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Six adult and three juvenile honey buzzards *Pernis apivorus* were radio-tracked by satellite during autumn migration from southwestern Sweden. All adults crossed the Mediterranean Sea at the Strait of Gibraltar and continued across the Sahara desert to winter in West Africa, from Sierra Leone to Cameroon. Analysing three main steps of the migration, (1) from the breeding site to the southern Mediterranean region, (2) across the Sahara and (3) from the southern Sahara to the wintering sites, the adults changed direction significantly between these steps, and migrated along a distinct large-scale detour. In contrast, the juveniles travelled in more southerly directions, crossed the Mediterranean Sea at various places, but still ended up in the same wintering areas as the adults. Average speeds maintained on travelling days were similar for the two age groups, about 170 km/day in Europe, 270 km/day across Sahara and 125 km/day in Africa south of Sahara. However, as the adults used fewer stopover days en route, they maintained higher mean overall speeds and completed migration in a shorter time (42 days) than the juveniles (64 days). Although the juveniles set out on more direct courses towards the wintering grounds, they did not cover significantly shorter distances than the adults, as they tended to show a larger directional scatter between shorter flight segments. The results corroborate previous suggestions that adult and juvenile honey buzzards follow different routes during autumn migration, and that the birds change migration strategy during their lifetime. While juveniles may use individual vector orientation, social influences and learning may be of great importance for the detour migration of adults. The remarkable and distinct age-dependent shift in migratory route and orientation of the honey buzzard provides a challenging evolutionary problem.

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The honey buzzard *Pernis apivorus* breeds over large parts of Europe and western Asia, and is a long-distance migrant which spends the winter mainly in West and Central Africa, between 10°N and 20°S (Cramp and Simmons 1980). Ringing recoveries and visual observations reveal that the majority of birds breeding in northwestern Europe winter in forest areas close to the West African coast. They mainly migrate through western or central Europe to cross the Mediterranean Sea at the Strait of Gibraltar or, to a much lesser extent, the Sicilian Channel. Ringing recoveries also show, however, that some birds breeding in this area may follow a route east of the Mediterranean Sea across the Bosporus to unknown wintering sites (Cramp and Simmons 1980, Stolt et al. 1992). Moreover, analyses of counts of migrating honey buzzards in autumn at migration "hot-spots" in Europe and around the Mediterranean Sea suggest that adults and juveniles use different migration routes (Schmid 2000). Adults circumfly the Mediterranean Sea to a high degree, whereas juveniles seem to cross the sea at more or less any site. Thus, birds may switch from one route to another during their lifetime, suggesting that the migration strategy of the species is complex and needs further investigation.

On migration, the honey buzzard mainly uses thermal soaring flight (Bruderer et al. 1994). However, it is also capable of using flapping (powered) flight, which makes it somewhat less restricted to narrow sea-crossings than birds relying almost exclusively on soaring flight, and also enables it to cross other geographical obstacles where thermal activity is less predictable and wind conditions more complex, e.g. mountain ranges such as the Alps (Bruderer and Jenni 1990). This suggests that honey buzzards may follow fairly straight migrational courses on their way to the wintering grounds, and that they may extend the daily time available for migration and migrate on days with overall poor thermal activity (Bruderer et al. 1994). Thus, they may be able to cover longer distances on days of active migration than birds of prey relying almost exclusively on soaring flight, e.g. species belonging to the genera *Aquila* and *Buteo* (Rudebeck 1950, Bruderer et al. 1994, Spaar and Bruderer 1996). However, the honey buzzard may cover shorter daily distances than species which extend the daily time available for migration even more, e.g. the osprey *Pandion haliaetus*, which regularly supports soaring flight with a high proportion of flapping flight (Kerlinger 1989, Kjellén et al. 1997, 2001) and which flies at a higher speed. Also, medium sized and large birds of prey may be expected to migrate faster on days with strong thermal activity, as there seems to be a positive correlation between body size and cross-country speed under such conditions (Spaar 1997). As ringing recoveries provide limited information about details of the migration, these aspects have not been analysed.

The overall migration strategy of a species also depends on its wintering ecology. For birds defending home-ranges or territories, it may be of primary importance to arrive at the wintering grounds as early as possible to ensure a good territory, i.e. to minimise the time of migration (Alerstam and Lindström 1990). This is probably the case for many ospreys, as indicated by observations at the wintering grounds (Prevost 1982) and by satellite tracking (Kjellén et al. 1997, Hake et al. 2001). For species living a nomadic life during the winter, e.g. many *Aquila* eagles and *Ciconia* storks (Berthold et al. 1992, 1995, Meyburg et al. 1995a, b), early arrival may be of less importance and instead they may be adapted for minimising the energy expenditure during migration (Alerstam and Lindström 1990). Little is known about this aspect of the wintering ecology of the honey buzzard.

In this study, we investigate the migration performance of nine honey buzzards by satellite tracking and provide information about migration routes, stopover and wintering sites, timing and speed of migration and movements at the wintering sites. During the last decade, studies using satellite telemetry have provided information about the migration performance of many birds of prey, e.g. falcons, eagles and the osprey (see above), permitting comparisons with the honey buzzard.

Information from satellite tracking may also be useful in conservation work for honey buzzards breeding in Sweden as well as in other parts of northwestern Europe. The number of honey buzzards counted on autumn migration at Falsterbo, southwesternmost Sweden, has declined significantly during the last three decades (Roos 1996), and there has been an estimated reduction of the Swedish breeding population by about 30% (2000–3000 pairs) since the late 1970's (Ahlén and Tjernberg 1996). Since the honey buzzard is a long-distance migrant, spending about eight months away from the breeding grounds, this decline may fully or partly be caused by factors affecting the survival of the birds along the migration route and/or at the wintering grounds. One such threat may be the destruction of suitable wintering habitat due to logging of tropical forests, which seems to be the preferred habitat during winter based on information from ringing recoveries (Cramp and Simmons 1980, Stolt et al. 1992). Hence, to identify potential hazards for the birds during the non-breeding season, it is important to have as detailed information as possible about their migration and wintering strategy.

