

Migration and wintering of adult European honey buzzards (*Pernis apivorus*) breeding in Germany, as revealed by satellite telemetry

Migrácia a zimovanie dospelých včelárov lesných (*Pernis apivorus*) hniezdiacich v Nemecku, ako to odhalila satelitná telemetria

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Abstract: Twelve adult European honey buzzards (*Pernis apivorus*) were tracked for up to five years. The females left the breeding area approximately eight days earlier than the males. Ten of the birds appeared to die during the telemetry period. In autumn, all of the birds migrated to West Africa, reaching as far south as the Republic of the Congo via France and Spain. In most cases (13 out of 20 migrations involving nine birds), they crossed the western third of the Pyrenees. Most of them used the Strait of Gibraltar to reach Africa (16 migrations involving 10 birds), but in some cases (three migrations involving two birds) they flew long distances over the Mediterranean sea instead. The routes of individual birds varied from year to year. In spring, the birds generally migrated farther east than in autumn. Three honey buzzards wintered in Nigeria, two in Liberia and one in each of Cameroon, Gabon and the Republic of the Congo. The distances travelled between the breeding grounds and wintering areas ranged from 6,128 km to Liberia to 8,645 km to the Republic of the Congo. The autumn migration lasted between 36 and 99 days, while the spring migration lasted between 23 and 55 days. This depended on the length of the migration route, the duration of stopovers and other factors. Birds travelled up to 600 km per day, reaching a maximum speed of 109 km/h. Winter site fidelity over consecutive years was recorded for four individuals over up to four winters. The home ranges of two wintering honey buzzards were calculated from up to 97 GPS fixes. These birds had small winter home ranges of 1.55 and 3.40 km² (MCP95), and 4.43 and 7.44 km² (KDE95), respectively.

Abstrakt: Dvanásť dospelých včelárov lesných (*Pernis apivorus*) bolo sledovaných viac ako päť rokov. Samice opúšťajú hniezdne oblasti v približne o osem dní skôr ako samce. Počas obdobia sledovania pravdepodobne došlo k úhynu desiatich z monitorovaných vtákov. Jesenná migrácia všetkých jedincov smerovala do západnej Afriky. Ich trasa viedla cez Francúzsko a Španielsko až na juh Konžskej republiky. Najčastejšia trasa videla cez západnú tretinu Pyrenej (13 z 20 migrácií týkajúcich sa jedincov). Ku dosiahnutiu Afriky väčšinou využili Gibraltársky prieliv (16 migrácií týkajúcich sa 10 jedincov), ale v niektorých prípadoch (tri migrácie zahŕňajúce dvoch vtákov) preleteli aj dlhé vzdialenosti nad Stredozemným morom. Trasy jednotlivých vtákov sa z roka na rok líšili. Na jar vtáky zvyčajne migrovali ďalej východnejšie ako na jeseň. Tri včeláre zimovali v Nigérii, dva v Libérii a po jednom v Kamerune, Gabone a Konžskej demokratickej republike. Vzdialenosti medzi hniezdiskami a zimoviskami sa pohybovali od 6128 km do Libérie po 8645 km do regiónu Kongo. Jesenná migrácia trvala 36 až 99 dní, zatiaľ čo jarná migrácia trvala 23 až 55 dní, v závislosti od dĺžky migračnej trasy, trvania medzipristátí a ďalších faktorov. Vtáky preleteli až 600 km za deň a dosiahli maximálnu rýchlosť 109 km/h. Vernosť zimovískam v priebehu po sebe idúcich rokov bola zaznamenaná u štyroch jedincov počas až štyroch zim. Domovské areály dvoch zimujúcich včelárov boli vypočítané na základe až 97 GPS polôh. Tieto vtáky mali malé zimné domovské areály s rozlohou 1,55 a 3,40 km² (MCP95) a 4,43 a 7,44 km² (KDE95).

Key words: migration, wintering, satellite telemetry, GPS tagging, migration routes, migration speed, raptors, birds of prey

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Earth. J. von Rönn reshaped the haversine formula to work with a German version of Excel. D. Holte helped to interpret weather data. C. Meyburg prepared migration maps and calculated various migration parameters. I. Krause provided invaluable assistance in preparing the data. C. Panter calculated the winter home range sizes, created the illustrations and improved the English text. The World Working Group on Birds of Prey (WWGBP) covered the costs of the transmitters and the data transmission via the Argos system. N. Agostini and M. Kouba made substantial improvements to the manuscript.

Introduction

European honey buzzards (*Pernis apivorus*, hereafter ‘honey buzzard’) are primarily forest dwellers that only spend about four months in their breeding grounds. Due to their secretive lifestyle, there is uncertainty regarding the status of their population and the causes of potential population declines (Bijlsma et al. 2012). After years of studying breeding biology, population dynamics and VHF radio tracking in the breeding area (Ziesemer 1997, 2019, 2024; Ziesemer et al. 2021), we decided in 2001 to use satellite telemetry to gain insights into migration and wintering areas as well.

Honey buzzards spend most of the year undertaking long-distance migration and overwintering in sub-Saharan Africa. They mostly use thermals and deflection updrafts over land to migrate, but they can also cross large bodies of water by flying long, nonstop flapping flights (Vansteelant & Agostini 2021).

The birds return very late from their African wintering grounds, ensuring that the rearing of young coincides with the highest wasp abundance in midsummer. After a short breeding season, adult honey buzzards leave Europe in late August. They spend more than half the year in the forests and tree savannahs of sub-Saharan Africa, with some individuals travelling as far as southern Africa, particularly females and juveniles (Howes et al. 2019). Honey buzzards are difficult to study on their breeding grounds, and even less is known about their lives in Africa outside of the breeding season.

The honey buzzard is the most abundant soaring bird at almost all major migration monitoring sites in Europe and the Middle East (Vansteelant & Agostini 2021). Despite the difficulty of obtaining reliable population estimates for this secretive woodland species, evidence suggests that the honey buzzard population is stable throughout most of its range (BirdLife 2020, Online Datazone, status: Least Concern). The total population in Germany is estimated to be around 5,200 pairs (Mebs & Schmidt 2014), or 3,600–3,800 pairs according to Ferguson-Lees & Christie (2001).

This study provides information on the migration and wintering areas of German honey buzzards. It describes their migration routes and stopover sites, as well as the timing, speed, and home range sizes in their wintering

areas. Some of the results have already been published: Ziesemer & Meyburg (2015) described behaviour in the breeding area, while Meyburg & Ziesemer (2024) and Meyburg & Gries (2024) discussed mortality. However, the entire migration and wintering period has not previously been analysed comprehensively.

