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# Migratory movements of Central and Eastern European Saker Falcons *(Falco cherrug)* from juvenile dispersal to adulthood

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**ABSTRACT—**The Saker Falcon is a partial migrant species of Eurasia, but there is little information on the species' migratory movements. This article attempts to compile the available information describing the migratory movements of Sakers breeding in Europe. In addition, data from satellite-tracking of 45 juvenile Saker Falcons tagged in the frame of a LIFE project were analysed. The results suggest that juveniles show partial and parallel autumn migration in their first calendar year starting in October–November. Regardless of their starting position, all migrating juvenile Sakers migrate southwest (210° on average). The distance of the autumn movements varies between a few dozen to a few thousand kilometres. They cross large water bodies on a broad front and do not congregate at straits as soaring raptors do. Females travel further for winter than males. The main wintering areas for the birds leaving the breeding range of the species are in the Central Mediterranean region. To date, only juvenile females have been proven to spend the winter in the Sahel. First spring migration starts late March–early April and slower than autumn migration. From the second year, Sakers return to their previous wintering sites in the subsequent years and the time spent in the wintering areas becomes shorter.

**Keywords:** *Falco cherrug*, temporary settlement area, migration, satellite tracking, ringing data, Hungary, Slovakia

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## Introduction

In their European range Saker Falcons breed in the European part of Kazakhstan, Russia, Turkey, Georgia, Ukraine, Moldova, Romania, Serbia, Croatia, Hungary, Slovakia, Austria and the Czech Republic. Sakers have no recent confirmed breeding records in Macedonia and Bulgaria although once the used to breed there. Occasional breeding of 1-2 pairs have been confirmed at least once in the past in Germany and Poland. There is no confirmed historical or recent record of Sakers breeding in other European countries; however the species may occur in most of them on passage or as vagrant *(Baumgart, 1991; Baumgart & Haraszthy, 1997; Orta, 1994; Makatsch, 1950; Sielicki et al., 2009; Augst, 2000; Ragyov et al., 2006).*

According to the literature, the Saker is a partly migratory species *(Porter & Beaman 1985)*; a certain part of the population is resident, another part migrates, while some birds leave their breeding area only when weather conditions become unfavourable *(Baumgart, 1991).* Sakers in Mongolia, located in the northern part of the distribution range of the spe-

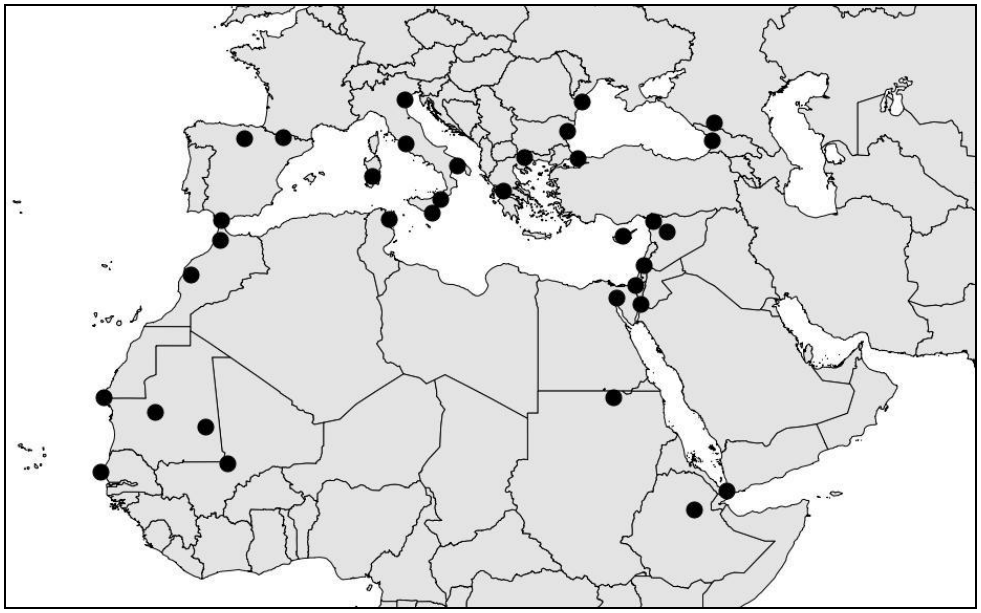

**Figure 1.** Relevant sites within the Eurafrican region where occurrence of Saker was indicated during migration or wintering in the literature (those records where exact location was missing and literature data describing the movements of satellite-tracked individuals were both omitted)

cies, can be either nomadic or migratory or stay in the breeding area all year round *(Potapov, 2002).* All the descriptions that can be found in the literature are based on visual observations, a few recoveries and satellite-tracking of a few individuals. Detailed studies based on well replicated samples of ringing or satellite-tracking data are not available for the migration of Sakers.

In this article we attempt to describe the migration patterns of the Central-Eastern European populations of the species and map their passage and wintering areas by analyzing available literature and ringing data and the results of a large-scale satellite-tracking project.

### *Review of literature data on the migration of Sakers*

The following review is based on extensive research of both the printed literature and internet soruces relating to raptor surveys at the most relevant migration bottlenecks (the most important data were summarised in Appendix 1 and relevant wintering sites mentioned in the literature are sown in Figure 1). The discussed sites are—apart from Măcin Mts. in Romania—outside the recent breeding range of Sakers *(Orta, 1994)*, hence, data refer to true migrants or stragglers. Some notes on winter findings of Sakers outside of their breeding range are also provided.

*Middle East*

The most important raptor migration bottleneck for Western Palearctic raptors is situated south of the Caucasus (Georgia) where thousands of raptors migrate. Only single birds pass through there. During wintering only four Sakers were recorded in December 1998 south of the Caucasus *(Galushin & Moseikin, 2000).*

The species may breed in Central and Eastern Turkey; however it is more widespread on passage and winter *(Acar et al., 1975).* On the well-known passing site at Bosporus the species is seen only in small numbers during autumn *(Porter & Willis, 1968; Sutherland & Brooks, 1981; Üner et al., 2010).* Individuals are seen occasionally also elsewhere (Camili, Artvin, *Perktaş & Turan, 2007;* Belen Pass, *Acar et al., 1975).*

In Israel, the Saker is a rare passage migrant, generally seen during migration after mid October with fewer than 20 records each year *(Christensen et al., 1982; Géroudet & Juillard, 1990; Alon et al., 2004; CITES, 2004)*. It is also a winter visitor in small numbers here, mainly in the lowlands of northern and central Israel and the Negev Desert *(Shirihai, 1996; Shirihai et al., 2000; Alon et al., 2004).*

