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Can vector summation describe the orientation system of juvenile ospreys and honey buzzards? – An analysis of ring recoveries and satellite tracking

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Juvenile bird migrants are generally believed to use a clock-and-compass migratory orientation strategy. According to such a strategy migrants accomplish their migration by flying a number of successive flight steps with direction and number of steps controlled by an endogenous programme. One powerful way of testing this is by comparing predictions from a model of such a strategy with observed patterns. We used data from ringing and satellite-based radio telemetry to investigate the orientation system of juvenile ospreys (*Pandion haliaetus*) and honey buzzards (*Pernis apivorus*) migrating from Sweden to tropical west Africa. The ring recoveries showed a much larger scatter in the orientation of ospreys than of honey buzzards, but there was only a slight such difference in the satellite tracks. These tracks of individuals of both species were rather straight with a high directional concentration per step. The honey buzzard data showed a close fit to a simple vector summation model, which is expected if birds follow a clock-and-compass strategy. However, the osprey data did not fit such a simple model, as ring recoveries showed a significantly greater deviation at short distances than predicted on the basis of long distance data. Satellite tracking also indicated less concentrated orientation on short distances. The pattern observed for the osprey can generally be explained by an extended vector summation model, including an important element of pre-migration dispersal. The existence of extensive dispersal in the osprey stands in contrast to the apparent absence of such dispersal in the honey buzzard. The explanation for this difference between the species is unclear. The model of orientation by vector summation is very sensitive to the existence of differences in mean direction between individuals. Assuming such differences, as tentatively indicated by the satellite tracking data, makes simple compass orientation by vector summation inconsistent with the distribution of ring recoveries at long distances, with a high proportion of misoriented birds falling outside the normal winter range.

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Migration patterns are relatively well described for many bird species, and orientation mechanisms have been the target of many studies, demonstrating several compass mechanisms and an endogenous time scheme. However, relatively little is known about the migratory orientation system in free-flying migrants (Alerstam 1996). Comparing predictions from theoretical models of bird orientation with observed migration patterns can provide a powerful tool for evaluating the possible orientation systems of birds (Wehner 2001). Still, only few such studies have been made (Rabøl 1978, Mouritsen 1998, Sandberg and Holmquist 1998, Mouritsen

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and Mouritsen 2000, Thorup et al. 2000, Thorup and Rabøl 2001).

Rabøl (1978) pointed out the possibility that the migration of birds could be described by summation of successive flight steps (vectors), where the orientation varies between each flight step according to a circular probability distribution around the primary (mean) direction. The variation in orientation between flight steps may be caused by limitations in the precision of the birds' compass mechanisms as well as by external influences of e.g. wind drift. Given a step length and a directional variability between steps, expressed by the concentration measure r for circular distributions (where $r = 0$ for a uniform circular distribution and $r = 1$ for a unidirectional distribution without scatter; Batschelet 1981), the process of migration by vector summation may be simulated. The background of the vector summation procedure is further described by Alerstam (2000).

Rabøl (1978) showed how migrants drawing their orientation during each flight step from a circular probability distribution with a given angular scatter will, by the effect of vector summation over many flight steps, produce long-distance ring recoveries with a much more restricted angular scatter than the initial directional variability. Mouritsen (1998) and Mouritsen and Mouritsen (2000) investigated this idea further and claimed that such simple vector orientation is sufficient to explain the geographic distribution of ring recoveries of juvenile night-migrating passerines like the pied flycatcher (*Ficedula hypoleuca*) and the European robin (*Erithacus rubecula*). This would support the 'clock-and-compass' concept, according to which migration of juveniles is regulated exclusively by an endogenous temporal/directional programme (Berthold 1996, Gwinner 1996) without any elements of compensation for geographic displacement or of goal area navigation (Rabøl 1978).

However, Mouritsen (1998) in his calculations assumed that there is no difference in primary (mean) direction between individuals. Thorup et al. (2000) indicated that, taking the probable existence of such variation into account, the long-distance ring recoveries of flycatchers were less scattered than predicted on the basis of vector summation only. Furthermore, Thorup and Rabøl (2001) pointed out that it is difficult to explain the high precision orientation to very restricted winter ranges in some species of long-distance passerine migrants by simple vector summation.