Adult honey buzzards were also satellite tracked in the Netherlands (n = 13), Sweden (n = 6) and in the Czech Republic (n = 2). These birds used the West African–Eurasian flyway, crossing the Mediterranean via the Strait of Gibraltar during autumn (Šena 2025) and spring migration (Hake et al. 2003; Strandberg et al. 2009; Vansteelant et al. 2014, 2017b). Conversely, a tracking study of adult birds from Finland revealed migration routes across the eastern Mediterranean (Vansteelant et al. 2017a). A majority of experienced adults in the Finnish breeding population was found to readily engage in long sea-crossings, leaving Europe mostly via Greece and the Aegean islands, probably taking advantage of frequent tailwinds during their post-breeding migration (Vansteelant & Agostini 2021). Of five males from north-eastern Poland, only one used the route via Gibraltar, the others crossed the Mediterranean via Italy and Greece or circumvented it via the Bosphorus (Mirski et al. 2026). These routes cannot be directly compared with those taken during outward migration from northern Germany via Gibraltar and are therefore not considered here.

Material and methods

We analysed data from twelve adult honey buzzards (seven males, five females) breeding in northern Germany, one in each of the federal states of Brandenburg and Mecklenburg-Western Pomerania, and the others in Schleswig-Holstein (Tab. 1). The birds were caught in 2001–2011 during the nestling stage close to the eyrie using mist nets and decoys. Birds were fitted with 18- to 22-g solar-powered satellite transmitters (PTTs) made by Microwave Telemetry, Inc. (USA) and NorthStar (USA) as backpacks (Meyburg & Fuller 2007), which used the Argos satellite system to locate and track the honey buzzards. From 2001 to 2009, only transmitters with Argos Doppler-shift locations were available due to the species’ small size. In 2009, we began using six GPS-enhanced tags that also transmitted data

Tab.1. Overview of tagged honey buzzards.
Tab.1. Prehľad označených včelárov lesných.

Transmitter ID	Sex	First location	Last location	Transmission period (days)	Remarks
13288	♂	28.7.2001	2.5.2003	602	Probably drowned in the Mediterranean during its spring migration. Analysis of weather data online does not provide a clear indication of any unusual weather events. Did not return to its breeding ground afterwards.
1 st transmitter 13289*	♀	7.7.2001	2.9.2002	430	30.5.2003 observed at the nest, 26.6.2004 transmitter 13289 replaced by PTT 40867.
2 nd transmitter 40867*		26.6.2004	2.5.2006	625	
13290	♀	22.7.2001	8.10.2002	409	Spring and autumn migration routes in 2002 were very similar, in contrast to the significantly different autumn migration route along the Atlantic coast in 2001.
40868	♀	18.7.2009	27.10.2009	103	Female of male with tag 95771. Recaptured on 9 August 2011, weight 906 g, 23 g heavier than in 2009, transmitter removed.
41504	♂	19.7.2003	16.5.2006	1031	Recaptured on 30 July 2005 at a nest 2.3 km further southeast, transmitter not replaced; weight 30 g higher upon recapture
52033	♂	7.8.2010	5.12.2011	485	In 2012, two new, untagged but ringed individuals were breeding in this bird's nest, thus this individual most probably died in the wintering area on 05.12.2011 or shortly afterwards.
52035	♀	16.7.2011	29.9.2011	74	Last location in Côte d'Ivoire where the transmitter failed, since the bird was observed in the breeding area on 22 July 2012.
57029	♂	22.7.2006	11.10.2006	82	No remarks
68560	♀	15.7.2011	3.10.2011	80	Female of male with PTT 68561, died in the Sahara Desert on 14.9.11, locations received until 3.10.2011. See also below.
68561	♂	15.7.2011	10.10.2011	87	This is the male partner of the female with PTT 68560, who died on 17.9.2011 in the Sahara Desert. Locations received until 10.10.2011. His death three days after his female, 174 km northwest of her place of death, occurred after spending six days in the Sahara. Compared to his female, his migration was almost identical (delayed by two days). In particular, their movements in the Sahara indicate that both birds were exposed to very similar adverse migration conditions, which slowed their progress and caused them to travel in a zigzag pattern.
95770	♂	19.7.2009	12.7.2010	363	This male died in the Sahara Desert in Mauretania and was then taken to Mali by someone.
95771	♂	18.7.2009	8.1.2010	175	Male partner of the female with tag 40868. As the male was not observed in the breeding area in 2010 and thereafter, it can be assumed that the bird died in its wintering area on 8 January 2010.

*individual was retrapped and tagged with new transmitter

on flight direction and speed. Four of these provided altitude data up to a technical upper limit of 2,047 metres above sea level (ASL). The PTTs with Argos-Doppler positioning were programmed to record as many locations as possible, depending on the batteries' state of charge. The GPS/PTTs were programmed to acquire a GPS fix every hour. The combined weight of the transmitter and harness was always less than 3% of the birds' weight.

Locations obtained from Argos were checked for plausibility, and any obvious outliers were discarded. The GPS/PTTs provided both Doppler and GPS position estimates, enabling us to verify the estimates and, in some instances, supplement data from one system with data from the other.

All location data were analysed individually and entered into databases. We used a computer programme

(ArcView GIS 3.2a) to plot the birds' locations, measure the distances between them, and trace their migration routes. This programme is an integrated global mapping and digital display system that computes great-circle distances and dynamically displays both great-circle and constant-compass-bearing (rhumb) lines. Great-circle distances are the shortest possible distances on a globe. We calculated the distances between the wintering and summering areas, as well as between the different segments, by adding together the great-circle distances between all accepted neighbouring locations.

We analysed the GPS data using ArcView 3.2a and visualised it using Google Earth and other satellite imagery sources. For three cases involving birds crossing the Mediterranean Sea and the Sahara Desert, we collected wind information at various altitudes using the NCEP package (Kemp et al. 2012). This information

was downloaded as U and V vectors from the NCEP/NCAR reanalysis dataset (Kalnay et al. 1996), providing contextual information on atmospheric conditions potentially affecting migration. In three cases where the birds apparently died during migration, possibly due to adverse weather conditions in the Sahara Desert (ID 68560 and 68561) or over the Mediterranean Sea (ID 13288), no more detailed information could be obtained, as the available weather data are limited to large-scale patterns.

However, due to largely unquantifiable inaccuracies in the Argos locations, a high proportion of locations falling into low accuracy classes, and long intervals between successive locations, particularly in the early years of the study, it was not possible to estimate small-scale movements with any degree of confidence. In later years, however, improved transmitter technology and GPS data collection enabled us to investigate small-scale movements, including those within the breeding home range (Zieseimer & Meyburg 2015; Meyburg & Zieseimer 2024).

Because several individuals were tracked across multiple migrations, some tracks are not statistically independent. Therefore, the analyses are descriptive and should not be interpreted as independent population-level replicates.

To determine the duration and length of the crossing of the Sahara Desert, we defined its boundaries according to the methodology proposed by Olson et al. (2001), as described in `\\SASQUATCH\\DATA\\ecoregions\\version_2\\new_version\\wwf_terr_ecos.shp`.

