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Spatio-temporal distribution of migrating raptors: a comparison of ringing and satellite tracking

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We describe the migration performance of three long-distance migrating raptors, osprey *Pandion haliaetus*, honey buzzard *Pernis apivorus* and marsh harrier *Circus aeruginosus*, and one short-distance migrating raptor, common buzzard *Buteo buteo* based on Swedish ringing recoveries and satellite telemetry, respectively. Tracking by satellite can provide detailed information about the exact timing of migration, migration speed, migration directions, stopover sites, and detours, thereby overcoming many of the potential biases found in ring recoveries. Comparison of the results from these two methods revealed agreement in the geographical distribution of the studied Swedish raptor populations during autumn migration and the winter period. Satellite tracking, nevertheless, provided much more detailed information in Africa and revealed significantly faster migration progress than indicated by ring recoveries. The implications of our findings for interpretation of migratory connectivity and the understanding of migration are discussed.

The difficulties associated with following individual migrating birds over longer distances have prevented a thorough understanding of this critical aspect of their lives. Even describing overall migration patterns in detail have proved difficult, and such data are important in studies of avian ecology and conservation. For example migration counts and radar observations only record the phenology of migration at a specific locality (e.g. Rudebeck 1950, Alerstam 1990, Bednarz et al. 1990, Kjellén 1992, Bildstein and Klem 2001). In contrast, ringing provides information about large scale movements of individual birds. It is a relatively simple method that, due to the enthusiasm of thousands of volunteers, often involves large sample sizes. However, only a small fraction of the applied rings is recovered, at least for smaller birds, in which each individual ring is rarely recovered more than once, typically if the bird is found dead. As such, ring recoveries (including recaptures) provide information of samples of individuals. Currently, ringing is virtually the only adequate method to get information about migration patterns of small birds, in particular nocturnal passerines (Berthold 2001, Fransson and Pettersson 2001, Bønløkke et al. 2006).

Satellite telemetry (either relay of data from GPS tags or the Argos system that uses Doppler principles) is an alternative method to study migration patterns of individual birds and trace the movement throughout the migration between breeding and wintering grounds (Fuller et al. 2005). During the last twenty years it has been used for quantitative tracking of migration in a variety of bird species (e.g. Jouventin and Weimerskirch 1990, Fuller et al. 1998, Kjellén et al. 2001, Martell et al. 2001, Hake et al. 2003).

Both ringing and satellite tracking studies have their specific drawbacks. Ringing recovery data do not give a complete picture of bird migration due to bias in recovery rates (Perdeck 1977). Recoveries are scarce from uninhabited areas, which for example results in an over-representation of recoveries from the European part for the European-African migratory flyway. Also, a substantial proportion of recoveries came from hunting (Fransson and Pettersson 2001, Bønløkke et al. 2006), thus the spatial distribution of recoveries is to some degree reflecting hunting pressure in addition to migration intensity (Perdeck 1977, Newton 1979, McCulloch et al. 1992). Another important possible source of heterogeneity in ring recoveries may result from injured or diseased birds. Migratory performance of these individuals would presumably deteriorate, resulting in recoveries lagging behind the actual migration of normal, 'healthy' individuals. Satellite telemetry has two major disadvantages. Firstly, sample sizes are normally small since financial costs of satellite transmitters and data transfer are high. With a small sample size the effect of a single individual that behaves in an unusual way can be significant. Secondly, because transmitters are relatively heavy (the lightest at the moment weighs 9.5 g) the method can only be used for the largest birds, omitting approximately 85% of all species, and even for the larger species, carrying transmitters (especially with the relatively large cross-section of satellite transmitters) has more impact on the individual bird than a metal ring (e.g. Kenward 2001).

Both ringing and satellite telemetry studies have been used to derive information about the timing of migration, migratory routes and wintering areas (e.g. Hilden and Saurola 1982, Kjellén et al. 2001, Martell et al. 2001). In this study, we compare ring recoveries with satellite telemetry tracks of four species of raptors to investigate potential biases associated with ring recovery data. We focus mainly on the spatio-temporal distribution during autumn migration when birds are mobile and from which we have the most data. To ensure that any differences found do not result from including different populations in the analysis, we use ringing and satellite tracking data from approximately the same breeding areas.

Methods

From 1995–2006 we tracked the autumn migration of juvenile and adult individuals of four species of raptors using satellite telemetry: osprey *Pandion haliaetus* (Hake et al. 2001, Kjellén et al. 2001), honey buzzard *Pernis apivorus* (Hake et al. 2003), marsh harrier *Circus aeruginosus* (Strandberg et al. 2008) and common buzzard *Buteo buteo* (Strandberg et al. 2009). All birds were tagged at breeding sites (osprey and common buzzard at approximately 60° N, 15-16° E, honey buzzard: 57-59° N, 12-13° E, marsh harrier: 56° N, 14° E). Locations obtained from transmitters and provided by the Argos Doppler-based system are divided into different classes (labelled A, B and 0-3) depending on validation, number of messages received, and location accuracy. In this analysis, we used all high quality positions (location classes 1-3, accuracy most often within 1 km). Low quality positions (location classes A, B and 0, unspecified accuracy) were only used when considered accurate in relation to good quality positions received during adjacent transmitting periods (see also Kjellén et al. 2001).

From all Swedish ring recoveries of osprey, common buzzard, honey buzzard, and marsh harrier made between 1917 and 2005, we selected the records of individuals breeding within 10° of lat. and long. of where our radio-tagged birds originated from (osprey: 58-62° N, 11-19° E, honey buzzard: 55-67° N, 11-23° E, marsh harriers: 55-60° N, 12-18° E and common buzzard: 58-61° N, 11-19° E). We only used recoveries with a reporting error of no greater than 25 km and reported no more than 7 d after death (Swedish Museum of Natural History). We used data from Sept. to Nov. Data from August were excluded, because for that month the great majority of tracking positions and ring recoveries were from the breeding grounds. For Oct., no ring recoveries of adult honey buzzards were available.