Thus it is controversial if vector orientation according to an internal circannual temporal/directional programme is sufficient to explain the orientation of juveniles on their first autumn migration. Alternatively, pre-programmed responses to external geographic cues may also be involved in the process of guiding the birds along the proper migration route and to the right destination areas. There is evidence that hatchling loggerhead sea turtles respond to different combinations of geomagnetic intensity and inclination, reflecting different geographic locations in the Atlantic Ocean, by orienting in different directions so as to remain within their normal migratory range (Lohmann et al. 2001). There are also indications that geomagnetic cues, characteristic of certain latitudes or regions, affect the orientation (Beck and Wiltschko 1982) or fuel deposition (Fransson et al. 2001) of juvenile birds on their first migratory journey. The possibility that stellar cues affect the orientation of birds after geographic displacement has also been reported (Rabøl 1998, but see Mouritsen and Larsen 2001). Such responses towards certain target regions along the migratory route would reduce the increase in geographic scatter with increasing migration distance, which would be expected in a simple vector summation model. Also the proportion of misoriented individuals, ending up outside the geographic width (measured perpendicularly to the principal migratory direction) of the regular wintering area, would be reduced.

In this paper, we will try to carry the analysis one step further by using both ring recoveries and results obtained from satellite-based radio telemetry to test orientation by vector summation for juveniles of two species of raptors migrating between north Europe (Sweden) and tropical west Africa, namely the osprey (*Pandion haliaetus*) and honey buzzard (*Pernis apivorus*). These two species provide an interesting contrast, with ospreys migrating solitarily on a very broad front (Österlöf 1977, Saurola 1994, Fransson and Pettersson 2001) while juvenile honey buzzards are more concentrated and sometimes travel in small flocks (Schmid 2000, Fransson and Pettersson 2001). In both species, the juveniles migrate independently from the adults. The general migration performance of these two species in Europe and Africa has been analysed on the basis of satellite tracking results by Hake et al. (2001, 2003) and Kjellén et al. (1997, 2001). In this study we use and analyse the extensive ring recoveries of Swedish ospreys and honey buzzards (Fransson and Pettersson 2001) as well as the satellite tracking records of Swedish birds, obtained during the above-mentioned studies.

First we analyse the ringing data in order to identify the combinations of step length and directional scatter between steps (r_{step}) in a vector summation model which fit the observed distribution of ring recoveries best. We then use the segments between positions determined by satellite tracking (Hake et al. 2001) to calculate r_{step} and the associated step length for individual birds completing the journey between north Europe and west Africa. Comparing these estimates of r_{step}/step length between ringing and satellite data will tell us if the orientation performance of individual birds tracked by satellite is consistent with the distribution of ring recoveries and with a process of simple vector summation. We will also estimate the proportion of misoriented individuals depending on if there is a significant scatter in mean directions between individuals ($r_{between}$) or not, under different conditions of orientation performance.

Material and methods

Ring recoveries

The data set consists of recoveries of ospreys ($N = 766$) and honey buzzards ($N = 61$) ringed in Sweden as nestlings and recovered in the same autumn or winter (before 1 March). For each recovery, the direction and length of the loxodrome (constant compass course) between the ringing and recovery site were calculated. Only recoveries more than 100 km (loxodrome distance) from the ringing sites were used. Mean directions and directional concentrations r were calculated based on individual directions. As estimates of the r-value of the parent population (ρ) can be seriously biased when sample size and observed r-values are small, sample size has to be taken into account when comparing observed directional concentrations. This was done by fitting a von Mises distribution to the observed data, i.e. by estimating the parameter of concentration κ, using equations in Fisher (1995; page 88), and finding the corresponding adjusted estimate of the directional concentration ($\hat{\rho}$) for the population.

Satellite telemetry

We used the migratory segments obtained from satellite tracking using the Argos system by Hake et al. (2001, 2003) and Kjellén et al. (2001). The primary data set consisted of juveniles of the two species. Adult ospreys were included for comparison, but not adult honey buzzards as their migratory route involves directional changes (Hake et al. 2003). A maximum of one position per 24 hours was used, and the positions were separated by a minimum of 100 km. Segments that were obviously directed along southern coastlines in west Africa were excluded (presumably after arrival to the wintering areas). The accuracy of positions used was either within one kilometre (high quality; categories 3, 2 and 1 in the Argos system) or of unspecified accuracy (low quality; categories 0, A and B in the Argos system). Of 227 positions used, 40% (91) were of high quality. For the satellite tracks of juvenile ospreys and honey buzzards, the proportion of high-quality positions were 58 and 59%, respectively (the proportion of high quality readings for each group are given in Table 4).