Methods

During 1997–2000, we fitted satellite transmitters on ten honey buzzards. Four adult breeding birds (two females and two males) were captured at four different nests (at about 58.7°N/12.4°E) in early August 1997 (called Fe 48–97 and Ma 49–97 below) and 1998 (Fe 10–98, Ma 50–98) in the county of Dalsland, SW Sweden. Another two females were captured at two different nests (about 57.1°N/12.5°E) in the county of Halland, close to the Swedish west coast, in late July 2000 (Fe 09–00 and Fe 55–00). Captures were made in a net (10 × 4 m) placed above a stuffed goshawk *Accipiter gentilis* close to the nest. In 1998, we also put a transmitter on one adult male (Ma 12-98) which was found injured in a forest area (known breeding site for honey buzzards) just north of Göteborg (57.7°N/11.9°E). He was kept in an aviary and treated for three weeks before he was released, in perfect health, on 4 September. In addition, three juveniles were equipped with transmitters just before fledging, one from a brood of two at a nest 30 km north of Göteborg in 1998 (Juv 11-98), and two siblings (Juv 11-00 and Juv 12-00) from the same nest as Fe 09-00 in 2000. The transmitters were attached as backpacks with a harness made of nylon string covered by rubber tubing. After the transmitter was attached, the birds were immediately released (within one hour after capturing). We used transmitters with conventional batteries (Microwave

PICO PTT 100), weighing 20 g (about 2.5% of the body weight of the birds). The transmitters, which were tracked by CLS/Service Argos in Toulouse, France, were programmed to be active during 10 hours every second day to cover the whole autumn migration and part of the wintering period. Depending on satellite orbits and local conditions we received 0–8 positions during each 10-hour period. The batteries of the transmitters had a life-time of at least 400 hours.

Locations provided by the Argos system are divided into different classes (labelled A, B and 0–3) depending on validation, number of signals received and location accuracy. We have normally used all validated locations in this analysis, taking location accuracy into account only when relevant (see below). For three classes of locations (1–3), the accuracy is within 1 km, while the accuracy for the other classes (A, B and 0) is unspecified. Class 1–3 locations, which make up only about 20% of all locations in our data set, were mainly obtained when the birds were at, or close to the wintering grounds. During periods when the birds were stationary within a limited area (breeding or wintering site) it was obvious that locations of unspecified accuracy were sometimes 10–50 km from the correct position, and in a few extreme cases the deviation was up to 100 km. However, it seems appropriate to use all available locations in the analysis of migratory movements over substantial distances, as the location error will, in such cases, only affect the results to a minor degree. In analyses of movements made by the birds after they reached the wintering grounds, only high-quality locations (classes 1–3) were included. For Ma 12–98 and Juv 11-98, it was not possible to make such an analysis, as too few locations of high accuracy were obtained before the batteries were exhausted.

Since the transmitters were not active every day, we did not always know the exact date of departure from the breeding grounds and arrival at the wintering site. If these dates were not known, we used the average speed on travelling days to calculate the most likely date of departure and arrival. The total duration of stopovers has been determined using the same method. An area was considered to be a stopover site if the bird staged for at least 24 hours and moved less than 100 km within the area.

The daily pattern of migration activity was investigated by calculating speeds (in km/h) between two consecutive locations 1–5 hours apart. All positions from travelling days (excluding stopovers) have been used except for class "B" locations (least accurate) and positions which were obviously wrong (a few single positions located in a direction completely deviating from the mean migration route). For the evaluation of the daily pattern of migratory behaviour, location times in UTC were recalculated to true local times (based on the longitudinal position of the bird). The original times in UTC were used for calculating all time intervals between locations.

Distances and directions are based on standard calculations for loxodromes (rhumblines). The total distance migrated was obtained by using a maximum of one position per 24-hour period and adding the resulting segment distances between these positions. For plotting, the locations were transformed to coordinates according to the Mercator projection (Gudmundsson and Alerstam 1998). This map projection has the advantage of showing loxodromes as straight lines. However, it is true neither with respect to distance nor area, exaggerating geographical dimensions of high latitudes in comparison with equatorial areas. As a basis for evaluating the flight-routes and stopover sites, the Times Atlas of the World was used (scales of maps generally 1:2 500 000–5 000 000).

As it became obvious that the adults did not fly straight to their wintering grounds (see below), the differences in migration strategy between adults and juveniles were analysed in detail by dividing the total migratory journey into three different steps; "Europe", "Sahara" and "West Africa", with dividing points as close to the Strait of Gibraltar or North African coast of the Mediterranean Sea and the southern border of the Sahara desert as possible. For each bird, the locations closest to these areas were selected as dividing points (range adults = 32.3–36.2°N and 14.3–15.8°N; juveniles = 33.7–36.8°N and 14.4–16.8°N).

Means of directional data were calculated as mean vector directions along segments of the migration route according to Batschelet (1981). Movements over a minimum distance of 100 km and a minimum time of 9 hours were considered as segments (thus, excluding irregular changes in positions during stopover periods). The duty cycles of the transmitters and the availability of positions determined how many segments the migratory journey could be divided into for the different honey buzzards. Indexes of large- and medium-scale straightness were obtained by dividing direct distances between start and end positions by distances travelled along migratory segments. Small-scale deviations associated with circling and gliding between thermals could not be obtained from data provided by the satellite tracking.

Results

Timing and routes of migration

Of the ten honey buzzards provided with transmitters, nine (three females, males and juveniles, respectively) completed their autumn migration. Contact with Fe 48-97 was lost in the breeding area, probably because of transmitter failure. The breeding of Fe 10-98 was terminated due to predation when the young were half-grown in early August. We do not know whether Ma 12-98 was breeding when he was injured, but the four remaining adults produced fledged young.