Records from the Arab Peninsula are scarce. In the Syrian Desert, six Sakers were captured between 2000 and 2003 during autumn migration *(Serra et al., 2005a; 2005b)*. In Yemen, it has been recorded during autumn at two sites *(Porter & Christensen, 1987; Welch & Welch, 1989).* In Oman, the Saker is a passage migrant and winter visitor mostly from September to April. Some records may refer to ex-captive birds *(Sargeant et al., 2008).*

*Eastern Mediterranean region*

In the Balkans, data are available from Romania, Bulgaria, Macedonia, Serbia and Greece. In the Măcin Mountains of Romania several Sakers were recorded during the autumn raptor censuses *(Milvus, 2008),* but they may refer to individuals of the three resident breeding pairs near the observation sites. While no confirmed breeding of Sakers has been reported since 1998 in Bulgaria, it is regular on passage all over the country with most records concentrating in the Burgas region at the Black Sea coast *(Michev et al., 2011)*. The oldest record from Greece refers to a subadult Saker collected on the Rhodes island in 1913 (Turin Museum of Natural History). In recent years, there have been 2–4 verified records of Saker in Greece annually according to the reports of the *Hellenic Rarities Committee (2011).* Sakers are suspected to breed in North-Thrakia (*Handrinos & Dimitropoulos, 1983*). Saker Falcon for Macedonia was mentioned already by *Makatsch (1950)*, three further specimens are known in museums (Natural History Museum in Skopje) originating from Macedonia and one from Serbia (Vranje), from the autumn migration and/or wintering period (Ovche Pole, Skopsko Pole, Negotino). *Dimovski (1972)* mentions the species from Skopje Valley only during the migration.

In Cyprus, Saker Falcon is regarded as a scarce migrant in spring but commoner in autumn. It is reported sporadically in some years also in winter (December–January). Migration through the Akrotiri peninsula had been monitored on a daily basis in the period 2004–2007, when the number of passing Sakers were negligible compared to those in the 1960s *(M. Miltiadous,* pers. comm.).

*Western Mediterranean region*

The species used to be a fairly common wintering and passage bird in Italy from the 19th to the mid 20th centuries, when it apparently became much scarcer. It is considered now a regular winter visitor in Italy, with somewhat fewer records during spring and even fewer during autumn passage—most probably because there are far more observation surveys in spring in the country *(Corso & Harris, 2012,* with a detailed review of Italian data there). The Saker Falcon is a rare vagrant on the Maltese Islands during spring and autumn *(Sammut & Bonavia, 2004; Raine & Vella, 2007; Galea & Vella, 2012).* Out of the 49 records between 1908 and 2007, 69% were seen in the autumn months, 27% were observed in spring, while 4% were recorded in the winter (*R. Vella,* pers. comm.). Sixteen records relating to 20 individuals of Sakers have been accepted in France up to 2010 *(Reeber & le CHN, 2011).* The first official record for Spain was accepted in 2004 *(De Juana, 2006).* Another record, a satellite tagged Hungarian bird was reported in 2009 *(Dies et al., 2011).* The first confirmed record for Portugal was also provided by the same individual detected in August 2009 in Guarda district *(Matias et al., 2011).*

*Africa*

The Saker has been known as a scarce winter migrant to Northwest and Northern tropical Africa south to Sudan, Ethiopia reaching the Equator in Kenya *(Brown et al., 1982).* According to more recent literature the species occurs throughout the Sahel region from Senegal to Sudan *(Dejonghe, 1980; Thiollay, 1989; Ash & Nikolaus, 1992; Dixon, 2005),* although Sakers can be seen still mainly in North Africa during the migration period and in winter *(Global Raptor Information Network, 2012)*. In Tunisia Sakers are passage migrants and winter residents in small numbers *(de Balsac & Mayaud, 1962; Isenmann et al., 2005)* with most data from Cap Bon during spring passage between the end of March and May *(Thiollay, 1977; De Jong et al., 2009)*. A few winter records have also been recorded here *(Isenmann et al., 2005; Global Raptor Information Network, 2012)*.

There are further, unverified records indicating the occurrence of Sakers in the sub-Sahel countries. One Hungarian and one Slovak satellite-tracked Saker reached even Niger *(Issaka & Brouwer, 2012)*.

## Material and methods

### *Analysing ring recoveries*

Ringing and recovery data were collected from available papers relating to range states of Saker Falcons, data of ringing atlases *(Schröpfer, 2008; Bagyura & Szitta, 2009)* and reports. In case of Hungary, a total of 2570 ringing and 94 recovery data were analyzed with a special emphasis on the relationship between recovery distance and age.

### *Satellite-tracking*

Out of the different migration study methods available, satellite tracking provide the most accurate and detailed information on the movements of animals. Satellite-tracking of birds started in the early 1990s and by the mid 2000s the development of technology made

| | Total | Male | Female |
|---|---|---|---|
| Number of tagged birds | 45 | 19 | 26 |
| Sakers perished or PTTs broken before their 1st migration period | 13 | 6 | 7 |
| Bird migrated but no accurate data were available for analysis | 1 | 0 | 1 |
| Sakers providing satellite data during migration | 31 | 13 | 18 |
| **Types of movements according to migration distance** | | | |
| No migratory movement shown from the pre-migration TSA | 5 (16.1%) | 3 (23.0%) | 2 (11.1%) |
| Short-distance movements detected | 11 (35.4%) | 6 (46.1%) | 5 (27.7%) |
| Medium distance migration (Mediterranean Europe) | 10 (32.2%) | 4 (30.8%) | 6 (33.3%) |
| Long distance migration (Africa) | 5 (16.1%) | 0 | 5 (22.7%) |
| **Sakers showing migratory behaviour in total** | **26 (83.8%)** | **10 (76.9%)** | **16 (88.8%)** |

**Table 2.** Distribution of the numbers of satellite-tracked juvenile (1CY) Sakers according to migration type

it possible to apply the technique on a number of species *(Meyburg & Fuller, 2007).*

In Hungary 39 juvenile and 5 adult Sakers, in Slovakia 6 juveniles were tagged between 2007 and 2010. The tagged Sakers represented both sexes in a similar ratio (Table 1). In 2009 two adult males were tagged in western Hungary as part of an environmental impact assessment study of a planned wind farm *(Váczi & Prommer, 2010)*. Information was also used from an Austrian Saker satellite tracking project, where three captive-bred juvenile females were released with satellite transmitters (PTTs) in 2009 and 2010 *(Gamauf & Dosedel, 2012).* In total, over ten thousand fixes from 53 satellite-tracked Sakers were available in the Central European region.