Consecutive locations tend to be autocorrelated when time intervals between locations are small (Turchin 1998). Our data are for each individual a time-series of locations characterised by irregularly timed and serially correlated observations (Jonsen et al. 2006), with each location normally being strongly dependent on the previous location. In contrast, no more than one ring recovery is included for each ringed bird. To account for this discrepancy, we simply used average locations for each satellite tracked individual for each comparison with ringing data. Thus, to test for differences in timing between tracked and ringed raptors, we calculated for every track the average longitudinal position per month, and subsequently compared, for every month, the average positions of the tracked birds with the positions of the ringed birds, using a t-test (SPSS 16.0). In the case an F-test indicated that variances were unequal between groups (see below), we performed a t-test that assumes unequal variances, and vice versa. In a similar test for differences in geographical (longitudinal) distribution, we divided the positions into different categories based on latitudes rather than months. This was required since migration occurs within a northeast-southwest corridor.

This method makes direct comparisons of relevant summary measures such as monthly positions and average positions in certain geographical areas and thus avoids the complications of dependence in more advanced methods such as general linear models. Additionally, our method also allowed us to test for differences in variance directly. However, with our method the results of each test cannot be considered independent of the other tests.

For the geographical analyses, we divided the data into four latitudinal sectors: (1) northern Europe, 65-50° N, (2) Central/southern Europe, 50-40° N, (3) Mediterranean, 40-30° N, and (4) sub-Saharan Africa, 18-5° N (there were no ring recoveries in the Sahara Desert between 30-18° N and only osprey recoveries in sub-Saharan Africa). For common buzzards we made two different tests comparing tracks with recoveries in sector 1 (where tracks ended) and with all recoveries, respectively.

We also compared the spatial distribution of recoveries and tracks during winter (Dec. to Feb.) for ospreys (representing long-distance migrants) and common buzzards (representing short-distance migrants), to check for possible differences in migratory populations and for potential differences in geographic distribution during this stationary period (Sylvén 1978, Prevost 1982). Because ringed and tracked birds in this study are assumed to winter in the same geographical area and not to change temporal distribution during winter, data were in this case not restricted in latitudinal sectors for longitude tests. Honey buzzards (three recoveries), and marsh harriers (two recoveries), were not included in this analysis because of the lack of ring recovery data.

For both the temporal and geographical comparison we also compared the 'spread' of the locations between the two data sets, by calculating the variance. Differences in variances were evaluated by F-tests (Levene's test for equality of variances). Separate analyses were conducted for each combination of species and age class (adult and juvenile).

For plotting satellite telemetry tracks and ring recoveries, all coordinates were transformed to coordinates in the Mercator projection (see Gudmundsson and Alerstam 1998).

Results

Geographical patterns during autumn migration and wintering

In general, the geographical distributions of satellite tracks and ring recoveries were similar (Fig. 1), although no birds were recovered from the Sahara desert. The most obvious difference was that, except for ospreys, no recoveries were made south of Sahara during the autumn migration (Fig. 1). Correcting for latitude there were no significant differences in longitudinal positions between tracked and recovered birds (Table 1), except for juvenile honey buzzards and adult marsh harriers in the Mediterranean (40-30° N), with only one recovery included for the latter.

There were significant differences in the variation around the longitudinal mean for adult and juvenile honey buzzards in the Mediterranean, for adult and juvenile marsh harriers in Central/Southern Europe and for adult and

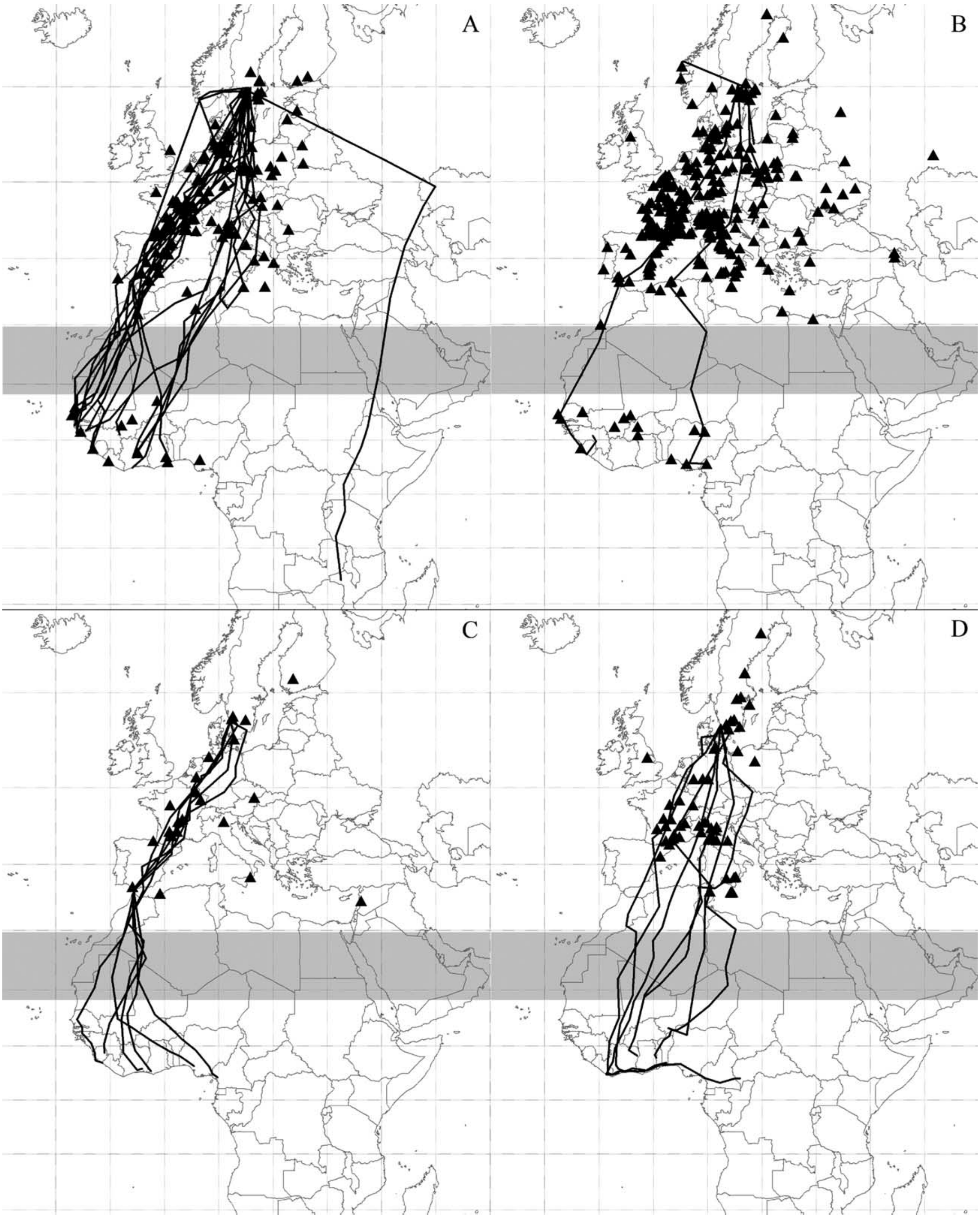

Figure 1 (*Continued*).