Winter home ranges were estimated using both Minimum Convex Polygon (MCP) and Kernel Density Estimation (KDE) approaches implemented in R (R Core Team 2024) using the „adehabitatHR“ package (Calenge 2024). Location data (longitude/latitude; WGS84 datum) were first projected into an equal-area coordinate system (Albers Equal Area; units in meters) to allow accurate area estimation using the „sp“ (Pebesma and Bivand 2005) and „sf“ (Pebesma and Bivand 2023) packages. MCPs were calculated at the 95% isopleths to represent the total home range area. KDEs were computed using a fixed kernel approach with the reference bandwidth ($h = h_{ref}$) as the smoothing parameter. Utilisation distributions were then converted to polygons representing the 95% volume contours using the `getverticeshr()` function within the „adehabitatHR“ package. Areas of these contours were calculated in km² from the projected data. The 95% KDE was used to characterise the overall home range extent.

The authors did not use generative AI technology in the preparation of the manuscript.

Results

Of the two birds marked in Brandenburg and Mecklenburg-Western Pomerania, it remains unknown whether they bred and, if so, with what success. All 10 other birds bred successfully in Schleswig-Holstein. Signals were transmitted for up to three years per tag. Except for the last six transmitters, which were equipped with GPS positioning and three-layer solar panels, data was transmitted almost exclusively during migration periods. During non-migration periods, the birds remained in vegetation that was too dense for earlier transmitters to recharge adequately.

Autumn migration routes

All of the birds migrated to West and Central Africa (Fig. 1). The duration and distances travelled between breeding and wintering areas are given in Table 2 (see also Appendix text T1).

All the honey buzzards started migrating south-west and maintained this direction as far as Spain (Fig. 1). After crossing Germany and France in a relatively broad front, the birds crossed the Pyrenees, most of them (13 of 20 migrations from 9 birds) concentrated in the western part. A broad front, running straight from the Pyrenees to Gibraltar, was again recorded in south-eastern Spain, between Madrid and the Mediterranean Sea. The migration route was strongly concentrated near the Strait of Gibraltar.

In Africa, after crossing the High Atlas, the migration front expanded to around 1,100 km across the El Jouv Desert in Mauritania and Mali. Most of the birds turned south-east here, heading for their wintering grounds. Birds with a more westerly destination continued further south (Fig. 1; see Appendix text T2 for details).

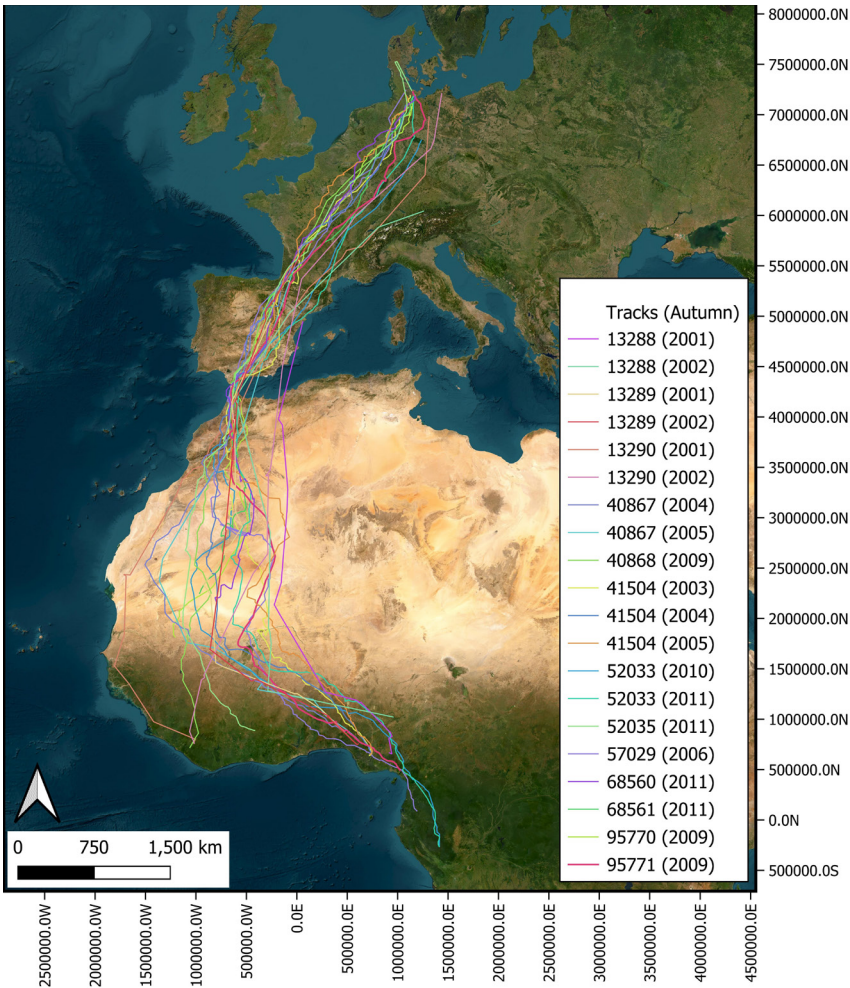
Spring migration routes

Overall, the spring migrations occurred farther east than the autumn migrations (Fig. 2). At 20° N, the migration front was at its widest, spanning almost 2,000 km. The birds migrated in a relatively straight line towards north-northwest. However, only one individual deviated by over 1,100 km from the direct route between the wintering area and the Strait of Gibraltar, migrating in an arc far to the west.

Unlike during their autumn migration, the birds crossed the Mediterranean not only near the Strait of Gibraltar. Bird 52033, which had wintered the farthest east and south in the Congo region, performed a loop migration, travelling north via Tunisia and Sicily to the Apennine peninsula.

Fig. 1. Autumn migration routes of tagged honey buzzards. While the autumn migration in Europe is concentrated in the Strait of Gibraltar, the routes across the Sahara Desert show a wide range of individual possibilities, likely in response to external conditions.

Obr. 1. Jesenné migračné trasy označených včelárov lesných. Kým jesenná migrácia v Európe sa sústreďuje cez Gibraltársky prieliv, trasy cez púšť Sahara vykazujú širokú škálu individuálnych možností, pravdepodobne v závislosti od vonkajších okolností.



Tab. 2. Distances travelled (km, mean $\pm$ standard deviation, if available) and duration (span, in days) of autumn and spring migration.
Tab. 2. Preletené vzdialenosti (km, priemer $\pm$ smerodajná odchýlka, ak je dostupná) a trvanie (v dňoch) jesennej a jarnej migrácie.

Individual ID	13288	13289 (40867)*	13290	40868	41504	52033	57029	95771
Autumn path	6523	7342	6764 $\pm$ 1237	6128	7471 $\pm$ 363	8455 $\pm$ 269	8116	7329
Spring path					6703 $\pm$ 703	7746		
Autumn duration		44	44–92	70	37–44	63–99	48	36
Spring duration			51		23–55	29		

*individual was retrapped and tagged with new transmitter

Individual birds demonstrated that they could navigate to their breeding grounds along different routes from year to year. Male bird 41504, while crossing the Strait of Gibraltar in 2004, reached the Mediterranean via different coastal sections in Algeria in both 2005 and 2006, taking the route via Ibiza each time.

Unlike in autumn, the Pyrenees were crossed in spring further east, north of Barcelona. Except for the bird that migrated via Italy, the others reached their breeding areas in northern Germany from the Spanish–French border in an almost straight line. See Appendix text T3 for details.