The satellite-tracked Sakers were fitted with solar-powered transmitters (so-called PTTs; Platform Transmitter Terminals). The Argos satellite system was used to communicate with the PTTs. In the Hungarian-Slovak LIFE project in 2007 five 20g solar Argos PTTs (NorthStar ST) were applied that did not have an embedded GPS unit but the Argos system located them by using the Doppler-effect. They did not work very accurately in Central Europe due to the high level of background noise in the used frequency. Another five units with GPS capability (manufactured by Microwave Telemetry Inc.) provided accurate data. Based on that experience, from 2008 only GPS-embedded 22g solar Argos/GPS PTT-100 units (Microwave Telemetry Inc) were used, which gave more accurate positions in Central Europe than simple Argos-located PTTs. In the wind farm project, as well as in the Austrian project, the same type of 22g solar Argos/GPS PTTs were again used. The PTTs represented ca. 2.6% of the mean weight of the males (730–950 g) and only 2% of the females (970–1300 g; *Cramp & Simmons, 1980*).

PTTs were mounted on the birds as a backpack by using a special teflon ribbon for harnessing. The teflon ribbon was run through the three loops of the PTT—one in the front and two on the flanks and fixed by sewing at the connections. We did not use metal crimps as they might cut the teflon ribbon as previous studies suggest *(Steenhof et al. 2006)*. End cuts of the teflon ribbon were folded back under itself before sewing and covered by small rings from the same material to prevent linting. Dental floss was used for sewing and finishing knots were fixed by using superglue. Three independent stitches were made at one sewing point. The harnesses were very similar to the ones used for the Marshall telemetry equip-

ment in falconry. Harness straps were crossed on the breast above the sternum and fixed with a sewn knot. PTTs were placed on the centre of the back of the birds to cause the least disturbance in the centre of gravity of the bird. Harnesses were just loose enough to let one finger fit between the PTT and the bird's back.

GPS-embedded PTTs are able to locate the bird with an accuracy of approximately $12 \times 20$ meters. Considering the weaker performance of the PTTs during the winter of 2007/2008, when they were set to locate the birds six times a day all year and to transmit the data on every third day, and considering the purpose of the tracking (studying dispersal and migration or habitat use), from 2008 the PTTs on juveniles in the Hungarian-Slovak project were set to locate the birds six times a day between 1 April and 30 September and three times a day in the rest of the year. PTTs were set to locate adult Sakers ten times a day all year round as the main aim in their case was to study habitat use. This latter setting resulted fewer locations in winter owing to lack of light; however the amount of data was still sufficient to evaluate the winter movement of those birds. As soon as the raw data arrived in the French-based database available online, they were downloaded, processed and evaluated. When mapping and analysing the dispersal data, movements on the temporary settlement areas (TSAs) and migration, the WGS84 system was used to map the locations of the birds. Satellite-tracked birds were also fitted with aluminium rings.

## Results and discussion

### *Ringing data*

Extensive ringing projects have been running only in three countries (Hungary, Slovakia and the Czech Republic) within the European range of the species, and even in those countries large-scale systematic ringing started only in the 1980s. The ringing activity has been focusing on ringing nestlings in all three countries mentioned above, which is occasionally complemented by trapping and ringing fledged juveniles and adults. Other European range countries that hold a significant Saker population—like Serbia, Ukraine and Austria—carry out no systematic, long term ringing projects.

#### *Czech Republic and Slovakia*

Up to 2002, 312 Sakers were ringed in the two countries including the period when they formed one country, Czechoslovakia *(Schröpfer, 2008).* Between 1999 and 2009 in the Czech Republic 151 Sakers were ringed *(Beran et al., 2012);* and between 2007–2010, 240 Saker nestlings were ringed in Slovakia. Most of the recoveries were in the Czech Republic, Slovakia and the neighbouring countries confirming a relationship between the Czech and Slovak and also with the Hungarian and Austrian populations. Recoveries confirm that some of the juveniles stay in the breeding area for winter. However, there are only a few recoveries providing further information on the migration and wintering habits. A juvenile ringed as a nestling in the Czech Republic on 20 May 1993 was found dead on 21 December in the same year near Venice, Italy. A Saker ringed on 21 May 2005 in the Czech Republic was found on 8 January 2006 in Western Hungary. Another Czech bird, ringed on 27

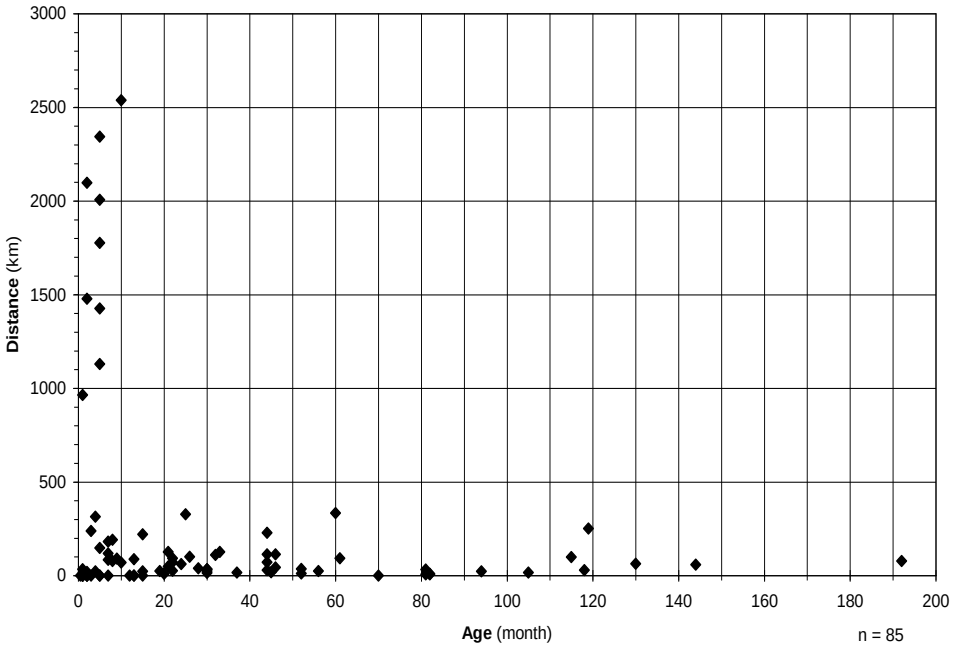


**Figure 1.** Age related distance of recoveries of Sakers ringed as pullus in Hungary (1950–2010)

May 1986, was found during its first winter in Western Hungary on 12 January 1987. An individual ringed in May as a nestling was trapped in October of the same year in Libya—2539 km away—by a falconer. Other recoveries can be considered as post-fledging dispersal, and as they are indirectly linked to migration movements they need to be mentioned. A Saker ringed as a nestling on 29 May 1982 collided with a small airplane two and a half months later, on 16 August near the town of Tarbes-Ossun-Lour, SW France *(Schröpfer, 2008).*