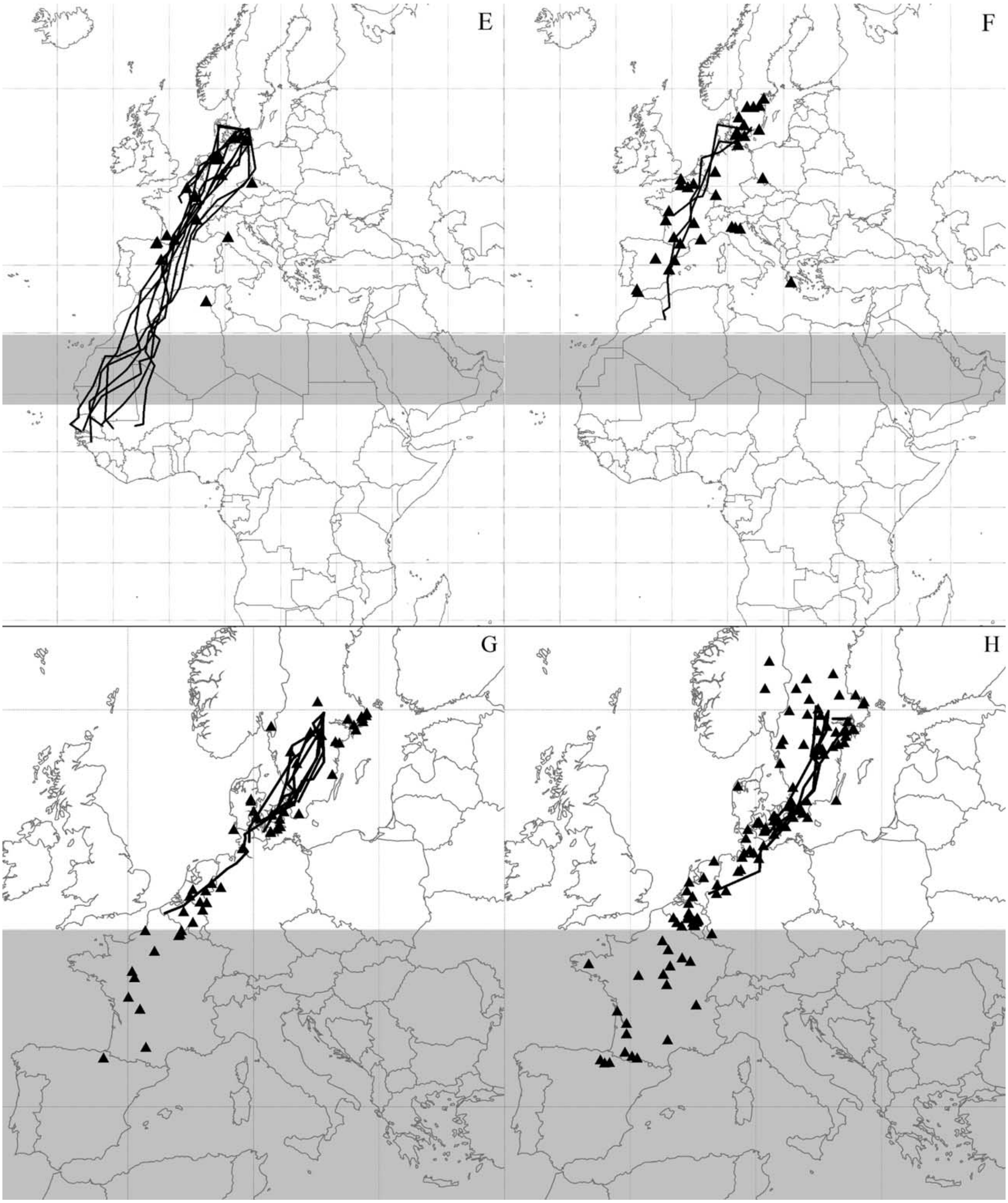

Figure 1. Geographical pattern of tracks (lines) and recoveries (black triangles) of raptors from southern Sweden during autumn migration: adult ospreys (A), juvenile ospreys (B), adult honey buzzards (C), juvenile honey buzzards (D), adult marsh harriers (E), juvenile marsh harriers (F), adult common buzzards (G), and juvenile common buzzards (H). Note that for two juvenile honey buzzards the autumn movement continued into December (from Ivory Coast and east to Benin and Central African Republic, respectively). The shaded zone shown over the Sahara represents the area without ring recoveries, which were excluded from the geographical analyses (A–F). The shaded zone in G and H indicates the latitudes that were never reached by the tracked common buzzards (range 2 in Table 1).

juvenile common buzzards in northern Europe (Table 1). Tracked adult honey buzzards (Mediterranean) were restricted to routes through Spain, as were recoveries with a few exceptions (Fig. 1C). For the juvenile honey buzzards, tracks and recoveries were evenly spread out over the western parts of southern Europe (Fig. 1D). Concerning the marsh harriers in Central/Southern Europe, tracks were more concentrated through Germany and France than

Table 1. Geographical distribution of autumn migration in raptors recovered and tracked from Sweden, based on results from t-tests of mean longitudinal positions (° E). The positions were divided into latitudinal sectors: (1) northern Europe, 65-50° N, (2) Central/southern Europe, 50-40° N, (3) Mediterranean, 40-30° N, and (4) sub-Saharan Africa, 18-5° N. There was only one ring recovery in the Mediterranean range for adult marsh harriers. N tracks = number of satellite tracks; n rings = number of ring recoveries; track long. = longitudinal mean position of tracked birds in different sectors; ring long. = longitudinal mean position of ring recoveries in different sectors; P variance = P-value of longitudinal variance from F-test. Note that 32 ring recoveries of common buzzards (presented in Table 2) were made in sector 2, an area not reached by the tracked birds. The P-values are bold when significant.