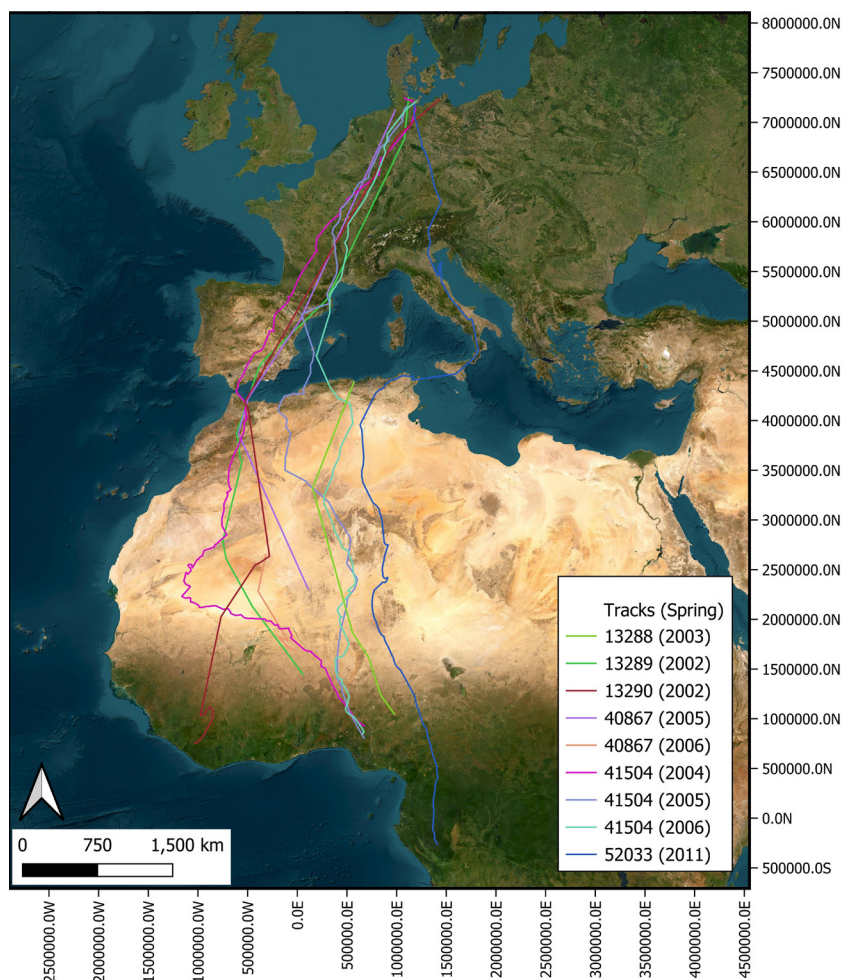


Fig. 2. Spring migration routes of tagged honey buzzards. The routes chosen for crossing the Sahara Desert and the Mediterranean Sea also show great diversity in spring.

Obr. 2. Jarné migračné trasy označených včelárov lesných. Trasy zvolené preletom cez púšť Sahara Stredozemné more vykazujú aj počas jari veľkú rôznorodosť.

Migration timing in relation to sex

The females left the breeding grounds and initiated the autumn migration between 15 and 25 August ($n = 5$, median = 18 August), while the males left between 13 and 29 August ($n = 9$, median = 26 August). On average, the females left eight days earlier. They reached their wintering areas between 13 September and 24 November (median 27 September, $n = 4$). The males arrived between 19 September and 25 November (median 9 October, $n = 7$), approximately 12 days later than the females. This difference is largely due to females travelling shorter distances than males: Three of the females undertook three migrations to Liberia and four to Nigeria. In contrast, five of the males undertook nine migrations: five to Nigeria, one to Cameroon, one to Gabon and two to the Republic of the Congo. Only limited data is available on departure from the wintering area, partly because the solar cells of the older

transmitters were insufficiently charged in these areas. Between 3 April and 1 May, four birds (three males and one female) began six homeward journeys. The majority (four trips by three males) began between 20 and 25 April. Arrival in the breeding area was documented for seven migrations by two males and two females. They arrived between 16 and 23 May. The only exception was male 41504, who was late in 2004 but reached the breeding area on 17 May 2005 and 16 May 2006. The duration of migration was 23–29 days for birds that migrated directly to the breeding area ($n = 3$), 51 days for female 13290 and 55 days for male 41504. See Appendix text T4 for details.

Migration speed

Migration speed varied greatly between individuals and between an individual's migratory routes from year to year (Tab. 3). Similarly, differences were observed between

Tab. 3. Comparison of honey buzzard migration speeds (km/day) in sections north, above, and south of the Sahara. Differences in the sample sizes are due to data gaps and to differences in the birds' lifespans.

Tab. 3. Porovnanie rýchlostí migrácie včelára lesného (km/deň) v úsekoch na sever, ponad a južne od Sahary. Rozdiely vo veľkosti vzoriek sú spôsobené chýbajúcimi údajmi a rozdielmi v dĺžke života vtákov.

	Autumn			Spring		
	Median	Range	n	Median	Range	n
North of the Sahara Desert	191	130–255	12	251	211–292	4
Above the Sahara Desert	277	216–475	18	301	180–333	7
South of the Sahara Desert	176	119–195	10	224	214–229	4

autumn and spring migrations, as well as between the individual migratory stages (Fig. 3, 4). On average, the birds migrated 38% faster in spring than in autumn. This was due to them having fewer stopover days (see below) and higher travel speeds on active migration days (23% faster). The difference was most pronounced on the route north of the Sahara to the breeding area, where migration was 62% faster than in autumn. It was least pronounced over the Sahara, where migration was 9% faster.

In general, average flight performance was highest over the desert. The length of migratory routes across the Sahara Desert ranged from 1,314 to 2,239 km (mean 1,712 km; median 1,645 km), and they took between 3.59 and 11.22 days (mean 5.99 days; median 5.56 days) to complete. In spring, the migration routes over the desert were longer (mean 2,010 km, median 2,121 km) than in autumn (mean 1,619 km, median 1,617 km). Consequently, crossing the Sahara took longer in spring (on average 7.24 days; median 6.39 days) than in autumn (mean 5.6 days; median 5.52 days). See Appendix text T5 and T6 for further details.

Stopovers

There was sufficient data from 13 autumn and four spring migrations to draw conclusions about stopover sites. Ten complete autumn migrations and four complete spring migrations involving seven birds were suitable for comparing the northern, southern, and Saharan parts of the migration route.

