority in Germany but also in Latvia, Slovakia, Namibia & Poland	MEYBURG <i>et al.</i> 1993, 1995a, 2001, 2002, 2004a, 2006, 2007a-b, 2005. Numerous results not yet published
Greater Spotted Eagle	14	Entirely adults in Poland (bar 1)	MEYBURG <i>et al.</i> 1995b 1998, 2005. Most of many results not yet published
Hybrid G'ter & Lesser Spotted Eagles	4	3 adult males in Poland and 1 juvenile in Germany	MEYBURG & MEYBURG 2007c. Results for hybrid adults unpublished
Imperial Eagle	19	In Saudi Arabia, Hungary & Slovakia	MEYBURG <i>et al.</i> , 1995d. Study of one juvenile published
Steppe Eagle	16	Mainly in Saudi Arabia	MEYBURG <i>et al.</i> , 2003. Ca. Half the data published
Osprey	16	Only adults in Germany	No results published to date
Red Kite	10	Adults & juveniles in Germany	No results published to date
Black Kite	6	Adults in Germany	No results published to date
Honey Buzzard	5	Adults in Germany	No results published to date
Short-toed Eagle	4	In France: 1 trapped & 3 rehabilitated	MEYBURG <i>et al.</i> , 1996, 1998a. About half the data published to date
Egyptian Vulture	4	Juveniles: 2 in France, 1 in Bulgaria 1 in Greece.	MEYBURG <i>et al.</i> , 2004b
Wahlberg's Eagle	2	Adults in Namibia & South Africa.	MEYBURG <i>et al.</i> , 1995c
White-tailed Eagle	1	Juvenile in Germany	MEYBURG <i>et al.</i> , 1994. Ca. half the results published
Steller's Sea Eagle	1	Juvenile in Kamchatka (Russia)	MEYBURG & LOBKOV, 1994
Peregrine Falcon	1	Adult in Saudi Arabia	No result published to date

TABLE III Topics and questions regarding raptors for which data from satellite telemetry have or are expected to provide information. Some references are provided and more can be found on the world wide web.

Annual cycle	Seasonal movements (1) Changes over the years (2)
Migration	Migration routes (3) Individual variations (4) Ecological barriers, guiding lines (sea, mountains, deserts) (5) Concentration points: do all Individuals pass through at one precise spot and on what dates (6) Navigation and orientation (7) Period of migration and timing (8) Differences according to sex and age, the nesting stage (9) Speed and height of migration (10) Variations during migration (11) Distances flown daily (12) Daytime behaviour, roosts, arrival and departure times, feeding (13) Weather conditions (14) Ecological conditions encountered on migration routes (15)
Wintering	Geographical situation of wintering grounds (16) Discovery of new wintering grounds(17) Size of wintering grounds Fidelity to these areas for several years running (18)
Breeding season	Size of territories, use of habitat and territorial behaviour (19) Dispersion, philopatry (20) Reasons for late arrival at nest site (weather conditions during migration, delayed departure from winter quarters) (21) Stability of pairs over a number of years (22) Behaviour of non-breeding adults (arrival, fidelity to nest site in event of failure, eventual nomadism)
Movements of immatures	Area of dispersion and emancipation Return to place of birth or prolonged stay in winter quarters (23)
Geographical behaviour	Survival, mortality threats Impact of human activity (24) Other factors (climatic, intraspecific competition) Survival and behaviour of birds returned to the wild (25)
Movements of hybrids	(26)
Some references:	(1) : BRODEUR <i>et al.</i> , 1996, FULLER <i>et al.</i> , 2003, MEYBURG <i>et al.</i> , 2003,2004a, STEENHOF <i>et al.</i> , 2005, (2) : ALERSTAM <i>et al.</i> , 2006, (3): MEYBURG <i>et al.</i> , 1995a, b, c, BRODEUR <i>et al.</i> , 1996, FULLER <i>et al.</i> , 1998 ELLIS <i>et al.</i> , 2001, HIGUCHI <i>et al.</i> , 2005 (4): ALERSTAM <i>et al.</i> , 2006, (5): MEYBURG <i>et al.</i> , 2002, 2003, (6) : (FULLER <i>et al.</i> , 1998, (7) : HAKE <i>et al.</i> , 2001, THORUP <i>et al.</i> , 2003a,b, (8): KJELLEN <i>et al.</i> , 2001, MEYBURG <i>et al.</i> , 2004b, 2007b, (9): UETA <i>et al.</i> , 2000, UETA & HIGUCHI 2002, HAKE <i>et al.</i> , 2003, MCGRADY <i>et al.</i> , 2003, MEYBURG <i>et al.</i> , 2005, 2007b, (10): MEYBURG <i>et al.</i> , 1995a,b,c, KJELLEN <i>et al.</i> , 2001, (11): MEYBURG <i>et al.</i> , 1998a, 2007b, (12): FULLER <i>et al.</i> , 1998, MEYBURG <i>et al.</i> , 1998a, 2004a, (13): MEYBURG <i>et al.</i> , 1998a, (14): MEYBURG <i>et al.</i> , 1998a, THORUP <i>et al.</i> , 2003, 2006, (15) : MARTELL <i>et al.</i> , 2001, HAINES <i>et al.</i> , 2003, (16): MEYBURG <i>et al.</i> , 1998b, (17): MCGRADY <i>et al.</i> , 2002, MEYBURG <i>et al.</i> , 2004a, (18): FULLER <i>et al.</i> , 2003, MEYBURG <i>et al.</i> , 2004a, MEYBURG & MEYBURG 2005, (19): MEYBURG <i>et al.</i> , 2006, (20): RAFANOMEZANTSOA <i>et al.</i> , (21): STEENHOF <i>et al.</i> , 2005, (21): MEYBURG <i>et al.</i> , 2007b, (22): MEYBURG <i>et al.</i> , 2007a, (23): MEYBURG <i>et al.</i> , 2004b, (24): EASTHAM <i>et al.</i> , 2000, (25) : MEYBURG <i>et al.</i> , 1996, (26): MEYBURG & MEYBURG 2007C