Species	Age	Lat. sector	n tracks	n rings	Track long.	SD	Ring long.	SD	F	df	P difference	P variance
Osprey	ad	1	11	51	12.6	3.3	14.4	5.8	3.64	60	0.304	0.061
Osprey	ad	2	15	57	8.4	12.6	5.8	6.2	3.97	70	0.265	0.050
Osprey	ad	3	17	14	0.7	12.2	3.7	9.7	0.01	29	0.469	0.941
Osprey	ad	4	17	12	−9.2	13.0	−7.1	7.7	0.32	27	0.635	0.575
Osprey	juv	1	5	97	14.2	5.3	15.0	7.9	0.84	100	0.819	0.363
Osprey	juv	2	3	171	12.0	8.4	8.6	8.5	0.00	172	0.485	0.983
Osprey	juv	3	2	51	−1.2	5.7	8.2	9.8	1.53	51	0.189	0.222
Osprey	juv	4	2	14	−1.5	14.3	−3.3	9.6	0.38	14	0.818	0.545
Honey buzzard	ad	1	3	7	10.8	3.3	13.0	5.7	0.29	8	0.560	0.607
Honey buzzard	ad	2	5	11	3.5	1.9	4.6	5.3	2.90	14	0.669	0.111
Honey buzzard	ad	3	6	4	−5.0	0.8	11.4	19.0	17.21	8	0.183	**0.003**
Honey buzzard	juv	1	8	18	11.5	2.1	13.4	4.9	2.26	24	0.290	0.145
Honey buzzard	juv	2	6	28	9.4	5.8	6.4	3.9	2.39	32	0.131	0.132
Honey buzzard	juv	3	7	8	6.0	5.9	14.0	1.5	14.46	13	**0.011**	**0.002**
Marsh harrier	ad	1	10	8	11.5	2.2	11.2	2.6	1.51	16	0.763	0.237
Marsh harrier	ad	2	10	11	3.9	2.0	2.6	4.0	5.44	19	0.362	**0.031**
Marsh harrier	ad	3	8	1	−2.0	1.4	6.7	–	–	7	**(0.001)**	–
Marsh harrier	juv	1	3	18	8.2	1.2	11.5	4.7	2.15	19	0.247	0.159
Marsh harrier	juv	2	3	13	3.3	0.8	4.1	5.1	5.65	14	0.609	**0.032**
Marsh harrier	juv	3	2	4	−0.8	0.5	2.2	13.1	3.15	4	0.774	0.151
Common buzzard	ad	1	8	47	13.1	1.3	11.9	4.4	8.53	53	0.147	**0.005**
Common buzzard	juv	1	4	99	13.0	1.4	11.4	4.3	4.53	101	0.109	**0.036**

recoveries, more so among juveniles. Finally, the tracked common buzzards (Northern Europe) were more centred through western Sweden and down through Denmark to the Benelux countries, even though the difference in variance is affected by the lack of tracks south of Denmark (only one male and one juvenile continuing to Belgium and the Netherlands, respectively).

In both ospreys and common buzzards, the mean and the spread of winter positions of adult birds differed between ring recoveries and satellite telemetry (Table 3, Fig. 3). Ring recoveries of ospreys were north and east of telemetry positions and ring recoveries of common buzzards were south and west of telemetry positions. The latitudinal spread of ring recoveries was much larger than tracked positions in both species, whereas the longitudinal spread was not different. In juveniles, significant differences were found only for ospreys. Both the latitudinal position and the spread of positions were larger for recoveries, which were found north of the tracked birds' winter positions (Table 3, Fig. 3).

Temporal patterns during autumn migration

We found pronounced differences in latitudinal mean position among adults and later in autumn when the birds approached their wintering grounds (Table 2). Most tracked birds reached their wintering areas by Nov. For the trans-Saharan migrants (osprey, honey buzzard, adult marsh harrier), all tracked birds (except for one female marsh harrier spending the winter in Camargue, France) had passed the Sahara before the end of October, while ring recoveries continued in Europe through Nov. (Fig. 2). Even for the osprey, the only species for which ring recoveries during autumn migration were available from tropical Africa, the majority of ring recoveries in Nov. (68%) came from Europe. Results from t-tests confirmed that ring recoveries of the trans-Saharan migrants lagged behind satellite tracks and the temporal difference typically increased later in the season (Table 2). The difference in latitudinal mean position in Nov. was more than 20°, i.e. the mean position of recovered birds was still in Europe while the tracked birds had already reached their wintering grounds in tropical Africa.

There were no differences in timing between tracked and recovered juvenile marsh harriers, which in fact behaved as short distance migrants, with mean positions in Europe for both recoveries and tracks throughout the autumn period, in contrast to the tracked adult birds.

There was a significant difference in timing of migration between tracks and recoveries for the short-distance migrating adult common buzzards (Table 2). However, the picture here was reversed with tracked birds lagging behind the recovered birds. Many buzzards were recovered south of the wintering positions of the tracked birds, with recoveries as far south as 37° N.

As seen in Table 2 and Fig. 2, there were significant differences in the variance around the latitudinal mean value in several cases. In general, this variance decreased for satellite tracks later in autumn, which to a large extent reflects individual differences in rate of progress along the migration route (see Discussion).

Discussion

Ring recoveries and satellite tracking provide much of the same picture concerning the geographical pattern for the combinations of age and species classes studied in this contribution. This was not unexpected because the tracked and ringed birds in this study involved only birds from approximately the same breeding origin in Sweden. However, for honey buzzards, at the passage of the Mediterranean, we found significant differences in the spread of positions. This was probably either caused by the small variation in routes taken via the Gibraltar Strait by adult birds tracked from Sweden, and by the high share among the recoveries of juvenile birds shot at the more eastern part of the migration corridor (passage through Italy to Tunisia, see also Hake et al. 2003), or by differences in routes taken by birds from different areas in Sweden (with ringed birds from a wider range than tracked birds).

Autumn ring recoveries are absent from the Sahara desert and southwards, with an exception for the osprey. Recoveries from other periods of the year can nevertheless be used to infer the routes through Africa of the long-distance migrants (Fransson and Pettersson 2001). The lack of recoveries from Sahara is most probably the result of the fact that this concerns vast areas without human settlements (Crissey 1955). Also factors such as poverty would contribute to the scarcity of recoveries from tropical Africa.