During their autumn migration, which lasted between 36 and 99 days, five out of seven birds made between one and 11 stopovers, each lasting between one and 53 days. Seventeen of the 30 stopovers lasted one day each, likely due to adverse weather conditions, and three lasted two

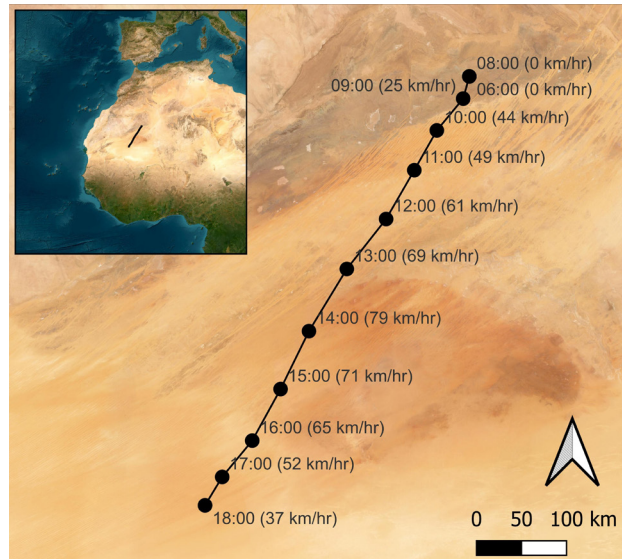


Fig. 3. Hourly flight speeds of male honey buzzard ID 95770 during the autumn migration over the Sahara Desert on 20 September 2009. The distances covered per hour rise and fall with the sun's position, adding up to a daily total of 551 km.

Fig. 3. Hodinové letové rýchlosti samca včelára ID 95770 počas jesenného sťahovania nad púšťou Sahara 20. septembra 2009. Vzdialenosti preletené za hodinu stúpajú a klesajú v závislosti od polohy slnka, pričom celkový denný výkon dosiahol 551 km.

days each. These short stopovers occurred in both Europe (eight times) and sub-Saharan Africa (12 times). One bird (ID 41504) stopped in Morocco for 8 days. There were no stopover days in the Sahara. The longest stopovers occurred during the autumn migration in 2001, just before the birds reached their winter quarters: one lasted 41 days (ID 40868) and another approximately 53 days (ID 13288). These may represent pre-wintering areas rather than stopovers.

In spring, the birds made no stopovers, except during the irregular migration of 41504 in 2004 (see Appendix text T7).

Winter home range size and habitat

Home range sizes could be calculated for two individuals using up to 97 GPS fixes in the periods: 28.10.2010–3.2.2011 (ID 52033) and 3.10.–16.11.2009 (ID 95771). These were small: 1.55 and 3.40 km² (MCP95) and 4.43 and 7.44 km² (KDE95).

Due to limited solar charging of transmitters, especially in dense vegetation, conclusions about habitat use remain limited. All individuals wintered in habitats with varying tree cover, ranging from closed rainforest to semi-open agricultural landscapes.

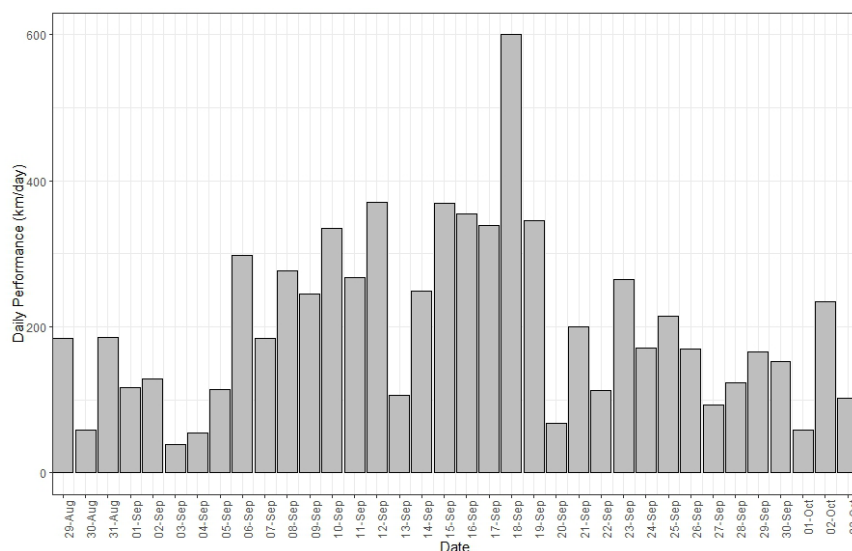


Fig. 4. Daily flight performance of male honey buzzard ID 95771 during autumn migration in 2009. Generally, the highest daily flight performances were measured over the Sahara Desert, up to 600 km in this example.

Obr. 4. Denný letový výkon samca včelára lesného ID 95771 počas jesenného sťahovania v roku 2009. Najvyššie denné letové výkony boli zaznamenané vo nad púšťou Sahara, v tomto prípade až 600 km.

Mortality

Ten birds disappeared during the monitoring period and were presumed dead: three during autumn migration, two during spring migration, four during winter and one in the breeding area. Mortality appeared to be higher during migration than during other periods, although this result should be interpreted with caution given the limited sample size.

Discussion

When we began our study, little was known about the migration of adult honey buzzards. Since then, several studies have been conducted in Central Europe and the Mediterranean region (e.g. Vansteelant et al. 2017b, Vansteelant & Agostini 2021). The broad outlines are now known. Here, we discuss individual aspects of migration and wintering that we find particularly noteworthy.

According to the median values, females began their autumn migration on average 8 days earlier than males. Studies on birds carrying VHF transmitters and video surveillance at nests have shown that both females and males can leave early, leaving their partner to care for the young (Ziesemer 1997; Ziesemer et al. 2021; Ziesemer & Meyburg 2015). In most cases, however, the female appears to leave earlier than the male. Consistent with this, three females tagged by Hake et al. (2003) left their Swedish breeding sites earlier than three males. Cento et al. (2021) also observed that adult females crossed the Strait of Messina on average five days earlier than males during autumn migration in Italy.

In spring, however, we were unable to detect a sex difference due to insufficient data. With two exceptions, the birds left their winter quarters between 20 and 25 April. Consistent with this, Vansteelant & Agostini (2021) reported that most individuals departed from sub-Saharan Africa around mid- to late April. At the Strait of Messina, males migrate on average six days earlier than females (Chiatante et al. 2024).

En route to Africa, the Pyrenees present the first obstacle, concentrating migration through mountain passes and around the entire mountain range. We considered the migration route in relation to the use of the important bird migration route of the Orgambideska Pass, where the hunting of migratory birds ceased in 1979.

In autumn, the Pyrenees were crossed 11 times to the west of the Orgambideska Pass (i.e., through the western fifth), but only eight times to the east (i.e., through the eastern four-fifths). It appears that no birds used the Orgambideska Pass, a known migration route for birds of prey, to cross the Pyrenees (Urcun & Bried 1998). However, for ID 13289=40867, this cannot be ruled out for the 2005 autumn migration, as there are insufficient fixes. Two other passes, widely used by common cranes (*Grus grus*) (Filippi-Codaccioni et al. 2011), appear to have held different significance for our honey buzzards. While there is a clear concentration of migration routes in the area around the Lindux Pass, located just under 30 km to the west, the Lizarrieta Pass, located 57 km to the northwest, was not used. Every autumn, between 6,500 and 21,500 honey buzzards cross the Orgambideska Pass; on average,

10,812 individuals were counted over 28 years (1981–2008) (Urcun & Bried 1998, Filippi-Codaccioni et al. 2010). In the eastern Pyrenees, the Col de la Perche/Eyne is a well-known passageway for soaring birds. In autumn, 11,000–15,000 honey buzzards pass through Eyne alone (www.migration.net). The density of our honey buzzard locations (ideally one per hour) does not usually permit precise assignment to individual passes. However, nine birds could have crossed one of the western Pyrenean passes at least once, and male 52033 most likely crossed the Col de la Perche/Eyne pass on 6 September 2011.