The adult females left the breeding grounds 16–23 August, i.e. somewhat earlier than the adult males, who departed 29 August and 7 September (Table 1). Juv 11-00 left on 5 September, whereas Ma 12-98 and the two remaining juveniles left considerably later, on 15 September. Five of the adults probably left Sweden close to Falsterbo, whereas Ma 49-97 seemed to cross the Baltic Sea further to the east. All the adults then migrated across Germany, France and Spain, crossed the Mediterranean Sea at the Strait of Gibraltar and continued across the western part of the Sahara desert to wintering sites in West Africa, between Sierra Leone and Cameroon (Table 1, Fig. 1). The adults reached their wintering sites between 21 September and 21 October in the same order as they departed from the breeding area (Table 1), i.e. the females arrived before the males. The juveniles migrated along more easterly routes (Fig. 2). Due to few locations in Europe and the Mediterranean region north of Africa, particularly for Juv 11-98 and Juv 12-00, we do not know exactly which route they followed in Europe, but they probably crossed the Mediterranean Sea from various points between eastern Spain and the Sicilian Channel. They then continued straight across the Sahara and reached the region south of the desert in early/mid-October (Table 1, 2, Fig. 2). Juv 11-00 and Juv 12-00 later continued further south to reach their wintering sites 11–13 November (Table 1). Based on information from honey buzzards ringed as nestlings in Sweden and Finland and recovered during their first winter (Stolt et al. 1992, Roland Staav in litt.), and judging from the behaviour of Juv 11-00 and Juv 12-00 after they crossed Sahara, we have reasons to believe that Juv 11-98 did not complete the migration before the transmitter failed, as locations with good accuracy were provided until 14 October only. Thus, data on this bird were not included in any analyses except when investigating differences between adults and juveniles during the migration across Europe and Sahara. The total distance covered on the entire migration was, on average, 6700 km, with no significant difference between adults and juveniles (Table 1; t-test; $t = 0.72$, df $= 6$, $P = 0.50$).

Fe 09-00 and Fe 55-00 made no obvious stopovers at all during the migration. The remaining four adults made stopovers on 1–3 occasions during a total of 3–10 days (Table 2). All these stopovers were made north of latitude 43°N, mainly north of 50°N. The juveniles also made 1–3 stopovers, but spent much more time at stopover sites than the adults; 17–28 days (Mann–Whitney test; $Z = 2.01$, $n_1 = 6$, $n_2 = 2$, $P = 0.04$). In contrast to the adults, almost all stopover days were spent after the crossing of Sahara, although Juv 11-00 also stopped for 10 days in northern Europe. Juv 11-98 made no stopovers during the migration over Europe and Sahara (Table 2). No stopovers at all were recorded when the birds crossed Sahara.

Table 1. Basic data on autumn migration of nine honey buzzards followed from the Swedish breeding grounds to West Africa 1997–2000. Approximate coordinates (decimal values) are given for wintering sites.

| Bird	Migration period	Wintering site (coordinates)	Total distance (km)	Total time (days)	Average speed (km/d)	No. of travelling days	Av. speed on travelling days (km/d)
Male 49-97	7 Sep–21 Oct	Ivory Coast (06.0N/03.8W)	6905	45	153	42	164
Male 50-98	29 Aug–10 Oct	Ghana (05.5N/02.1W)	6719	43	156	37	182
Male 12-98	(15 Sep)[a]–2 Nov	Sierra Leone (07.4N/11.5W)	6586	49	134	40	165
Female 10-98	23 Aug–5 Oct	Sierra Leone (08.8N/10.9W)	6299	45	140	35	180
Female 09-00	21 Aug–23 Sep	Nigeria (06.4N/05.9E)	7091	34	209	34	209
Female 55-00	16 Aug–21 Sep	Cameroon (04.4N/10.3E)	6880	37	186	37	186
Juvenile 11-98	15 Sep–(7 Oct)[b]	(Nigeria 12.1N/06.3E)	(5342)	(23)	(232)	(23)	(232)
Juvenile 11-00	5 Sep–13 Nov	Ivory Coast (05.2N/06.2W)	6541	70	93	42	156
Juvenile 12-00	15 Sep–11 Nov	Togo (07.7N/00.9E)	6652	58	115	41	162
Average adults	23 Aug–5 Oct[c]	(06.4N/02.0W)	6747	42	163	38	181
Average juv.	15 Sep–12 Nov[d]	(06.4N/02.6E)[d]	6596[d]	64[d]	104[d]	42[d]	159[d]
Average all	1 Sep–10 Oct[c,d]	(06.4N/02.2W)[d]	6709[d]	48[d]	148[d]	38[d]	176[d]

[a] Released from captivity 4 September.
[b] Migration probably not completed.
[c] Excluding male 12-98.
[d] Excluding juvenile 11-98.