The following recovery shows an opposite dispersal direction: a nestling, ringed on 14 May 2003 in eastern Slovakia, was found electrocuted in November in the same year, near Moscow, Russia, 1200 km away. A male sibling of this latter bird was also found on 20 January 2004 in Serbia, 450 km south of the nest showing a different dispersal and migration/wintering strategy *(Bagyura & Szitta, 2009).*

*Hungary*

Between 1954 and 2010, 2570 Sakers were ringed in Hungary (more than 95% as nestlings) and 94 recoveries have been recorded. Regardless of age, most of the recoveries occurred in Hungary or in neighbouring countries, mainly Slovakia, throughout the year. There are, however, recoveries suggesting that some Hungarian Sakers do migrate and

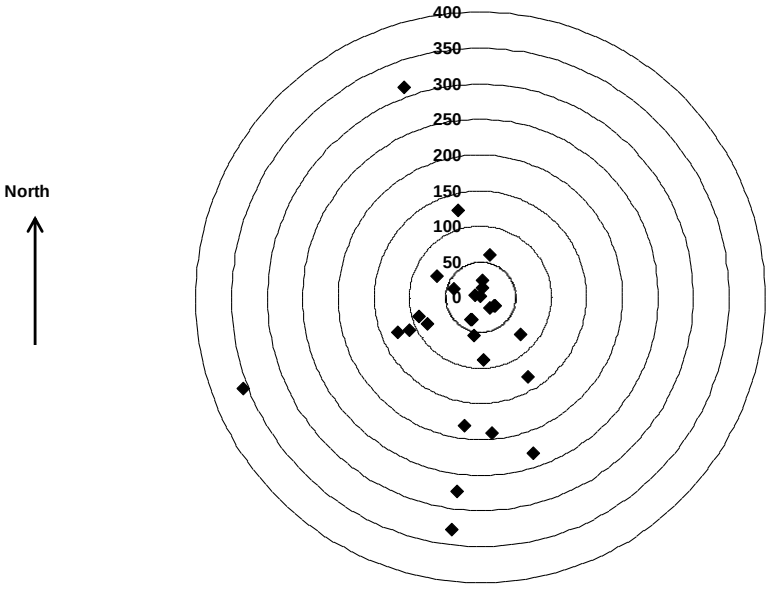


**Figure 2.** Directions and distances of recoveries of juvenile Sakers ringed in Hungary between 1951–2010 (circles represent distances in kilometres; diamonds show the distance of recovery and the direction from the ringing site)

foreign birds found in Hungary confirm that Sakers of more northern origin may spend their winter in Hungary. Age-related distance of recoveries strongly suggest that only juveniles migrate, as none of the recoveries exceeding 500 km is related to Sakers older than 11 months (Figure 1).

Juveniles recovered within 500 km tend to show clear southerly and south-westerly movements (Figure 2), while recoveries of adult birds (ringed as nestlings) were distributed in every direction except for north (Figure 3).

Long-distance recoveries can be divided into two groups: (1) Recoveries occurring during the post-fledging period, usually within 1-2 months after fledging, but before the migration season. A juvenile Saker ringed as a nestling in eastern Hungary on 31 May 1996 and was found dead on 26 July 1996, 1478 km away from the place of ringing. The bird had left the nest exceptionally early and covered a very long distance within a short time. One more post-fledging movement also deserves to be mentioned: a juvenile Saker ringed as nestling on 18 June 1983 in North Hungary was found dead in Germany (at a distance of 964 km) only 27 days later, on 15 July. (2) Long-distance recoveries related to migratory movements. Migration related movements are shown by the four recoveries from Libya between 1996 and 2009, all recoveries relating to juvenile Sakers (1st migration/winter) and they are from between October and March; one juvenile ringed as a nestling on 16 May 1993 was found on 15 October in the same year, near Poros, Greece; and a dead Saker was found in Malta on 12 October 1996 that had been ringed as a nestling on 25 May 1996.

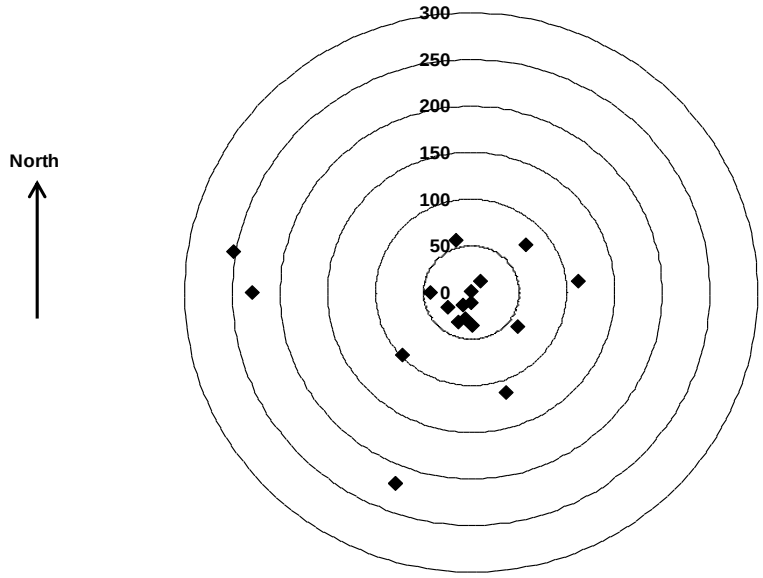


**Figure 3.** Directions and distances of recoveries of adult Sakers ringed in Hungary between 1951–2010 (circles represent distances in kilometres; diamonds show the distance of recovery and the direction from the ringing site)

Ring recoveries in the past 30 years have not demonstrated any gene exchange between the Hungarian and Eastern European (east from the Pannonian Basin) Saker populations. No emigration to or immigration from either population was observed. Recoveries of breeding adults prove the strong relatedness between the Hungarian and Slovak populations. Communication between the Czech and Hungarian populations is confirmed by ring recoveries, although only non-breeding juveniles have been recovered so far. The Hungarian population most likely relates also to the Austrian, Croatian and Serbian Saker populations, however, no ring recoveries have confirmed that theory yet.