The potential effect of including low accuracy positions in the analysis was simulated for the cases of ospreys tracked continuously (with solar-powered transmitters) and ospreys tracked every third day (transmitters powered by conventional batteries). This was done by adding an extra variation to the directional data corresponding to an added standard deviation of 50 km in location accuracy (Britten et al. 1999, Fernandez et al. 2001, Hays et al. 2001) and finding the maximum likelihood solution for the observed directional concentration. This extra variation in location scatter affected the estimates of directional concentration to a negligible degree. The directional concentrations thus seem relatively robust with respect to position scatter.

However, as some cases (e.g. when considering variation between individuals) could be rather sensitive to positional scatter, the effect of excluding readings of category B was investigated, as these are often excluded entirely in other studies (Fernández et al. 2001).

Directional concentrations r and $\hat{\rho}$ were calculated as described for ring recoveries.

Modelling using vector summation

We used vector summation to model the migratory orientation system. Each migratory step is considered a vector with a fixed length and a direction picked randomly (and independently) from a circular distribution (Rabøl 1978, Mouritsen 1998, Sandberg and Holmquist 1998, Mouritsen and Mouritsen 2000, Thorup and Rabøl 2001). In the present study, the circular distribution used was the von Mises distribution, which is the distribution normally used in circular statistics (Batschelet 1981, Fisher 1995). The basic parameters in the model are (1) the directional concentration of the circular distribution used for picking directions for each individual step (directional concentration per step r_{step}), (2) the directional concentration of the between-individuals distribution ($r_{between}$) and (3) the step length. The mean of the directional distribution in the model is assumed to equal the mean migration direction.

The contribution of variation between individuals was introduced by adding a direction picked randomly from a chosen between-individuals distribution to the resulting sample mean vector after the number of migratory steps had been added (Thorup et al. 2000).

The proportion of misoriented individuals was calculated as follows: For a given distance from the starting point, the proportion of modelled paths falling outside a given ± deviation (corresponding to half the width of the destination range) from the mean direction was calculated by adding vectors until the length of the sumvector exceeded the given distance. This was repeated a large number of times (100000), and the proportion of sum-vectors falling outside the given deviation and thus outside the goal range, was calculated.

The modelled migratory tracks in many cases crossed wide stretches of water or desert. With a step length shorter than these stretches, the model assumes that the step length between independent variations in orientation are unaffected by these passages. This may not be correct and one may argue that sea crossings should be treated as single prolonged flight steps (probably not valid for the desert crossings, when the ospreys and honey buzzards travelled by daily flight steps as over other land areas, Hake et al. 2001, 2003) However, the possible bias of assuming a constant step length irrespective of long sea crossings will be conservative, giving less scatter in the resulting tracks than with prolonged step lengths over the sea.

Results

Ring recoveries

The recoveries of Swedish ospreys and honey buzzards ringed as nestlings and recovered in their first autumn/winter are shown in Fig. 1 and 2, respectively. The mean directions are 195° for ospreys and 196° for honey buzzards, and the majority of winter recoveries for both species were made in western Africa south of the Sahara.

Calculating the concentration of ring recoveries in different distance intervals give the results in Table 1. As the data set of the honey buzzards was much smaller, rather large intervals were used to allow a reasonable number of recoveries in each interval.

The concentration of short-distance recoveries for ospreys is about 0.4, 0.75 and 0.8 for distances of 250, 500 and 750 km, respectively (interpolated from 100 km intervals). After approximately 2000 km (south/central Europe) as well as after approximately 3000 km (south Europe/Mediterranean), the concentration is about 0.95 (Table 1). For honey buzzards, the concentration is about 0.8 after a distance of 500 km (Table 1). For the honey buzzard, the concentrations after approximately 2000 km (south/central Europe) and after approximately 3000 km (south Europe/Mediterranean) are similar; about 0.99 (Table 1). Simulating a von Mises distribution using the concentrations after approximately 2000 km, we expect 95% of the ospreys to be within a band of 2600 km after 2000 km and for the honey buzzards within 1200 km.