Fig. 1. Map (Mercator projection) of the autumn migration routes of six adult honey buzzards tracked by satellite from their breeding sites in Sweden to the wintering grounds in Africa.
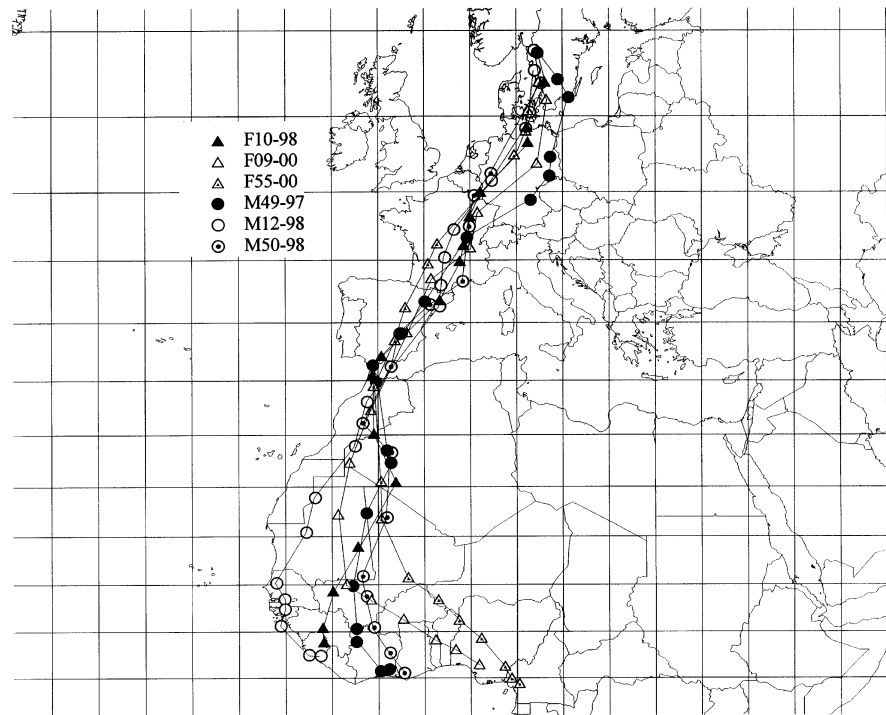
The adults seemed to go straight for a known wintering site after they had crossed Sahara. The five birds which could be followed after settling down in West Africa, remained stationary within a radius of 5 km (Fig. 3A). The two juveniles also seemed to move within a limited area after reaching their final destination (Fig. 3B).
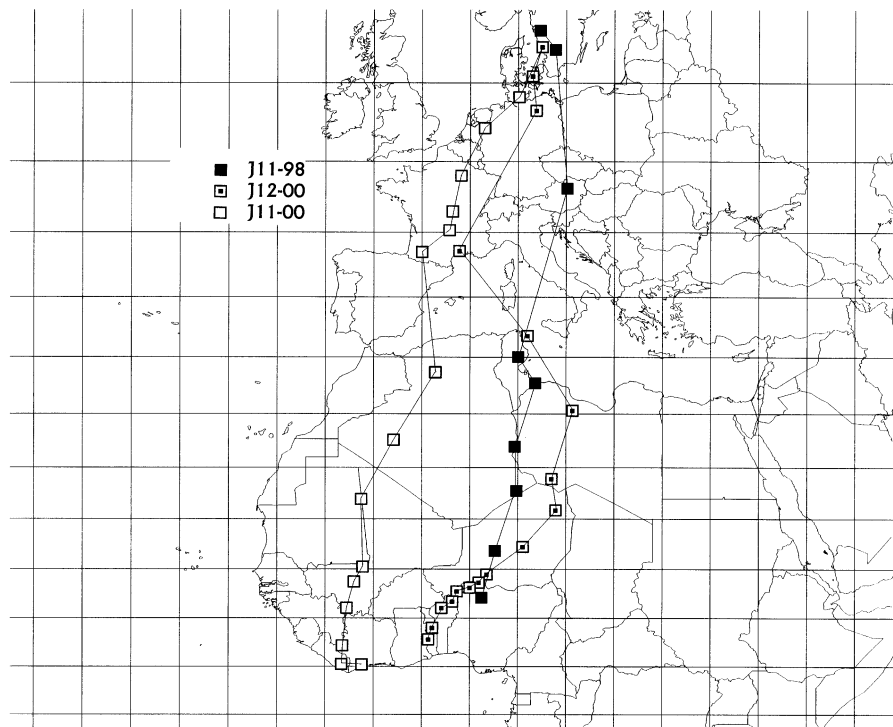

Fig. 2. Map (Mercator projection) of the autumn migration routes of three juvenile honey buzzards tracked by satellite from their nest sites in Sweden to the wintering grounds in Africa.

Table 2. Data on stopovers made by nine honey buzzards during autumn migration from the Swedish breeding grounds to West Africa 1997–2000. Approximate coordinates (decimal values) are given for stopover sites.

Bird	Number of stopover days				Dates and sites of stopovers (coordinates)	
	Europe	Sahara	West Africa	Total		
Male 49-97	3	0	0	3	12–13 Sep	NE Germany (52.4N/13.7E)
					16 Sep	NE Germany (51.1N/13.6E)
Male 50-98	6	0	0	6	4–9 Sep	W Germany (50.6N/06.3E)
Male 12-98	9	0	0	9	18 Sep	E Denmark (55.2N/11.5E)
					24–29 Sep	Central France (47.2N/03.2E)
					4–5 Oct	S France (43.0N/01.8E)
Female 10-98	10	0	0	10	25–27 Aug	N Germany (54.2N/10.9E)
					2–5 Sep	Luxemburg (50.0N/06.1E)
					7–9 Sep	NE France (48.0N/04.5E)
Female 09-00	0	0	0	0	–	
Female 55-00	0	0	0	0	–	
Juvenile 11-98	0	0	(0)	(0)	–	
Juvenile 11-00	10	0	18	28	9–18 Sep	N Germany (54.1N/10.2E)
					15 Oct–1 Nov	S Mali (11.0N/07.8W)
Juvenile 12-00	0	0	17	17	16–22 Oct	NW Nigeria (13.6N/05.8E)
					29 Oct–2 Nov	S Niger (11.0N/02.1E)
					5-9 Nov	Togo (09.0N/01.1E)
Mean adults	5	0	0	5		
Mean juveniles	3	0	18[a]	22[a]		
Mean all	4	0	4[a]	9[a]		

[a] Excluding juvenile 11-98.

Speed and daily pattern of migration

It took the honey buzzards, on average, 48 days to complete the autumn migration. Mean number of days
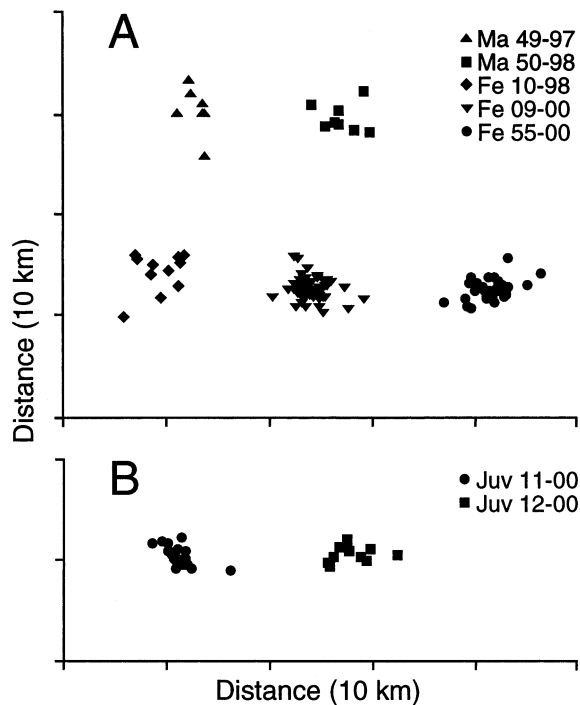