The winter distributions of tracked and ringed birds overlap (Fig. 3) even though there is a greater spread of recoveries and a significant difference in latitudinal mean position (except for juvenile common buzzards). For the osprey, differences are caused by a great number of ring recoveries in Europe (where no tracked birds wintered), which most probably relate to delayed birds. For the common buzzard a difference in winter distribution between tracked and ringed birds most probably reflects a change in wintering distribution in the last 30 years. This can for example be inferred from the fact that, despite an increase in ringing efforts during recent decades (Swedish Museum of Natural History), only seven out of 140 ring recoveries of common buzzards south of latitude 50° N have been made after 1980 (including all recoveries, no selection for season). Furthermore, the number of wintering buzzards in Sweden has showed a slight but significant increase during the last 20 years (Lindström and Svensson 2007), whereas the number of migrating common buzzards at Gibraltar (southern Spain) has decreased considerably between 1960 and 2005 (Bensusan et al. 2007).

There are, in most cases, clear differences in the timing of autumn migration between tracked and recovered adult raptors and these differences are increasing towards the end of the migration season. The pattern is not as obvious for juveniles which might be seen as an effect of their inexperience with migration. Juveniles are in a learning process and do not head for a certain wintering site as the adults do (e.g. Alerstam et al. 2006). Nevertheless, comparing the latitudes of the long-distance migrants' monthly positions, significant or not, the satellite tracked birds are in all except one group (juvenile marsh harriers in November), ahead of the ring recovery pattern. The opposite is true for the short-distance migrating common buzzard, with recoveries ahead of tracks, in which the difference in November

Table 2. Timing of autumn migration in raptors recovered and tracked from Sweden, based on results from t-tests of mean latitudinal positions (° N). Missing values for juvenile ospreys in Nov. were caused by transmitting failures/diseased birds and for adult honey buzzards in Oct. by lack of ring recoveries. Abbreviations in head line as for Table 1, with the difference that lat. = latitude. The P-values are bold when significant.

Species	Age	Month	n tracks	n rings	Track lat.	SD	Ring lat.	SD	F	df	P difference	P variance
Osprey	ad	Sept.	19	91	36.0	14.4	47.3	10.9	3.77	99	**0.003**	0.055
Osprey	ad	Oct.	18	33	16.7	11.8	40.1	12.1	0.09	49	< **0.001**	0.763
Osprey	ad	Nov.	17	10	9.4	7.1	36.9	19.5	19.53	25	**0.001**	< **0.001**
Osprey	juv	Sept.	5	190	47.5	13.2	48.1	6.4	8.99	193	0.914	**0.003**
Osprey	juv	Oct.	4	122	33.5	25.4	42.7	9.7	14.70	124	0.522	< **0.001**
Osprey	juv	Nov.	1	21	11.0	–	33.4	16.9	–	20	(0.211)	–
Honey buzzard	ad	Sept.	6	20	35.8	16.4	48.4	7.3	10.43	24	0.112	**0.004**
Honey buzzard	ad	Oct.	6	0	12.5	10.8	–	–	–	–	–	–
Honey buzzard	ad	Nov.	4	2	6.0	1.4	40.1	6.2	41.69	4	0.075	**0.003**
Honey buzzard	juv	Sept.	8	22	48.4	7.4	50.8	8.1	0.86	28	0.471	0.363
Honey buzzard	juv	Oct.	7	29	17.3	5.9	45.3	5.8	0.04	34	< **0.001**	0.852
Honey buzzard	juv	Nov.	6	3	9.0	5.0	42.9	6.3	0.27	7	< **0.001**	0.617
Marsh harrier	ad	Sept.	11	8	47.6	6.2	49.7	4.8	0.48	17	0.441	0.497
Marsh harrier	ad	Oct.	8	9	22.8	10.1	48.0	4.2	3.75	15	< **0.001**	0.072
Marsh harrier	ad	Nov.	7	3	14.2	0.9	43.7	10.5	20.17	8	**0.039**	**0.002**
Marsh harrier	juv	Sept.	3	16	50.0	10.7	53.3	6.9	1.22	17	0.484	0.285
Marsh harrier	juv	Oct.	3	16	45.5	11.7	46.8	5.4	5.51	17	0.865	**0.031**
Marsh harrier	juv	Nov.	2	3	46.8	1.5	42.3	5.3	5.21	3	0.345	0.107
Common buzzard	ad	Sept.	8	14	59.3	0.4	57.6	2.6	13.19	20	**0.032**	**0.002**
Common buzzard	ad	Oct.	8	25	56.2	1.2	53.9	4.5	5.95	31	**0.028**	**0.021**
Common buzzard	ad	Nov.	8	19	54.9	1.3	52.4	4.1	12.01	25	**0.026**	**0.002**
Common buzzard	juv	Sept.	4	41	59.1	1.0	58.2	3.2	1.31	43	0.576	0.259
Common buzzard	juv	Oct.	4	31	56.1	1.4	52.1	5.2	5.50	33	**0.003**	**0.025**
Common buzzard	juv	Nov.	3	48	54.1	1.6	51.7	3.5	1.63	49	0.258	0.208