*Other countries*

Ring recoveries show that Sakers from North Kazakhstan may migrate in a southwesterly direction using the Eastern European flyways. One Saker ringed in Naurzum State Reserve was shot in Georgia in November, 2040 km southwest from the place of ringing. Another Saker ringed in the same area was shot three years later in spring, near Chelkar railway station, 540 km southwest of Naurzum. Sakers in Southeast Kazakhstan seem to move also to a southwesterly direction according to Kazakh ring recoveries. However, they do not cross the border of Europe, but stay in Asia when migrating *(Gavrilov & Erokhov, 1994).*

Despite all ringing information one must note that ringing is not the most efficient way to study raptor movements due to the very low recovery rate. Recovery rates of birds of

**Figure 4.** Main directions of long-range post-fledging (pre-migration) dispersal of satellite-tracked juvenile Sakers (black diamonds show TSAs in the first summer established by some of the satellite-tracked birds and dark areas show the recent breeding range of Saker Falcon in Europe)

prey ringed in Hungary range between 0.6 and 9.5% but higher rates usually relate to colour-ringing projects. Only 3.6% of Saker Falcons ringed in Hungary between 1951 and 2006 were ever recovered *(Bagyura & Szitta, 2009).*

***Data from satellite-tracking in Hungary and Slovakia***

Transmitters of Saker Falcons tagged during the project were active during 10.4 months on average. Extreme values range from a few days to 51 months (and still working at the time of submitting this manuscript). Due to natural mortality and technical problems, we have data on 17 out of 45 satellite-tracked juvenile Sakers covering at least one full autumn migration and wintering period.

*Dispersal*

Although this paper aims to describe primarily the migration and wintering patterns of Central and Eastern European Sakers, some basic results of satellite-tracking about juvenile dispersal and roaming of immature birds must be presented for better understanding of the findings on migration and wintering.

Juveniles lefte the natal area one and a half month after fledging on average. The direction and distance of their first journeys varied greatly (Figure 4). In general, juveniles established their first TSA after an extended period of nomadic travel, although most of them stayed strictly within the Pannonian Basin and only few of them left it *(Sielicki et al., 2009; Uhrin & Chavko, 2008)*. Typically, juveniles used one or a few TSAs until the migration season. Using their TSAs as a base, juveniles made 'exploring trips' ranging from a few to several hundred kilometres in all directions. Post-fledging movements lasted until the mi-

gration season when most of the juveniles started to show other movement patterns.

A minority of juveniles show an entirely different movement pattern. They left their natal area very early, only about a month after fledging and covered great distances, sometimes over 1000 kilometres before they established their first TSA. In most cases they headed east and flew as far as eastern Ukraine, Southwest Russia or Western Kazakhstan. According to our results, survival chances of those juveniles were minimal.

Juveniles leaving their natal eyries in 'normal' time may also leave the Pannonian Basin before the migration season. During their migration they may behave in different ways, like the juveniles that stay in the Pannonian Basin.

As autumn migration starts from the last pre-migration TSA, the direction and the distance of dispersal determine the starting point of autumn movements. The location of the last TSA, however, does not affect the direction and length of the migration.

### *Migration*

Already at an early stage of the satellite-tracking programme it became clear that there are strong individual differences in the migration behaviour of juvenile Saker Falcons in their migration distance and routes *(Prommer & Bagyura, 2009; 2010)*. It is possible, however, to establish a few categories. According to our results satellite-tracked first calendar year (1CY) Sakers can be divided into the following groups according to the length of their migration route.

#### *Residents or short-distance migrants*

Almost half of all satellite-tracked falcons—and more than half of those surviving the first winter—stayed in the Pannonian Basin for winter. Even Sakers staying in the Pannonian Basin made a southward movement when the migration season arrived. Unlike long-distant migrants, however, they regularly did not cross the natural borders of the Pannonian Basin; they did not move more than 200-300 km at most.

#### *'True' (mid to long distance) migrants*

One-third of satellite-tracked juveniles left the Pannonian Basin in autumn. Juvenile Sakers started migration between early September and early December, the majority of them leaving typically between early October and mid November. Seemingly no direct trigger such as food shortage or weather conditions initiated migration. Of two satellite-tracked juvenile females having almost overlapping TSAs in Vojvodina, one moved to Africa in October and the other stayed to winter in the same area. It is thought, therefore, that more complex external conditions or/and genetic factors are likely to determine differences in their migration behaviour.

All mid and long distance satellite-tracked migrants showed a statistically identical angle of migration (190–200° south-southwest) confirmed by the *Welch'*s test: all birds started to migrate to the same direction regardless the location of the last pre-migratory TSAs (Figure 5). The longitude data of the position of the last TSA, therefore, determine the possible wintering range. Latitude did not play a role in this respect.

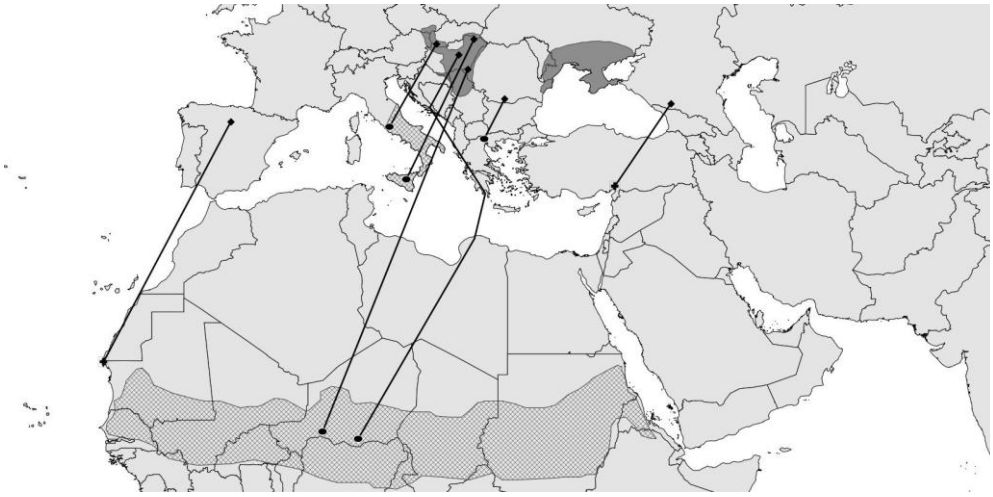

**Figure 5.** Main directions of migration routes of satellite-tracked first year Saker Falcons from the last pre-migration TSA (black square) to known wintering grounds (black ellipsoid in grey field) outside the known European breeding ground (dark grey). Crosses show when birds failed to reach the wintering ground (not every migrating bird with satellite data were shown; however, all typical routes are represented)

Average speed during migration was almost identically 40-50 km/h over sea and approximately 30 km/h over mainland in case of all satellite-tracked Sakers. Compared to movements during post-fledging dispersal—when Sakers tend to restrict their movements to the lowlands—they may cross high ridges and extensive mountain ranges on migration, but they prefer to follow the valleys where possible rather than crossing high altitude barriers directly.