Fig. 3. High-quality locations (accuracy better than 1 km) provided by satellite tracking of five adult (A) and two juvenile (B) honey buzzards after reaching the wintering sites in West Africa.

used by the adults was 42, which was significantly less than the 64 recorded for the juveniles (Table 1; t-test; $t = -4.33$, df = 6, $P = 0.005$). The mean number of travelling days used (excluding stopovers) was 38, with no difference between age groups (Table 1; $t = -1.77$, $P = 0.13$). The birds travelled at an average speed of 148 km/day over the entire migration, and the mean of 163 km/day recorded for adults was higher than the 104 km/day recorded for juveniles (Table 1; $t = 2.67$, $P = 0.037$). The speed on travelling days was, on average, 176 km/day. Adults travelled faster than juveniles, although the difference was not supported by statistical significance. (Table 1; 181 and 159 km/day, respectively, $t = 1.78$, $P = 0.13$).

Adults travelled at overall mean speeds of 141 km/day in Europe, 269 km/day across Sahara, and 137 km/day in West Africa. The corresponding speeds for the juveniles were 156, 269 and 40 km/day, respectively. Thus, there were no differences between age groups in overall mean speed of migration maintained during the three migrational steps (two-way ANOVA; $F_{1,18} = 3.07$, $P = 0.13$). However, mean speeds of all birds differed between steps ($F_{2,18} = 79.27$, $P < 0.0001$), and were 146 km/day in Europe, 269 km/day across Sahara and 113 km/day in West Africa (Fig. 4). There was also a significant interaction effect between age class and migrational step ($F_{2,18} = 6.78$, $P = 0.01$). Juveniles seemed to travel slightly faster over Europe, but more slowly over West Africa than adults. Similar differences emerged in an analysis of the speed maintained on travelling days (Table 3; $F_{1,18} = 0.92$, $P = 0.37$ for difference between age groups and $F_{2,18} = 96.10$, $P < 0.0001$ for difference between steps), although the interaction effect was reduced to a tendency ($F_{2,18} =$

Fig. 4. Overall speed (km/day) during autumn migration in relation to latitude for six adult (A) and three juvenile (B) honey buzzards tracked by satellite from Sweden to West Africa. The maximum speed recorded for each bird is indicated by an arrow.
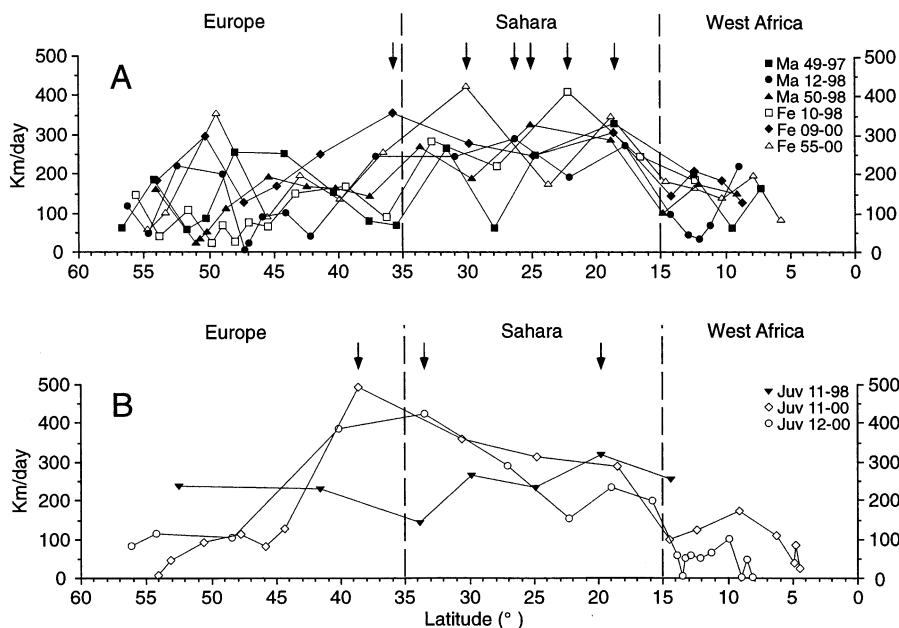
2.90, $P = 0.09$). Maximum speeds were recorded between latitude 15–40°N, i.e. when the birds crossed the Mediterranean Sea and Sahara (Fig. 4). The overall peak value was recorded for Juv 11-00, who travelled 494 km/day during a two-day flight between southern France and northern Libya (Fig. 2, 4B).

The honey buzzards seemed to travel almost exclusively between 8 am and 6 pm local time (Fig. 5). We have no indications that any of the birds migrated during the night.

Table 3. Mean speed (km/day) on travelling days along three main steps (see methods section) of the autumn migration route of nine honey buzzards tracked by satellite from Sweden to West Africa 1997–2000. The number of travelling days during the different parts of the journey are given within parenthesis.

Bird	Europe	Sahara	West Africa
Male 49–97	153 (22)	232 (10)	123 (10)
Male 50-98	154 (18)	250 (10)	141 (9)
Male 12-98	167 (19)	251 (9)	96 (12)
Female 10-98	140 (22)	288 (9)	155 (4)
Female 09-00	205 (16)	283 (7)	167 (11)
Female 55-00	170 (17)	308 (7)	141 (13)
Juvenile 11-98	221 (12)	238 (9)	(275) (2)
Juvenile 11-00	153 (19)	321 (7)	87 (16)
Juvenile 12-00	146 (18)	248 (12)	96 (11)
Mean adults	165 (19)	269 (9)	137 (10)
Mean juveniles	173 (16)	269 (9)	92[a] (14)[a]
Mean all	168 (18)	269 (9)	126[a] (11)[a]

[a] Excluding juvenile 11-98 (two travelling days only).