The importance of the other passes for honey buzzards is unknown, as counting only begins after 15 September, i.e., after the main honey buzzard migration period (Filippi-Codaccioni et al. 2011).

Vansteelant et al. (2017b) found that 12 Dutch honey buzzards consistently migrated through the western third of the Pyrenees in autumn. However, in spring, they dispersed widely. The authors concluded that honey buzzards can cross the Pyrenees over a wide area when tailwinds prevail over Europe in spring, but must circumvent this obstacle in autumn (Vansteelant et al. 2017b). Our study also revealed a preference for the western third of the Pyrenees in autumn (nine birds, fourteen migration routes), though at least three birds crossed the eastern two-thirds of the Pyrenees twice. At the eastern end of the Pyrenees, most honey buzzards are observed during the autumn migration on days when the wind blows from the north-west over southern France at altitudes between 1000 and 1500 metres (Garcia & Trabolon 2014). In spring, four birds on six migration routes crossed the eastern two-thirds five times and the western third once. This is consistent with the findings of Vansteelant et al. (2017b).

While the crossing of the Mediterranean Sea was concentrated near Gibraltar in autumn, in spring, individual birds deviated more strongly, sometimes successfully, from different points along the north coast of Africa. Some birds chose different routes from year to year.

A variant first recorded for German honey buzzards involves a loop migration via the Strait of Gibraltar in autumn and via the Italian peninsula in spring, with an attempt to cross the Adriatic (ID 52033). A similar case has been documented by Agostini et al. (2019), who described repeated autumn and spring migrations of an adult honey buzzard breeding in Hungary and wintering in Cameroon. In that study, the bird followed a longer route during autumn via the Strait of Gibraltar, interpreted as a risk-minimisation strategy avoiding long

sea crossings, whereas in spring it adopted more direct routes, minimising overall migration duration despite encountering headwinds over the Sahara and undertaking extensive sea crossings across the central Mediterranean. Vansteelant & Agostini (2021) hypothesise that substantial numbers of birds breeding north of the Balkan Peninsula employ this strategy. Mirski et al. (2026) confirmed this idea by tracking five males from north-eastern Poland and finding different types of loop migrations, some crossing the Adriatic Sea and some not.

In autumn, adult honey buzzards cross the Sahara quickly when there are northeasterly winds, travelling over 250 km per day. Only after crossing do they compensate for the drift and navigate towards their wintering grounds. Over the Sahel and tropical forests, they typically reach speeds of 170–180 km per day (Vansteelant & Agostini 2021). We also measured comparable speeds. Notable are the individual differences, as well as daily performances of up to 600 km across the Sahara (Fig. 4). Migration in spring is generally faster than in autumn, even though the route is longer, because birds use tailwinds (Vansteelant et al. 2017b). The westerly route that male 41504 took in spring 2004 (Fig. 5) is consistent with population-level patterns of wind-shaped migration routes described for honey buzzards breeding in the Netherlands and wintering in Western Africa (Vansteelant et al. 2017b).

The journey's duration could vary greatly. Autumn migration duration varied from 36 to 99 days depending on the distance between breeding and wintering areas, daily flight performance and the number and duration of stopovers. Adult birds from the Netherlands took approximately 25 days to complete the autumn migration. They are typically able to exploit favourable winds and avoid lengthy stopovers (Vansteelant & Agostini 2021). In spring, birds migrated faster: three individuals that migrated directly to the breeding area took 23–29 days, while two birds that made longer stopovers took 51 and 55 days, respectively (this study).

In the wintering areas, all of our birds visited only a single wintering site, except for individuals 40868 and 13288. The data suggest that the birds migrated to specific wintering areas they were already familiar with. 'The same area' could be very small, as with males 95771 and 52033, or large and vary from year to year, even within the same region. This is difficult to determine due to the gaps in the locations provided by the old transmitters. Female 13289=40867 spent four winters in the same area during the tracking period (autumn 2001 to spring 2006), although no data was available for winter 2003/2004 due to transmitter failure. Her male counterpart, ID 41504,

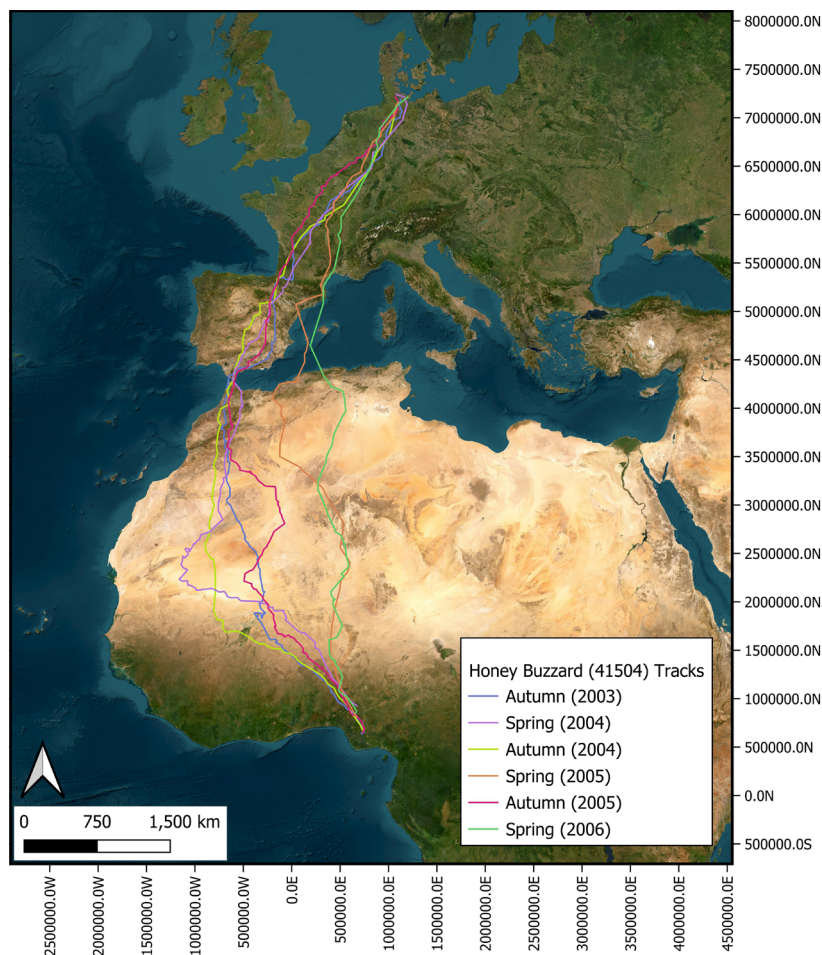


Fig. 5. The migration routes of male honey buzzard ID 41504. The bird showed significant variability in its route choices. During its autumn migration, it consistently crossed the western part of the Pyrenees and the Strait of Gibraltar. During its spring migration in 2004, however, it first flew far to the west before crossing the Strait of Gibraltar again. However, in 2005 and 2006, it crossed the Mediterranean via Ibiza and flew around the eastern side of the Pyrenees.