All satellite-tracked long-distance migrants that crossed the Mediterranean Sea were females. They used the same routes from the Pannonian Basin to the Adriatic coast as medium distance migrants, but unlike those medium distance migrants crossing the sea, three out of four long-distance migrants turned to south and followed the coastline to Greece. They crossed the Mediterranean Sea between the Greek islands and the North-African coast (Libya and Egypt). They always took off in the morning and their flights over the sea lasted 8–13 hours. Once they arrived at the African coast they immediately adjusted their route to the initial southwesterly direction and continued crossing the Sahara Desert.

One female Saker tagged in Slovakia chose a different route: she crossed the Adriatic Sea like medium distance migrants, but then carried on towards the southwest making an exceptional 24-hour non-stop flight from Montenegro to Tripoli, Libya covering 1100 km over the sea (average speed approximately 46 km/h).

As the direction of the migration was almost identical for different individuals, but the starting point (the location of the last pre-migratory TSA) varied, juveniles used different routes and they had different wintering areas depending on whether they dispersed from the Pannonian Basin to the west or to the east. One satellite-tracked male, which fledged in

Southeast Hungary, spent the summer in Dobrugea, Romania. In autumn, he migrated southwest and ended up in North Greece, where he spent the winter. A female fledged in western Hungary moved as far as North Spain, from where she was visiting several sites including Portugal. In autumn, she started to head south-southwest, crossed the Gibraltar Straits and continued her way along the Atlantic coast as far as the peninsula at Nouadhibou, North Mauritania. There she perished as the peninsula—without prey and fresh water—works as a natural trap for birds of prey having several hundred kilometres of desert behind it. The site was just a few kilometres away from the place where another dead Saker had been found during the winter of 1978/1979 in the water of Star Bay *(Dejonghe, 1980).* In both cases 1st calendar year (1CY) Sakers started their autumn migration in southwesterly direction, exactly like the juveniles remaining within the Pannonian Basin.

*'Multiple migrants'*

Multiple migrations within one—first autumn—migration season were also recorded. Two satellite-tracked females covered the Pannonian Basin—Italy distance multiple times (one flew there and back, and the other one there and back and there again) within one autumn migration season.

Analyzing the migration data of those 1CY Sakers ($n$ = 26) clearly showing migratory behaviour by using the *Welch's* test, we received the following results. There was a significant difference between the migration distance and time of males and females. Females migrated further and for a longer time ($p$ = 0.05) when compared to males; no significant difference was found in the speed and in the direction of migration.

*Migration of subadult Sakers*

Satellite tracking revealed that the migration pattern of Sakers changed after the first winter. They were imprinted on revisiting their previous wintering sites and they returned there regardless where they had spent the summer. In general, summer dispersal of young males covered even shorter distances each year until they established their own eyrie. After that they stopped summer nomadism. However, satellite-tracked males re-visited their traditional wintering sites even after their first active breeding period.

Satellite-tracked females showed a different summer nomadic behaviour in their second calendar year. Female Sakers staying in the Pannonian Basin did not disperse after their first winter. Females dispersing beyond the Pannonian Basin and wintering further away returned after the winter and remained for summer. For more detailed information on the migration patterns of subadult female Sakers, however, more birds need to be tagged.

*Migration of adult Sakers*

Satellite-tracked adult males did not migrate and they did not show nomadic movements, either. However, the possibility cannot be excluded that adults do migrate in certain cases, as the winter disappearance of some—untagged—individuals from certain eyries suggests. None out of the five adult male Sakers occupying eyries in western Hungary (n = 2), Central Hungary (n = 2) or East Hungary (n = 1) left the region throughout the year. They happened to leave to a few dozen kilometres for shorter periods (weeks) when

weather conditions (snow, cold) reduced prey availability, but even in those cases they visited the nest site from time to time. Otherwise they spent the winter within a few kilometres of the nest site.

Fewer data are available on adult females. There was only one adult female that had been tagged and provided information for two years. She spent only the breeding period at the nest. Outside the breeding season she followed a similar movement pattern in both years having three different TSAs according to seasons. She occasionally visited other areas as well.

*Timing of migration*

The timing of migration depended on the age of the bird and on the season. In the first calendar year Sakers started their autumn migration between late September and mid November, with most of them leaving in early October. Spring migration until the second year was more uniform: all the eight satellite-tracked falcons that survived until the second year left the wintering area between 26 March and 8 April regardless of whether they spent the winter within the Pannonian Basin or in Africa. The birds wintering in the Pannonian Basin left the wintering ground a few days earlier (end of March) than the birds wintering further away (first days of April). Individuals often returned to the area of their last TSA before autumn migration, however usually they did not stay there for long, and they continued wandering instead. Spring migration in the second calendar year was slower than the autumn migration in the first.

The start of autumn migration of older birds showed individual differences, spring migration, however, started earlier as the birds got older. During the spring of the third calendar year satellite-tracked males left the wintering ground in early/mid March and from the fourth calendar year they left the wintering ground as early as the end of February. A satellite-tracked adult female wintering in the Pannonian Basin—some distance from her eyrie—also left for the breeding site at the end of February.

## Conclusions

### *Migration studies of similar falcon species*

Movements of three other large falcon species—the Gyrfalcon *(Falco rusticolus)*, the Prairie Falcon *(Falco mexicanus)* and the Peregrine Falcon *(Falco peregrinus)*—were studied extensively by using ringing and satellite-tracking. Based on our findings the movements of Sakers show different patterns from theirs. Although a massive satellite-tracking programme on Saker Falcons was carried out in Central Asia, a detailed analysis of the results has not been published yet (*A. Dixon*, pers. comm.).

The movement patterns of Gyrfalcons, the closest relative of Sakers, are somewhat similar—e.g. adults tend to remain around the eyrie all year in some areas of the distribution range—but Sakers show an even more complex migration pattern compared to them. According to ringing and satellite-tracking data, movements of Gyrfalcons are determined by food supply rather than by instincts *(Sale & Potapov, 2005; Burnham & Newton, 2011)*.

Prairie Falcons, which occupy habitats in North America very similar to those used by

Sakers in Eurasia, migrate on two separate routes and use grassland areas consistently. According to Canadian ringing results, adults also migrate from the northern edge of the distribution range *(Schmutz et al., 1991)*.