Orientation

The mean direction for a straight loxodrome between the breeding site and the final destination of the honey buzzards was 193°, with little variation between birds (Table 4). There was no difference between age classes in overall mean directions (Table 4; two-way ANOVA; $F_{1,18} = 3.58$, $P = 0.11$). However, mean directions differed significantly between steps ($F_{2,18} = 12.04$, $P = 0.0014$), and there was a significant interaction effect on direction between age group and step of migration ($F_{2,18} = 6.42$, $P = 0.013$). While the juveniles followed routes with no consistent course variations between the three steps, the adults first moved SSW to the Gibraltar region, then shifted to more southerly courses across Sahara, and then generally moved towards southeast in West Africa (Table 4, Fig. 1, 2). Thus, the main large-scale deviation from a straight migrational course was the detour made by the adults when circumflying the Mediterranean Sea. There were also other deviations. Ma 49-97 and Fe 09-00 made easterly detours in Europe during the early stage of the migration, but then turned back to the route followed by the other adults (Fig. 1), and Juv 12-00 made a detour towards west before crossing the Mediterranean Sea (Fig. 2).

The route along the three steps of migration in Europe, Sahara and West Africa, respectively, had a mean large-scale straightness of 0.925 for the adults (Table 5). This means that the detour along this route is $1/0.925 = 1.08$ times (8%) longer than the direct route to the destination. In addition, the course varied also within each of the three steps of the migration route, corresponding to a mean medium-scale straightness of

0.95 for the adults. Combining the medium- and large-scale effects gives a total straightness of 0.878 for the adults, i.e. their recorded satellite tracks were, on average, $1/0.878 = 1.14$ times (14%) longer than the ideal loxodromes to the destination. The juveniles did not make a similar large-scale detour as the adults, and had a mean large-scale straightness of 0.98. However, they showed a larger variation in course between the shorter flight segments, with a medium-scale straightness of 0.895. The number of individuals is small, and the differences between adults and juveniles were not supported by any statistical significance, neither for the large-scale (Mann–Whitney test), nor for the medium-scale straightness (Friedman test). As a result, total straightness and actual travel distance were similar for juveniles and adults (Table 5).
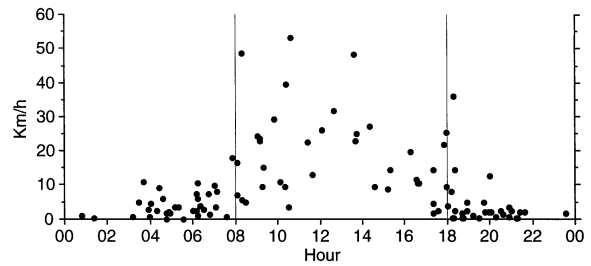

Fig. 5. Activity pattern (speed in km/h) over 24-hours (exact local times) for nine honey buzzards tracked by satellite during autumn migration between Sweden and West Africa. The mid-interval times of the intervals are depicted. The figure is based on a total number of 101 intervals (2–24 of each bird). Speeds below 15 km/h were most likely primarily due to variation in location accuracy. The general lack of position data between 10 pm and 2 am may depend on satellite orbits.

Table 4. Straight compass directions (degrees) between the first and last location of the three main steps (see methods section) of the autumn migration route, as well as directions straight from the breeding site to the final position for nine honey buzzards tracked by satellite from Sweden to West Africa 1997–2000.

Bird	Europe	Sahara	West Africa	Straight loxodrome
Male 49-97	206°	187°	157°	194°
Male 50-98	204°	188°	157°	192°
Male 12-98	207°	206°	149°	200°
Female 10-98	207°	190°	190°	200°
Female 09-00	207°	188°	121°	186°
Female 55-00	209°	170°	134°	182°
Juvenile 11-98	184°	187°	(196°)	(186°)
Juvenile 11-00	198°	200°	180°	196°
Juvenile 12-00	183°	190°	222°	191°
Mean adults	207°	188°	151°	192°
Mean juveniles	188°	192°	201°[a]	194°[a]
Mean all	201°	190°	164°[a]	193°[a]

[a] Excluding juvenile 11-98 (migration probably not completed).

Table 5. Straightness (direct distance divided by the distance along migratory segments) of migratory trajectories along three main steps (see methods section) of the autumn migration route of nine honey buzzards tracked by satellite from Sweden to West Africa 1997–2000. The number of segments used are given within parenthesis. The straightness of columns 1–3 combined is designated as medium-scale straightness, given in column 4. Large-scale straightness is calculated as the distance of the loxodrome between breeding and wintering sites divided by the sum of the three loxodrome distances between start and end locations of the three main steps of the migration route. Multiplying column 4 with column 5 gives the total straightness for the entire route.

Bird	Europe	Sahara	West Africa	Medium-scale straightness	Large-scale straightness	Total
Male 49-97	0.879 (10)	0.967 (4)	0.881 (4)	0.909 (18)	0.962	0.874
Male 50-98	0.939 (8)	0.912 (4)	0.982 (4)	0.937 (16)	0.962	0.901
Male 12-98	0.968 (8)	0.984 (4)	0.871 (5)	0.957 (17)	0.945	0.904
Female 10-98	0.944 (10)	0.923 (4)	(0.987) (2)	0.940 (16)	0.997	0.937
Female 09-00	0.944 (7)	0.977 (3)	0.999 (5)	0.967 (15)	0.825	0.798
Female 55-00	0.988 (8)	0.984 (3)	0.992 (6)	0.988 (17)	0.862	0.852
Juvenile 11-98	0.966 (3)	0.950 (4)	(1.000) (1)	(0.963) (8)	(0.997)	(0.960)
Juvenile 11-00	0.942 (7)	0.971 (3)	0.806 (5)	0.923 (15)	0.994	0.917
Juvenile 12-00	0.860 (4)	0.847 (5)	0.940 (7)	0.867 (16)	0.967	0.838
Mean adults	0.944	0.958	0.945[a]	0.950	0.925	0.878
Mean juveniles	0.923	0.923	0.873[b]	0.895[b]	0.980[b]	0.877[b]
Mean all	0.937	0.946	0.924[a,b]	0.936[b]	0.939[b]	0.878[b]

[a] Excluding female 10-98 (two segments only).
[b] Excluding juvenile 11-98 (one segment only/migration probably not completed).