Obr.5. Migračné trasy samca včelára lesného ID 41504. Vták vykazoval značnú variabilitu vo výbere trasy. Počas jesenného sťahovania pravidelne prelietal západnú časť Pyrenejí a Gibraltársky prieliv. Počas jarneho sťahovania v roku 2004 však najskôr letel západnejším smerom, než opäť preletel Gibraltársky prieliv. V rokoch 2005 a 2006 však preletel Stredozemné more cez Ibizu a obletel východnú stranu Pyrenejí.

overwintered 160 km away. Female 40868 spent the winter in Liberia, 2,100 km away from her partner, male 95771, who spent the winter in Cameroon. Vansteelant & Agostini (2021) observed large differences in mobility among their birds within sub-Saharan Africa, with some individuals exploiting up to three distinct wintering sites each year.

Considering the sex ratio in the wintering area, Howes et al. (2019) found that females far outnumbered males among adult birds in southern Africa when they evaluated internet photos. They interpreted this as supporting the hypothesis that the sex responsible for establishing the breeding territory (the male honey buzzard) spends the non-breeding period closer to the breeding grounds. However, such behaviour is not reflected in the data of the honey buzzards we tracked in West Africa, whereas in our sample, females stayed closer to the breeding grounds. Unlike the other birds, male 41504 returned to the

breeding area in 2004, but arrived far too late to breed. The autumn migration of 2003 was unusual in that the bird stopped over in Morocco from 12 to 21 September. It is possible that it was already in poor condition at this time of year. Evidence supporting this hypothesis includes the late departure for the spring migration, the choice of a comparatively safe long-distance migration route, and the 21-day stopover in Spain. Ultimately, a series of peculiarities led the bird to arrive too late in the breeding area. The fact that, in subsequent years, male 41504 optimised its migratory behaviour by crossing the open Mediterranean Sea from Algeria via Ibiza in spring 2005 and 2006 could also suggest impaired fitness at the time. In 2003 and 2005, i.e., before and after the Sabbatical Year, the male bred successfully. When we recaptured the bird on 30 July 2005, it weighed 30 g more than on 19 July 2003 and was in good condition.

A male that arrived in Poland after a particularly long return migration on 19 June, when another male occupied the nest and paired with the female (Mirski et al. 2026), may also not have bred. Non-breeding following late return migration has also been observed in other raptors, e.g., ospreys (*Pandion haliaetus*) and lesser spotted eagles (*Clanga pomarina*) (Meyburg & Holte 2025). Years in which birds do not breed for no apparent reason are rarely recorded, but are known to occur in many bird species (Kazama et al. 2013).

In two cases, we were able to tag both the male and female of a pair. As with all other pairs of birds of prey that we have tracked using telemetry (Meyburg et al. 2005 and unpublished), it became apparent that the pair does not stay together outside of the breeding season. Their offspring also go their separate ways. In most cases, especially with the lesser spotted eagle, young birds are fed by the males until they leave the breeding site. They then suddenly must fend for themselves, which can pose problems for both migrating along the optimal route and acquiring food (Meyburg et al. 2005, 2017).

This study began in 2001, making it the earliest satellite telemetry study of this comparatively small species. In addition, the first transmitters used were not nearly as sophisticated as those used today. As it remains the only study in Germany to date, further research using GSM transmitters, whose data is no longer transmitted via the Argos system, would be beneficial. GPS fixes at much shorter intervals and the ability to recharge the transmitters, even in dense deciduous forests, could provide data on the foraging behaviour of this species, which differs greatly from that of other birds of prey. The possibilities offered by research into flight behaviour are also interesting. Flight altitude can now be studied without restriction and with much greater accuracy. This also applies to home range sizes, habitat use, and so on. All these studies can now be conducted not only in the breeding area, but also in non-breeding areas and during migration.

Ethical approval statement

The State Office for the Environment and the Helgoland Ringing Centre have authorised the capture, ringing and tagging of honey buzzards in the federal state of Schleswig-Holstein, Germany. The permits for capturing the birds and fitting the transmitters were kindly issued by the state ministries of the federal states of Mecklenburg-Vorpommern and Brandenburg, Germany. The permits to ring Honey Buzzards were issued by the Hiddensee ringing station.

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Appendix:

T1: Routes between breeding site and wintering grounds

Three examples demonstrate that birds can choose different routes between their breeding site and their wintering grounds from one year to the next.

Male 41504 spent the winter in Nigeria. He migrated 7,759 km in autumn 2003; however, in autumn 2004, he flew only 7,063 km. He travelled 7,506 km in spring 2004 and 7,590 km in autumn 2005. In autumn 2001, female 13290 attempted to cross the Sahara Desert from Morocco. She then retreated over 400 km north-west of the Middle Atlas Mountains, before following the Atlantic coast to Liberia. The following autumn, she took a more direct route, crossing the Sahara in a relatively straight line from Algeria to Liberia.

Male 52033 wintered in the Republic of the Congo. The southernmost point was 2°22'S/12°42'E. In autumn 2010, he travelled 8,645 km in 63 days, averaging 137 km per day. The following spring, he undertook a loop migration across Sicily, covering 7,746 km in 29 days at an average speed of 267 km per day. The bird did not avoid high mountains. In autumn, it spent the night at an altitude of 1,725 metres above sea level in the Pyrenees on 10–11 September. In spring, it crossed the Austrian Alps at an altitude of around 3,000 metres above sea level. Its attempt to cross the Adriatic Sea was abandoned after four hours.

T2: Autumn migration routes

Compared to the others, the bird from Brandenburg (ID 13288) flew slightly more southerly, then turned further west in northern Bavaria. One female bird from Schleswig-Holstein (ID 52035) initially travelled 185 km north-northwest to Denmark. Most of the birds flew over western Germany along a 230 km-wide path. Around half of the honey buzzards migrated over Luxembourg and the Ardennes in south-eastern Belgium. To the south-east of Paris, they crossed a front around 320 km wide. Near Bordeaux, the group dwindled to just three birds, one of which flew south-east of Toulouse twice.

Only four migration routes for two birds crossed the central and eastern part of the Pyrenees. Most crossings (13 migrations from nine birds) occurred in the western third. Eleven of these took place in the 37 km-wide area in the north-west of the Pyrenees.