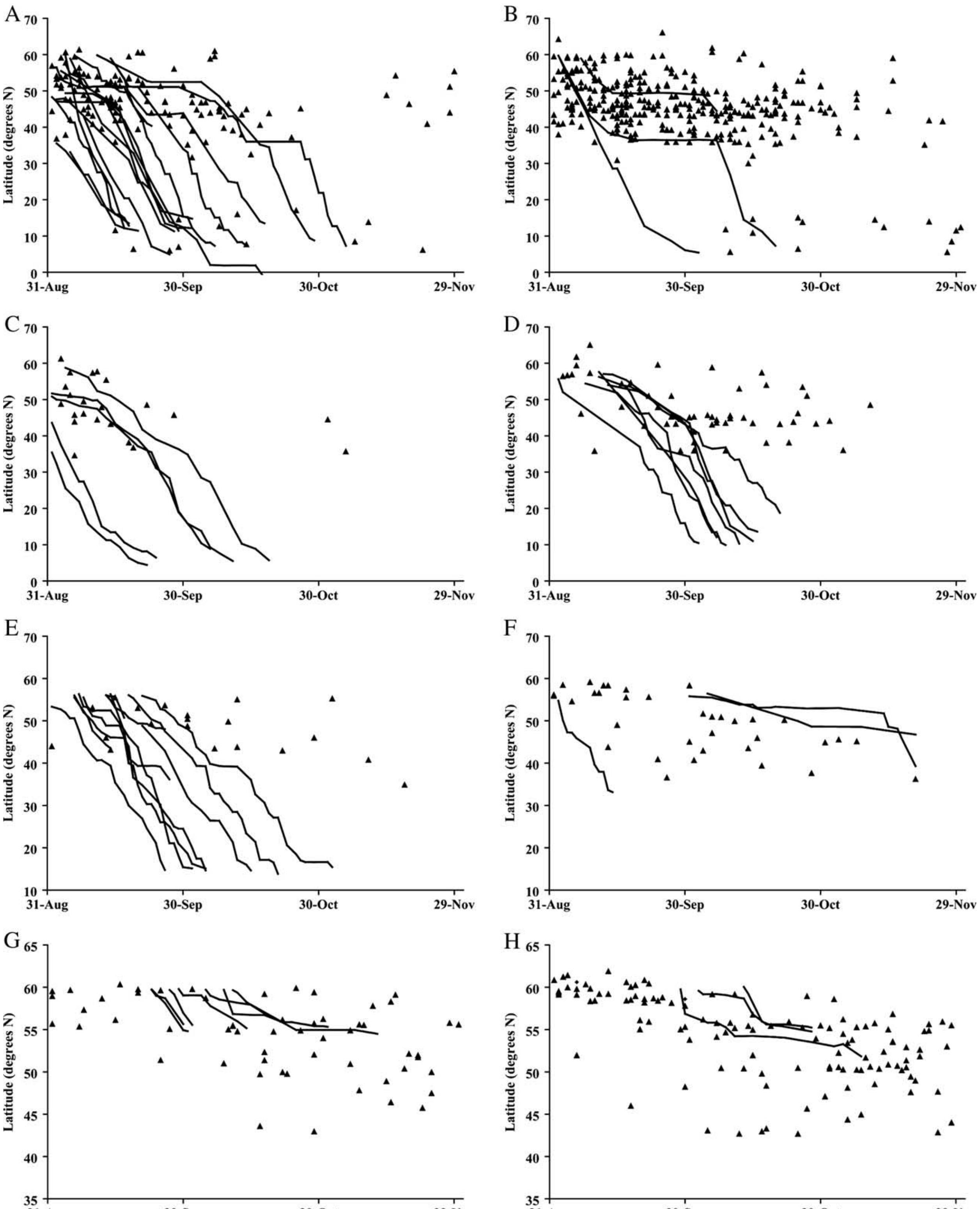

Figure 2. Temporal latitudinal positions of raptors from southern Sweden during autumn migration: adult ospreys (A), juvenile ospreys (B), adult honey buzzards (C), juvenile honey buzzards (D), adult marsh harriers (E), juvenile marsh harriers (F), adult common buzzards (G) and juvenile common buzzards (H). Filled triangles = recoveries, lines = tracks. Note that the tracks have been cut off before and after the migration movement, when and if birds were stationary in either breeding areas or wintering areas.

corresponds to about three degrees of latitude. This result is explained by the shift in wintering quarters over the years (see above). There are three possible explanations of why ring recoveries lag behind trackings for long-distance migrants. First, recoveries are scarce from Africa, resulting in an over-representation of European recoveries, and thus a bias towards Europe, especially later in the season (when most birds would have moved into Africa). Second, for a correct timing of recovery data it is important that the moment the bird died has been assessed correctly. Any misjudgement towards the bird being dead for a shorter time results in a bias towards a later timing of migration, as demonstrated by Kenward (1993) in recoveries of ringed and radio-tagged goshawks. Third, birds with a worsened condition will migrate at a lower speed (if migrating at all), and may be, due to a reduced manoeuvrability, more easily found or hunted. In other words, birds with a deteriorated condition have a higher probability to remain at higher latitudes and to be found. This will also increase the variance in timing for ring recoveries. Generally, among tracked