Discussion

Timing and routes of migration

Honey buzzards departed from their breeding area between 16 August and 15 September, with adults (disregarding the injured male) preceding juveniles by 2–3 weeks. This difference is in agreement with the timing of autumn migration recorded at Falsterbo, Sweden, where median dates for adults and juveniles are 27 August and 11 September, respectively (Kjellén 1992). Little is known whether there is a general difference in departure date between breeding males and females or between successful and non-successful breeders of the same sex as recorded in satellite tracking studies of the osprey (Kjellén et al. 1997, 2001). Females departed earlier than males in this study, but as we have data on only a few birds, it is not possible to draw any conclusions. At Falsterbo, median migration dates for adult males and females are similar (Kjellén 1992), suggesting no difference between the sexes in time of departure.

Before this study, the 1832 honey buzzards ringed (mainly as chicks) in Sweden up to 1997 had generated 164 recoveries (Stolt et al. 1992, Roland Staav in litt.), showing that Swedish birds mainly follow two different migration routes on their way to Africa. Most adults travel through western Europe across the Strait of Gibraltar, whereas a high proportion of juveniles follow a route through central Europe and the central Mediterranean region, suggesting a distinct age-dependent difference in migration strategy (Søgård and Østerby 1989, Stolt et al. 1992). Schmid (2000), who analysed recoveries of birds ringed in northwestern Europe and compared the proportions of adults and juveniles counted at migration "hotspots" all over Europe in autumn, came to the same conclusion. Adults generally circumfly the Mediterranean Sea via Gibraltar and the Bosporus, whereas juveniles travel in a more southerly direction and cross the Mediterranean Sea between any points. This is further supported by radar studies along the coast in southeastern Spain, where adult honey buzzards travelled along the coastline towards Gibraltar, whereas juveniles were seen heading out over the sea (Meyer et al. 2000). The results of our study agree well with this picture, as the adults made a large-scale detour, whereas the juveniles set out on more direct routes to the wintering grounds (Fig. 1, 2).

Although the adults made a large-scale detour, they maintained straighter courses than the juveniles during the migrational segments. Thus, they did not cover longer distance than the juveniles. However, we could not analyse small-scale deviations, and if the adults migrated mainly by termal soaring and the juveniles used flapping flight to a high extent, the adults may still have covered a longer distance. For honey buzzards using soaring flight, small-scale deviations associated with circling and gliding between thermals may extend the distance covered by up to 34% (Leshem and Yom-Tov 1996).

The main wintering region for Swedish honey buzzards is the tropical forest area close to the West African coast. All the 17 ringing recoveries from the winter have been made in this area, from Ivory Coast east to Congo-Brazzaville (Stolt et al. 1992), and the wintering sites chosen by the birds in this study fit well into this picture, although two of the birds wintered west of the area where recoveries previously have been made (Table 1, Fig. 1).

Speed of migration

The average overall speed of 163 km/day for the adult honey buzzards in this study does not differ much from the migration speeds recorded for other adult birds of prey tracked by satellite, e.g. *Aquila* eagles, (Meyburg et al. 1995a, b, B.-U. Meyburg, cited in Spaar and Bruderer 1996), ospreys (Kjellén et al. 2001, Martell et al. 2001) and peregrine falcons (Fuller et al. 1998), which showed average speeds of 150–175 km/day. Thus, there seems to be no clear differences in overall average travelling speed recorded for species using different strategies on migration. Radar studies of migrating birds of prey in desert areas in southern Israel have revealed a positive correlation between body size and cross-country speed maintained by birds in soaring flight on days with good thermal activity (Spaar and Bruderer 1996, Spaar 1997). Moreover, theoretical predictions suggest that there is a positive correlation between body size and overall speed of migration for birds of prey using thermal soaring under favourable weather conditions (Hedenström 1993). On the other hand, small- and medium-sized raptors may be more inclined to extend the daily migration time by mixed flapping and soaring flight during periods with poor thermal conditions (Hedenström 1993). This may contribute to reduce the differences in overall migration speed between some of the species studied. Also, to determine the exact duration of the total migration, it is necessary to include the number of days a bird spend accumulating energy reserves before leaving the breeding area (Alerstam and Lindström 1990). There is no information about this for the birds studied by satellite tracking, which makes it even more difficult to compare their overall migration speed.

Assuming that thermal soaring migrants like buzzards or ospreys use the days during their migratory period either as travelling days (travelling during 8–10 hours when thermals permit and resting during the remaining hours of a travelling day) or as fuel deposition days, one may predict the relative number of travelling and fuel deposition days on the basis of estimates of thermal soaring performance, energy con-