Out of the discussed species Peregrine Falcons were studied at the broadest geographical scale, but this species shows the least similarity to Saker Falcon. Most of the Peregrine studies focussed on the entirely migratory Arctic population. Individuals of the North American population travel to South America *(Fuller et al., 1998)*, while the North Russian population shows a fan-shaped migration with diverting routes from the breeding grounds to the wintering grounds *(Dixon et al., 2012)*. Satellite-tracking studies of Peregrines at lower latitudes reveal more individual variation in migration, but apparently those are less systematic than the migratory movements of Sakers *(Gahbauer, 2008; Mojica et al., 2011)*.

***Juvenile Saker Falcons in their first calendar year***

European juveniles are partial migrants. Almost all 1CY Sakers move southwest in autumn, but only about one-third of them leave the breeding range of the species and show medium or long distance migration. The rest of the birds remain within the breeding range and show only local or regional movements in the same direction—or no movement at all. The direction of the movements of 1CY Sakers is between 180° and 240° and seems to be universal: it is applicable to 1CY juveniles from Austria (Spain) as well as from western Kazakhstan.

Apart from ring recoveries mentioned above, satellite tracking studies also confirmed the southwesterly autumn movements of 1CY Sakers in West Kazakhstan (*A. Dixon*, pers. comm.). Juveniles of more eastern populations (Southern parts of Asian Russia, Altai Mountains, Mongolia), however, show a fan-shaped migration from the breeding ground to central and west China *(Eastham, 1998; Eastham et al., 2000; Karyakin et al., 2004; 2005; Potapov et al., 2001; 2002; Sumya et al., 2001; Batbayar et al., 2009).* Based on the data, the frontier between Sakers showing the 'Western' or 'European', and those moving on the 'Eastern' or 'Asian' migration patterns may be somewhere in the Altay-Sayan region. The two different migration patterns suggest that they have evolved separately by adapting to the geomorphologic features of the occupied areas in parallel with the gradual segregation of the two populations.

Uniformity of the migration patterns of 1CY Sakers suggests that direction (it seems to be uniformly southwesterly between 180°and 240° for 1CY Sakers in Central and Eastern Europe), timing of migration as well as the distance of the movements (of the given individual) are driven by inherited instincts.

The universal southwesterly autumn movement results in a parallel movement—or parallel migration—of 1CY juvenile Saker Falcons. The last pre-migratory TSA, as the starting point of autumn migration and the 'pre-set' direction for migration, therefore, determines the migration routes and the location of the potential wintering areas. The parallel migration explains why Sakers—according to data from observations—do not concentrate during migration as soaring raptors: individuals travel on a broad front and they are able to cross large water bodies by using powered flight.

As a result of parallel migration, wintering Sakers are sparsely scattered along the appropriate habitats mainly in the Central Mediterranean region in Europe and in the Sahel in

North Africa. However, as Central European Sakers may establish a TSA in Eastern Europe, juveniles seen on migration e.g. along the western Black Sea coast, are not necessarily East European Sakers, but may come from Central Europe.

Indirect data support the hypothesis of parallel migration. Literature data presented above shows that the number of migrating and wintering Sakers dropped dramatically by the 1950s–1960s in southern Italy, as well as in Sardinia. Similarly, the number of migrating Sakers in Cyprus declined after the 1960s—beforehand, the species was considered a relatively frequent autumn visitor. That was exactly the time, when Sakers in Central and Eastern Europe decreased significantly, due to habitat change (caused by human land use), persecution, nest robbing and other unknown factors. Since the 1990s, the number of migrating and wintering Sakers has been increasing in southern Italy, reflecting the positive trend of the Central European breeding population *(Corso & Harris, 2012; Bagyura et al., 2012)*. The number of Saker observations, however, has not increased in Cyprus despite a more systematic autumn raptor censussing on the island *(M. Miltiadous,* pers. comm.). It is in line with the parallel migration theory suggesting that Sakers visiting Cyprus come from the easternmost parts of Europe (European Russia and western Kazakhstan) and westernmost parts of Asia (East Turkey), where the population still has not recovered (*Dixon et al., 2009; I. Karyakin*, pers. comm.).

Autumn movements start between early September and early December with no obvious trigger (like weather or abundance of food supply) for timing found. During their autumn movements Sakers keep strictly to southwest and some individuals showing a long-distance migratory behaviour are able to cross considerable geographical barriers (e.g. the Mediterranean Sea). Those barriers, however, may temporarily diverge a certain number of individuals. Some of the migrating Sakers of the Pannonian Basin did not cross the Adriatic Sea, but continued moving southward, along the Adriatic coast deviating from the original south-western direction. However, they always crossed the Mediterranean Sea once they reached the tip of the Greek islands and they never turned to east to continue the migration over the mainland. Arriving in Africa, they returned to the original southwestern direction up to their wintering ground in Sahel (when crossing the sea between Greece and Africa they chose the southern direction probably to minimize the time spent above the open sea).

The first spring migration (in the second calendar year) starts in a very narrow time window—from late March to early April—regardless the distance between the wintering site. Spring migration after the first winter is slower than autumn migration beforehand.

***Immature (second calendar year) and 'floater' birds***

Sakers follow a different strategy from their second autumn on. Once they overwintered successfully, they return to the same place in subsequent winters, regardless where they spent the summer.

Floater males—those non-breeding adults that do not possess their own eyrie—migrate as well. No information on floater females is available as yet. With the progress of their age spring migration of Sakers starts earlier. Floater males in their fourth calendar year may start the spring migration already at the end of February.

***Breeding adults***

Tagged breeding males occupying their eyries did not migrate, but stayed in or near the eyrie all-year-round. It cannot be excluded, however, that some of the adult males of established pairs migrate as well, as some observations suggest.

Limited data on adult females of established pairs suggest that they visit the same places in the same periods of the year, regardless whether they remain around the eyrie with the male or show a special dispersal pattern in the non-breeding period within the breeding range. It is most likely a learnt behaviour and probably follows a food-availability pattern throughout the year; however more research is needed to confirm that.

***Wintering areas***

The main wintering areas of the migrating Central European Sakers are in Italy south of the Rome–Ancona line. According to the calculation of *Corso & Harris (2012)*, from the Hungarian population alone a few dozen individuals may winter in Italy. There are also wintering areas in Northeastern Greece; those areas host, however, fewer individuals considering the smaller size of East European populations.

In Africa the main wintering area is the Sahel, where Sakers can be found sparsely scattered from the Atlantic Ocean to Sudan occupying the appropriate habitats. They prefer dry semi-desert areas and grasslands. Study on a Hungarian satellite-tracked Saker wintering in Niger showed that the bird used millet fields and open areas with 20-70 trees/ha on average *(Issaka & Brouwer, 2012).* Some individuals may travel further south and spend the winter on the savannas of Kenya and Tanzania; it is unclear however, which part of the distribution range they are from.