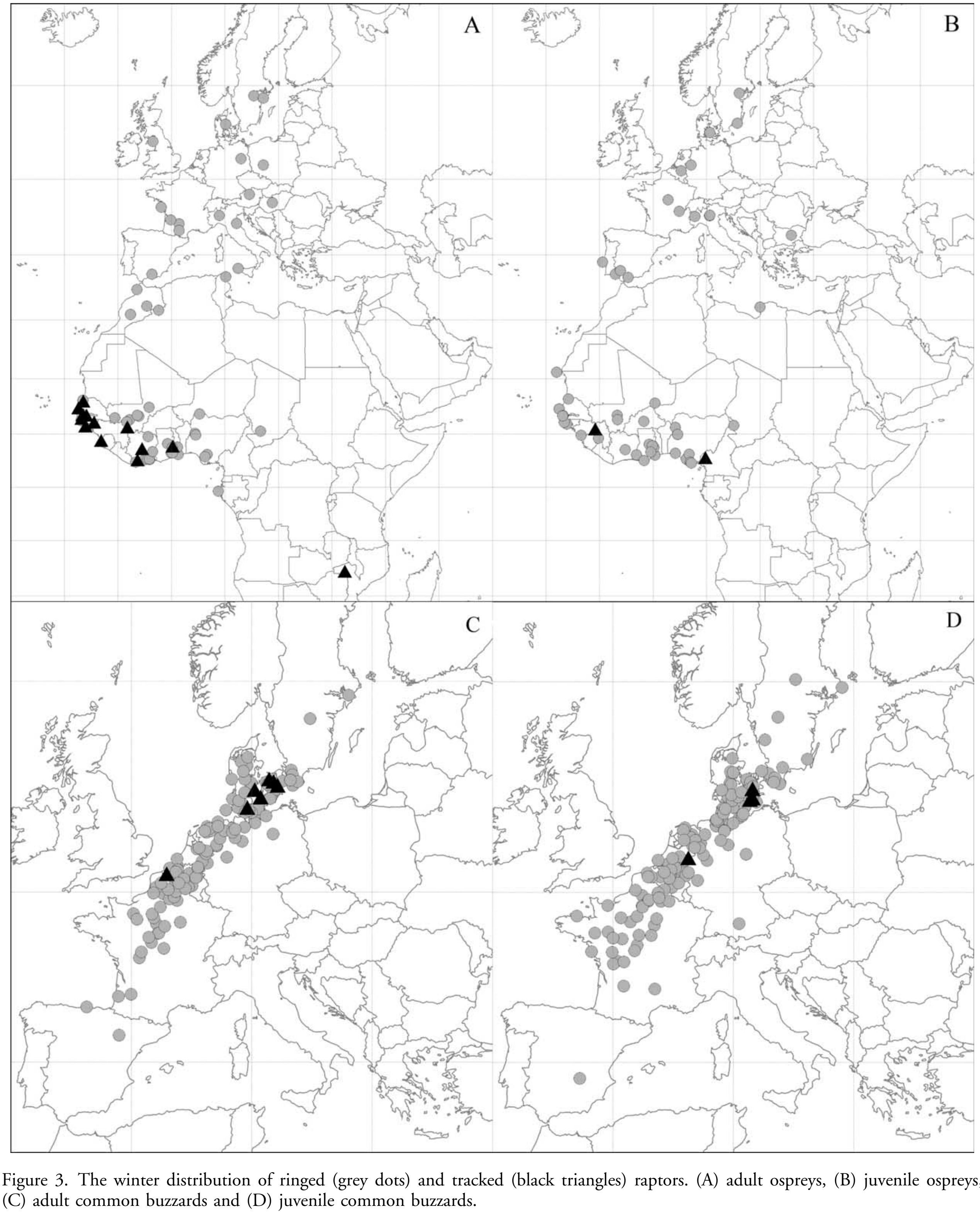

Figure 3. The winter distribution of ringed (grey dots) and tracked (black triangles) raptors. (A) adult ospreys, (B) juvenile ospreys, (C) adult common buzzards and (D) juvenile common buzzards.

long-distance migrants, the initiation of migration takes place during a wide time range with birds leaving northern Europe from late July to early Oct., while the great majority reach their wintering grounds during a narrower time range in late Oct. to early Nov. In Nov. all tracked birds have reached the winter grounds and are gathered in tropical West Africa. This would count for relatively high variance in latitudinal distribution early in the season. Such a pattern was not found in the recovery data of long-distance migrants (or in the results of the short-distance migrant common buzzard). However, there was greater variance among recoveries than among tracked common buzzards in all periods, among adults as well as juveniles (Table 3).

Difference in longitudinal variance between the tracks and recoveries is not as easy to address as for the latitudinal variance, and at least part of this may be explained by our statistical treatment where the ring recovery data include recoveries from throughout a month whereas in the satellite tracking data individual monthly averages are used. This might also be influenced by the greater sample area of ringed birds as is obvious for honey buzzards with three of the easternmost recoveries belonging to birds ringed north of 65° N, possibly using an eastern migration flyway. Otherwise, such differences could result from birds off the track being more easily recovered because of their odd behaviour or physical state.

In this comparison we used ringing data spanning over almost a century, whereas satellite telemetry data were only available for a little more than a decade, as this is a relatively recent technique. Migration patterns seem to be affected by the recent changes in climate and habitat (Robinson et al. 2005). Comparing two datasets that differ so much is time span might thus be problematic. Nevertheless, the general routes of the raptors that use the European-West African migration flyway seems not to have changed dramatically as tracks nicely match ring recoveries (at least in cases where the latter are available). Only for the short-distance migrating common buzzard we could detect a change in migration distance (Fransson and Pettersson 2001). For the time being, climate change seems to affect mostly the timing and possibly the duration of migration (Jonzén et al. 2006), and migratory birds are rather traditional in their migratory routes. The increase of wintering (mainly juvenile) marsh harriers in northern Europe (Castelijns and Castelijns 2008) is however an indication that also wintering areas and possibly routes for long-distance migrants are beginning to change.

Conclusions

We conclude that care should be taken in the interpretation of ring recovery data. For our raptor data, both methods show approximately the same general migration routes, but with recoveries biased to areas with more dense human populations. More problematic is the interpretation of the temporal patterns from recovery data. Differences between satellite telemetry and ringing recovery data can in part be explained by changes in the birds' behaviour (common buzzard) but, for long-distance migrants, illustrates an important problem with the ring recoveries, i.e. that recoveries provide a delayed picture of migration. Some

Table 3. Winter distribution (Dec.–Feb.) of ospreys and common buzzards recovered and tracked from Sweden, based on results from t-tests of mean latitudinal and longitudinal positions (degrees N and E). Abbreviations in head line as for Table 1. The P-values are bold when significant.

Species	Age	Test category	n tracks	n rings	Track mean position	SD	Ring mean position	SD	F	df	P difference	P variance
Osprey	ad	Lat.	13	52	9.1	8.1	23.4	18.8	31.83	63	**<0.001**	**<0.001**
		Long.	13	52	−8.8	13.6	0.7	9.3	0.33	63	**0.004**	0.567
Osprey	juv	Lat.	2	47	8.3	3.8	22.2	17.8	5.71	47	**0.023**	**0.021**
		Long.	2	47	−0.5	14.6	−0.2	10.9	0.12	47	0.974	0.733
Common buzzard	ad	Lat.	8	118	54.6	1.5	52.1	3.1	5.12	123	**0.002**	**0.025**
		Long.	8	118	10.0	3.0	6.7	4.0	3.35	123	**0.023**	0.070
Common buzzard	juv	Lat.	4	138	54.1	1.6	52.2	3.3	2.37	140	0.238	0.126
		Long.	4	138	10.2	2.6	7.1	4.3	2.04	140	0.151	0.155

of these biases are possibly less pronounced for smaller species such as passerines, but, nevertheless, care should be taken when reconstructing the timing of migration based on ring recoveries until alternative study techniques become available.

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References

Alerstam, T. 1990. Bird migration. – Cambridge Univ. Press.

Alerstam, T., Hake, M. and Kjellén, N. 2006. Temporal and spatial patterns of repeated migratory journeys by ospreys. – Anim. Behav. 71: 555–566.