sumption during soaring and resting, and fuel deposition rate. Given such estimates for the osprey, Kjellén et al. (2001) predicted that the fraction of days used for travelling should be about 50%, with the remaining 50% of the days used for fuel deposition. Conditions and estimates are very similar for the honey buzzard, and we expect this general prediction to apply to honey buzzards as well as ospreys. As seen from Table 1, the adult honey buzzards used 78–100% of the days between departure from the breeding site and arrival at the winter site as travelling days, and the juveniles used a similar proportion of travelling days to reach West Africa, i.e. to cover about 80% of the total distance travelled (Table 1, 2). Hence, even if the stopover days recorded were used very efficiently for fuel deposition, they are probably much too few to provide sufficient energy for the whole migratory journey, given the physiological restrictions for maximal energy deposition rates in birds (Lindström 1991). According to the prediction above, a total number of about 35 fuel deposition days are required to provide sufficient fuel for a migratory journey lasting about 35 travelling days (thermal soaring migration), which is close to the average number of travelling days used by the honey buzzards (Table 1). If the adults spent 3–10 days only on stopover (and probable fuel deposition) along the route, it seems reasonable to assume that the remaining expected fuel deposition time, almost 30 days, must have occurred before departure from the breeding site. This is supported by marked increases in weight prior to departure reported for adults breeding in central Europe. Mean body masses in August of males and females were 840 and 960 g, respectively, which is distinctly higher than the corresponding mean masses of 630 and 620 g in June (Glutz von Blotzheim et al. 1971). If this mass increase is due to storing of fat prior to autumn migration, the honey buzzards should be able to complete the entire journey from Europe to tropical Africa by thermal soaring migration without additional food (Smith et al. 1986, Alerstam 1990, 2000, Candler and Kennedy 1995). Thus, it seems likely that our honey buzzards stored most or all of their fuel for the migratory journey before departure from the breeding area. While some of the birds probably made some complementary fuel deposition on the relatively small number of stopover days along the route, others apparently had fuel reserves enough to complete the entire journey without a single stopover day. In this reasoning, we have assumed that foraging and fuel deposition of honey buzzards on travelling days, i.e. in the mornings and afternoons before and after the daily thermal soaring period, are of minor importance.

The maximum speeds of between 292 and 494 km/day of the honey buzzards were higher than recorded for members of the three species of *Aquila* eagles mentioned above, which showed maximum daily movements of 220–290 km/day. However, maximum speeds were lower than for species which may use a higher proportion of flapping flight on migration. Of 13 ospreys tracked by satellite, seven travelled at maximum speeds of more than 400 km/day, with a highest value of 746 km/day (Kjellén et al. 2001), while peregrines may cover up to 1045 km per day (Cochran and Applegate 1986).

Maximum speeds of the honey buzzards were recorded either when the birds crossed the Mediterranean Sea or Sahara. Likely explanations for this are that the birds use a higher proportion of flapping flight and may be forced to extend the daily time of migration when flying over the sea (juveniles), and that they can travel fast over the desert, where thermals are stronger and more frequent than elsewhere, because they may afford steep and fast inter-thermal gliding (Bruderer et al. 1994). There were no indications that the birds migrated during the night (Fig. 5). Hence, assuming a daily migration period of 10 hours, the maximum daily movements correspond to an average cross-country speed of 37 km/h, which agrees well with the prediction made by Bruderer et al. (1994) based on radar studies of honey buzzards migrating through desert areas in southern Israel.

Evolution of age-dependent differences in migration routes and orientation

Schmid (2000) suggested that the difference in migration strategy between adult and juvenile honey buzzards may partly depend on differences in the timing of migration. Adults mainly migrate across Europe in late August/early September, when it is still possible to travel by soaring flight to a high degree. Thus, they use the more comfortable and safe overland detour, as this is compensated by the low energy costs of soaring, compared to flapping flight. The juveniles migrate about two to three weeks later, when meterological thermal models suggest that conditions for using soaring flight are getting poor (Schmid 2000). Thus, they may as well use flapping flight and go the shortest way to West Africa. Although this may contribute to the difference in migration strategy between adults and juveniles, it seems doubtful whether this can be the only explanation for the shift in optimum route from the Gibraltar detour to a more direct route. Also, this suggests that juvenile honey buzzards should reach the wintering area faster than adults (Schmid 2000), which was not supported by the satellite tracking. Another possible explanation is that the detour via Gibraltar, as used by the adults, remains the most favourable route (Alerstam 2001), but the juveniles cannot use it because, travelling later than the adults, they do not have the possibility of obtaining guidance by experienced adults.

Adult honey buzzards use thermal soaring flight to an important degree on migration (Bruderer et al. 1994), and tend to avoid flying over wide stretches of open water. This pattern was evident in this study, as the adults seemed to cross most larger water bodies at narrow straits (Fig. 1). However, Ma 49-97 obviously left Sweden at southeastern Scania, and not at the narrow sea passages between Sweden and Denmark, e.g. at Falsterbo (Fig. 1). Juv 11-98 seemed to use the same initial route, and all the juveniles probably flew over wide stretches of water when crossing the Mediterranean Sea (Fig. 2). This, as well as the straight migration courses followed by all birds during the migration over Europe, Sahara and West Africa, respectively, with crossings of other geographical obstacles such as the Pyrenees and the Atlas mountains (Fig. 1; Bruderer and Jenni 1990), show that honey buzzards are capable of using flapping flight as an alternative to soaring flight on migration. Hence, adult honey buzzards seem to make a decision to follow the overland route rather than being forced to make a detour by the absence of thermal winds over water. This supports the suggestions that the Gibraltar detour is the most favourable route, and that social influence plays an important role for the orientation of adults. An increased reluctance against sea crossings will help to funnel the adults towards Gibraltar. The adults presumably have learnt cues which make it possible for them to correct for the displacement associated with the detour and navigate back to their previous winter sites after reaching West Africa (Perdeck 1958). In contrast, the juveniles may be constrained by their endogenous spatiotemporal migration programme (Gwinner 1996) from following a more complex route like the adults during their first autumn migration, and must rely on a more stereotype inherited orientation behaviour to reach the wintering area. They may learn another route only later, by joining different groups of experienced individuals on their first spring migration, after their first season in the breeding range, or even later, as indicated by ringing recoveries in the Central Mediterranean region, where the age of adult birds recovered was much lower than of adults recovered along the western and eastern detour (Schmid 2000). This is consistent with the high degree of synchronisation of migration of the honey buzzard (Kjellén 1992), and the habit of adults to travel in flocks (Schmid 2000, Alerstam, unpubl.).

While it is easy to see how such a distinct age-dependent shift in orientation principles and migratory route can continue to exist and be reinforced once there are enough experienced adults to learn the detour from, it is less obvious how such a system started to evolve. The age-dependent shift in migratory route and orientation of the honey buzzard, as corroborated by the satellite tracking results, is of a unique interest from an evolutionary perspective concerning the adaptive values of the separate routes, the importance of different orientation constraints for adults and juveniles and possible scenarios of evolution.

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