***Other findings***

When comparing the data of ringing records and those of satellite tracking, the extensive and long-term ringing of Sakers swhowed the main directions of their large-scale movement (juvenile dispersal and migration) even if the recovery rate was only 3.6% for the species. Ringing, however, failed to reveal any fine movement patterns as well as a possible individual fidelity to a certain site (TSA or wintering site) in consecutive years. Ringing as a method, at that scale, is not adequate to describe accurately the movement patterns of those raptors using active (non-soaring) flight during migration like the Saker Falcon.

Satellite-tracking and ringing results suggest that there is no significant gene exchange between the disconnected Central European and Eastern European populations, although their flyways overlap significantly. Flyways of juvenile Central European Sakers certainly overlap with the western Asian (West- and Central-Kazakh) Sakers, but after a certain time of dispersal all nomadising birds return to their respective natal areas. Ring recoveries confirm that Sakers show the largest movements in their first year then they tend to find their own eyrie around their natal area. Our research has not confirmed that Sakers have a nomadic behaviour as it was suggested by *Ellis et al. (2011)*.

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**Appendix 1.** Review of migration of Saker Falcon data related to its Central and Eastern European populations (data from regular and long-term monitoring programmes were included to the table; the Eastern Mediterranean region includes the Balkan countries also, n.d. = no data available)

| Country | Site | Date / *Period* | No. of raptors | No. of Sakers | Reference |
|---|---|---|---|---|---|
| **Middle East** | | | | | |
| Georgia | Batumi | Autumn 2002 | n.d. | 31 | *Balmer & Betton (2003)* |
| | | Autumn 2008–2009 | 1 658 170 | 6 | *Verhelst et al. (2011)* |
| | southern Caucasus | 26 Aug.–29 Oct. 1997 | 120 000 | 11 | *Galushin & Moseikin (2000)* |
| Israel | "Northern Valleys Survey" | 1990–1999 | n.d. | 4 | *Alon et al. (2004)* |
| | Eilat | 1969–1980 | n.d. | 1 | *Christensen et al. (1982)* |
| | Haifa | 7 Apr 1987 | n.d. | 2 | *Géroudet & Juillard (1990)* |
| Russia | Kislovodsk | 12 and Sep. 1998 | n.d. | 3 | *Galushin & Moseikin (2000)* |
| Syria | | Sep.–Nov. 2000–2003 | n.d. | 6 (trapped) | *Serra et al. (2005a, 2005b)* |
| Turkey | Belen Pass | Autumn 1976 | n.d. | 1 | *Acar et al. (1975)* |
| | Bosporus | 13 Sep.–1 Oct 1956, Autumn 1957, 20 Aug.–8 Oct. 1966 | n.d. | 23 | *Porter & Willis (1968)* |
| | | 18 Mar.–31 May 2006 | n.d. | 1 | *Üner et al. (2010)* |
| Yemen | Bab-el-Mandeb Straits | 15 Oct..–1 Nov. 1985 | n.d. | 3 | *Welch & Welch (1989)* |
| | Mafraq al Mukha | 4 Nov. 1985 | n.d. | 1 | *Porter & Christensen (1987)* |
| **Eastern Mediterranean region** | | | | | |
| Bulgaria | Bourgas (Burgas) | Autumn 1979–2003 | 770 674 | 151 | *Michev et al. (2011)* |
| | NE & S Bulgaria, Bourgas (Burgas) | Sep.–Oct. 2007 | n.d. | 6 | *D. Ragyov (pers.comm.), www.netfugl.dk (leg. P.E. Pedersen)* |
| Cyprus | Akrotiri Peninsula | Sep.–Nov. 2006 | n.d. | 7 | *M. Miltiadous* (pers.comm.) |
| | | Autumn 2004–2007 | n.d. | individuals | *M. Miltiadous* (pers.comm.) |
| Greece | Antikythira | Autumn 2007–2009 | 4 106 | 2 | *Lucia et al. (2011)* |
| | | Spring 2007–2008 | 797 | 0 | *Lucia et al. (2011)* |
| Romania | Măcin | Autumn 2002–2007 | 66 952 | 17 | *Milvus (2008)* |
| **Western Mediterranean region** | | | | | |
| France | | 1901–2012 | n.d. | 5 | *Mission Migration Project (www.migraction.net)* |
| Italy | Apuan Alps (Alpi Apuane) | 1–30 Sep. 2012 | 2 400 | 1 | *Premuda (2012)* |
| | Monte Conero | 20 Mar.–20 May 2004; Spring 2009; 15 Apr.–31 May 2012 | 18 957 | 3 | *Premuda et al. (2008), Borioni & Baldoni (2009), Fusari (2012)* |
| | Monte San Bartolo | 23 Apr.–7 May 2005; 10 Mar.–31 May 2009; 14 Mar.–31 May 2010 | 6 286 | 3 | *Premuda et al. (2008), Sonet et al. (2009, 2010)* |
| | Panarea | 20 Apr.–20 May 2005; 20 Apr.–20 May 2007 | 4 809 | 2 | *Gustin (2005, 2007)* |
| | Strait of Messina (Stretto di Messina) | Apr.–May 1986–2006 | n.d. | 20 | *Giordano (1991)* |
| | | Spring 1996–2000; 14 Apr.–21 May 2006; 2 Apr. – 27 May 2008; 1 Apr.–27 May 2009; 27 Mar.–26 May 2012 | 266 020 | 17 | *Corso (2001), Chiofalo et al. (2006), Cutini et al. (2008), Ricciardi et al. (2009), Giordano et al. (2012)* |
| Malta | Buskett | 2001 | n.d. | 3 | *Sammut & Bonavia (2004)* |
| | Buskett | 8–23 Sep 2007, 25 Aug–26 Oct 2012 | 6 309 | 3 | *Raine & Vella (2007); Galea & Vella (2012)* |
| | | 1908–2007 | n.d. | 49 | *R. Vella (pers.comm.)* |
| **Northern Africa & Sahel** | | | | | |
| Tunisia | Cape Bon | Mar.–Apr. 1974; 1–20 May 1975; Mar.–May 1977 | n.d. | 35 | *Thiollay (1977), De Jong et al. (2009)* |
| Ethiopia | Awash area | Nov. 2004 | n.d. | 27 | *Dixon (2005)* |
| Sudan | Lake Nasser area | Autumn 1986 | n.d. | 1–2 | *Ash & Nikolaus (1992)* |