A broad front, running straight from the Pyrenees to Gibraltar, was recorded in south-eastern Spain, between Madrid and the Mediterranean Sea. The migration route was heavily concentrated near the Strait of Gibraltar. The Mediterranean was apparently crossed only three to four times, well to the east of Gibraltar. This is indicated by the patchy Argos locations over land before and after crossing the sea. One individual (ID 68560) flew 105 km across the Atlantic, staying close to the coast, up to 27 km from the African shore. This flight began near the village of Zahara de los Atunes, 26 km north-west of Tarifa. At this location, the wind was blowing from the east at speeds of 20–25 km/h (<https://www.farsiweather.com/102411585/Gibraltar-Gibraltar/observations-history>).

In Morocco, the migration front was quite narrow, spanning approximately 115 km at 34.5° North. With two exceptions, all birds crossed the High Atlas over a 360 km stretch. After that, the migration front expanded to around 1,100 km across the El Jof Desert in Mauritania and Mali, near Tombouctou, except for one bird. Most birds turned south-east here, heading for their wintering grounds. One female (ID 13290), on its way to Liberia, flew along the coast of the continent for about 100 km. A second female (ID 40868) continued south to Liberia, and a third one (ID 52035) flew slightly further south than the majority, with its last location in Côte d'Ivoire at a possible wintering site. The two birds that travelled furthest south, reaching Gabon and the Republic of the Congo, flew closest to the coast near Douala in Cameroon.

T3: Spring migration routes

Two migration routes led from Algeria across the Mediterranean, passing Ibiza, to north-east Spain. Bird 52033, which had wintered the farthest east and south in the Congo region, travelled north via Tunisia and Sicily to the Apennine peninsula. Close to San Marino, it left the mainland to continue north across the Adriatic Sea. Around halfway through the journey, at approximately 115 km, it probably encountered adverse weather conditions and retraced its steps almost exactly (see Meyburg & Ziesemer 2024 for details). Subsequently, the migration continued north along the coast and over the Alps, reaching altitudes of over 2,000 metres at times. West of Gais in northern Italy, the direction changed to north-east. Shortly before reaching the Bavarian Forest, it took a northerly course towards its breeding grounds in Schleswig-Holstein.

Another bird (13288) also attempted to cross the Mediterranean Sea. It was last located on the coast, 180 km east of Algiers in Algeria. This bird was not observed in the breeding area afterwards. It is likely that this attempt was unsuccessful (see Meyburg and Ziesemer 2024, for details).

Two other individuals appear to have crossed the Mediterranean Sea approximately 130 km east of Gibraltar, with one (ID 40867) being located over the sea. There are only two direct routes across the Strait of Gibraltar.

Of the four migrations for which the locations were sufficiently accurate, three crossed the Pyrenees close to the Mediterranean. Only one bird crossed the mountains near Jaca in the central region, which are approximately 2,000 metres high.

T4: Migration timing in relation to sex

The wide variation in departure dates from the wintering area is due to two unusual migration patterns. Female 13290 left her wintering grounds in Liberia on 3 April, but remained in the area between north-west Côte d'Ivoire and Guinea until 25 April before beginning her homeward journey. Male 41504 did not leave Nigeria until 1 May 2004 and took several long breaks along the way. He did not arrive until 24 June, which was much too late for breeding.

T5: Flight altitude

Flight altitude data were obtained from GPS tracking of two honey buzzards (IDs: 52033 and 52035). Male 52033 completed three migration routes. Overall, recorded altitudes ranged from ground level to 2,047 m, with an average of 580 ± 450 (SD) m (median = 418 m, $n = 1,551$).

When the male 52033 data were examined by migration route, the autumn 2010 migration showed flight altitudes ranging from 19 m to 1,993 m, with a mean altitude of 616 ± 466 m and a median of 444 m ($n = 499$ data points). During the spring 2011 migration, the bird flew between ground level and 1,984 m, reaching a mean altitude of 736 ± 484 m ($\pm$ SD) (median = 676 m, $n = 303$). During the autumn 2011 migration, the bird flew between ground level and over 2,047 m (technical upper limit of altitude measurements), reaching a mean altitude of 494 ± 403 m (SD) (median = 366 m, $n = 749$).

Similarly, during its autumn migration from Central Europe to Côte d'Ivoire in West Africa, female 52035 exhibited significant variations in flight altitude. On average, she travelled at an altitude of 709.4 ± 508 m ($\pm$ SD) (median = 597 m, $n = 90$).

T6: Migration speed

Due to the relatively small sample size (12 individuals over 20 autumn migrations and nine spring migrations) and unquantifiable inaccuracies in the Argos locations, we did not consider statistically analysing variations in migration speed. Nevertheless, descriptive comparisons can be made.

While the median flight speed when crossing the Sahara Desert was 277 km per day in autumn and 301 km per day in spring, two individuals (ID 95771, 95770) achieved averages of 452 km and 475 km per day, respectively. The highest recorded performance was 600 km per day on 18 September 2009 (Fig. 4), respectively 109 km per hour (ID 95770, on 21 September 2009 from 11 a.m. to 12 noon). Although the daily flight distances north and south of the Sahara were relatively similar, the median values were substantially smaller at 54–69% and 73–83%, respectively, than those over the Sahara Desert.

The data on migratory routes over the Sahara was collected from 16 autumn and 5 spring migrations of birds that survived crossing the desert. Where precise duration calculation was prevented by data gaps, values were extrapolated from sections of the migration route that covered more than 50%.

T7: Birds tracked for more than one year

Honey buzzards tracked across multiple migrations provide insight into individual variability in migration behaviour. One male (ID 41504) was tracked for three autumn and three spring migrations (Fig. 5). The three autumn migrations were largely similar, but the routes differed slightly each time. They all crossed the Strait of Gibraltar, although slight variations occurred. The crossing of the Pyrenees became more direct over time: On 6 September 2003, the bird encountered the Pyrenees in an area south of Tarbes in France, where they are particularly high. Rather than continuing its migration in a straight line, the bird flew 115 km along the northern edge of the mountains to the west before crossing them at a lower altitude. The following autumn and the year after that, it crossed this lower area directly at Roncevalles.

In spring, the same individual showed flexibility, crossing different parts of the mountain range in different years. During spring migration in 2004, this bird exhibited unusual behaviour, departing late (1 May) and following a markedly more westerly route, resulting in a migration 1,100–1,300 km longer than in subsequent years. It also made a 21-day stopover in Spain, and the total migration lasted 55 days, rather than 23–27 days in other years. As a result, the bird arrived too late to breed. In both 2005 and 2006 the bird used shorter routes for his spring migrations. He reached the Mediterranean via different coastal sections in Algeria, taking the route via Ibiza each time (Fig. 5). Two transmitters (13289 and 40867), attached to a female bird, allowed documentation of four autumn and two spring migrations. This bird also used a shorter route across the Sahara in spring.

The male 52033, which wintered farthest south (in the Republic of the Congo), showed the most pronounced loop migration, with a deviation of 1,300 km between autumn and spring routes.

Eight of the 12 tracked honey buzzards reached wintering areas in Liberia (two birds), Nigeria (three birds), Cameroon, Gabon, and the Republic of the Congo (Meyburg & Ziesemer 2024). Of the five birds tracked over multiple winters, four showed site tenacity. One individual (ID 13288) shifted its wintering location by 370 km.