Bednarz, J. C., Klem, D. Jr., Goodrich, L. J. and Senner, S. E. 1990. Migration counts of raptors at Hawk Mountain, Pennsylvania, as indicators of population trends, 1934–1986. – Auk 107: 96–109.

Bensusan, K. J., Garcia, E. F. J. and Cortes, J. E. 2007. Trends in abundance of migrating raptors at Gibraltar in spring. – Ardea 95: 83–90.

Berthold, P. 2001. Bird Migration: A general survey. Second edition. – Oxford Univ. Press.

Bildstein, K. L. and Klem, D. Jr. (Eds.) 2001. Hawkwatching in the Americas. – Hawk migration association of North America, North Wales, pp. 119–141.

Bønløkke, J., Madsen, J. J., Thorup, K., Pedersen, K. T., Bjerrum, M. and Rahbek, C. 2006. – Dansk trækfugleatlas, Humlebæk.

Castelijns, H. and Castelijns, W. 2008. Het overwinteren van de Bruine Kiekendief *Circus aeruginosus* in Zeeland. – Limosa, 81: 41–49. (in Dutch)

Crissey, W. F. 1955. The use of banding data in determining waterfowl migration and distribution. – J. Wildl. Mgmt. 19: 75–84.

Fransson, T. and Pettersson, J. 2001. Svensk ringmärkningsatlas. Vol 1. – Naturhistoriska Riksmuseet, Stockholm, pp. 167–173. (in Swedish)

Fuller, M. R., Seegar, W. S. and Schueck, L. S. 1998. Routes and travel rates of migrating peregrine falcons *Falco peregrinus* and Swainson's hawks *Buteo swainsoni* in the western Hemisphere. – J. Avian Biol. 29: 433–440.

Fuller, M. R., Church, K. E., Millspaugh, J. J. and Kenward, R. E. 2005. Wildlife radiotelemetry. – In: Braun, C. L. (ed.). Manual of wildlife management techniques. Wildlife society, USA, pp. 377–417.

Gudmundsson, G. A. and Alerstam, T. 1998. Optimal map projections for analysing long-distance migration routes. – J. Avian Biol. 29: 597–605.

Hake, M., Kjellén, N. and Alerstam, T. 2001. Satellite tracking of Swedish ospreys *Pandion haliaetus*: autumn migration routes and orientation. – J. Avian Biol. 32: 47–56.

Hake, M., Kjellén, N. and Alerstam, T. 2003. Age-dependent migration strategy in honey buzzards *Pernis apivorus* tracked by satellite. – Oikos 103: 385–396.

Hilden, O. and Saurola, P. 1982. Speed of autumn migration of birds ringed in Finland. – Ornis Fenn. 59: 140–143.

Jonsen, I. D., Myers, R. A. and James, M. C. 2006. Robust hierarchical state–space models reveal diel variation in travel rates of migrating leatherback turtles. – J. Anim. Ecol. 75: 1046–1057.

Jonzén, N., Lindén, A., Ergon, T., Knudsen, E., Vik, J.O., Rubolini, D., Piacentini, D., Brinch, C., Brinch, C., Spina, F., Karlsson, L., Stervander, M., Andersson, A., Waldenström, J., Lehikoinen, A., Edvardsen, E., Solvang, R. and Stenseth, N. C. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. – Science 312: 1959–1961.

Jouventin, P. and Weimerskirch, H. 1990. Satellite tracking of wandering albatrosses. – Nature 343: 746–748.

Kenward, R. E. 1993. Modelling raptor populations: to ring or to radio tag? – In: LeBreton, J. D. and North, P. M. (eds.). The use of marked individuals in the study of bird population dynamics: models, methods and software. – Birkhauser, Basle, pp. 157–167.

Kenward, R. E. 2001. A manual for wildlife radio-tagging. – Academic Press, London.

Kjellén, N. 1992. Differential timing of autumn migration between sex and age groups in raptors at Falsterbo, Sweden. – Ornis Scand. 23: 420–434.

Kjellén, N., Hake, M. and Alerstam, T. 2001. Timing and speed of migration in male, female and juvenile ospreys *Pandion haliaetus* between Sweden and Africa as revealed by field observations, radar and satellite tracking. – J. Avian Biol. 32: 57–67.

Lindström, Å. and Svensson, S. 2007. Monitoring population changes of birds in Sweden. – Ann. rep. 2006, Dep. of Ecol., Lund Univ.

Martell, M. S., Henny, C. J., Nye, P. E. and Solensky, M. J. 2001. Fall migration routes, timing, and wintering sites of North American ospreys as determined by satellite telemetry. – Condor 103: 715–724.

McCulloch, M. N., Tucker, G. M. and Baillie, S. R. 1992. The hunting of migratory birds in Europe: a ringing recovery analysis. – Ibis 134: 55–65.

Newton, I. 1979. Population ecology of raptors. – Buteo Books, Vermillion.

Perdeck, A. C. 1977. The analysis of ringing data: pitfalls and prospects. – Vogelwarte 29: 33–44.

Prevost, Y. A. 1982. The wintering ecology of ospreys in Senegambia. – PhD thesis, Univ. of Edinburgh.

Robinson, R. A., Learmonth, J. A., Hutson, A. M., Macleod, C. D., Sparks, T. H, Leech, D. I., Pierce, G. J., Rehfisch, M. M. and Crick, H. Q. P. 2005. Climate change and migratory species. – BTO research report 414, British Trust for Ornithology, Norfolk.

Rudebeck, G. 1950. Studies of bird migration. – Vår Fågelvärld, Suppl. 1.

Strandberg, R., Klaassen, R. H. G., Hake, M., Olofsson, P., Thorup, K. and Alerstam, T. 2008. Complex timing of marsh harrier *Circus aeruginosus* migration due to pre- and post-migratory movements. – Ardea 96: 159–171.

Strandberg, R., Alerstam, T., Hake, M. and Kjellén, N. 2009. Short-distance migration of the common buzzard *Buteo buteo* recorded by satellite tracking. – Ibis 151: 200–206.

Sylvén, M. 1978. Interspecific relations between sympatrically wintering common buzzards *Buteo buteo* and rough-legged buzzards *Buteo lagopus*. – Ornis Scand. 9: 197–206.

Turchin, P. 1998. Quantitative analyses of movement: measuring and modelling population redistribution in animals and plants. – Sinauer Ass. Inc. Publ., Sunderland.