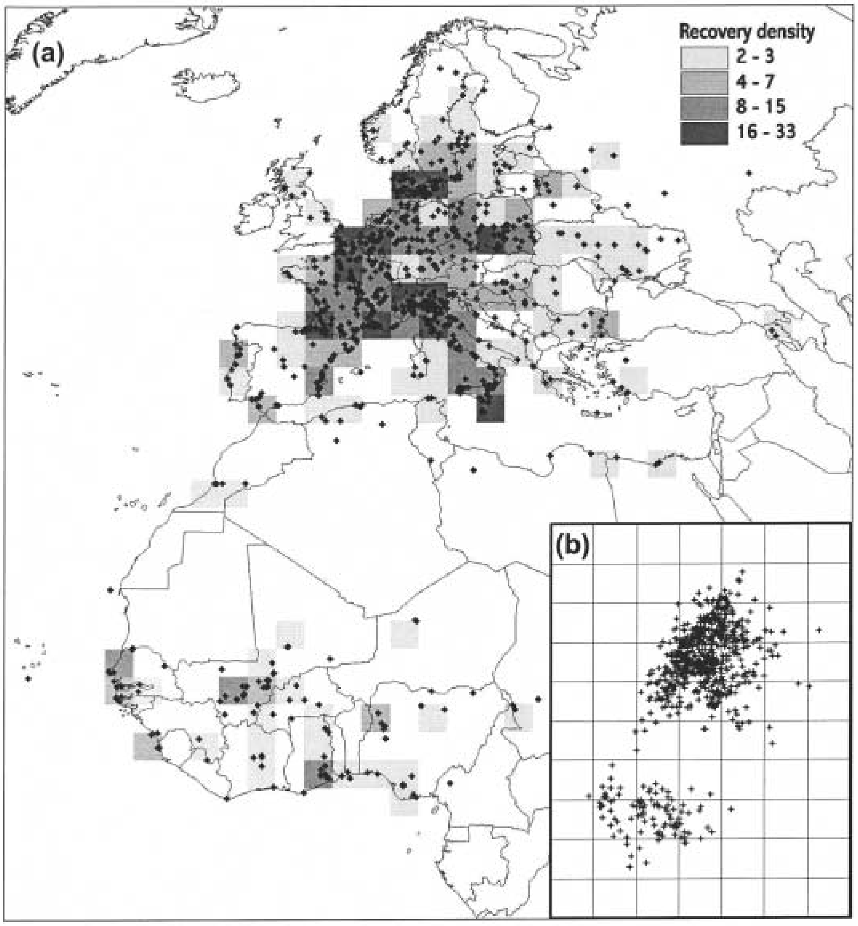

Fig. 1. Ring recoveries (+) of ospreys (N = 766) ringed as nestlings in Sweden and recovered in their first autumn/winter. (a) Equal-area projection. (b) Distance and direction (circle denotes point of origin; gridcells are 1000 km × 1000 km).

Table 1. Summary of the directional concentration r and corresponding $\hat{\rho}$ of ring recoveries of ospreys ($N = 766$) and honey buzzards ($N = 61$) ringed as nestlings and recovered in their first autumn/winter. All distributions differ from random. P-values denote the probability that the concentrations of ospreys and honey buzzards are the same according to the parametric test for the concentration parameter (Batschelet 1981). Recoveries for the intervals 100–750 and 750–1500 km have been lumped to increase sample size for honey buzzards.

Distance (km)	Osprey			Honey buzzard			Equal conc.
	N	r	$\hat{\rho}$	N	r	$\hat{\rho}$	P
100–750	107	0.636	0.630	8	0.886	0.817	}0.05
750–1500	195	0.874	0.871	8	0.957	0.934	
1500–2250	237	0.948	0.947	26	0.990	0.989	0.00
2250–3000	106	0.949	0.948	11	0.991	0.989	0.01
3000–5000	20	0.947	0.937	2			
5000–7000	101	0.992	0.991	6	0.995	0.991	0.92

The concentration of ring recoveries in the winter quarters in Africa (distance > 4500 km) is $r = 0.992$ for ospreys and $r = 0.995$ for honey buzzards with $\hat{\rho}$ of 0.991 for both species (Table 1). The distribution of directions of osprey recoveries in Africa could not be distinguished from a von Mises distribution ($P > 0.25$, Watson's U-test), but a wrapped Cauchy distribution (Batschelet 1981, Fisher 1995) is not a suitable model for these data ($P \ll 0.005$, Watson's U-test). Simulating a von Mises distribution using estimated concentrations results in estimates of the width of the wintering range enclosing 95% of the Swedish populations of 3200 km for both species.

The recoveries of ospreys and honey buzzards are not concentrated along the Atlantic Ocean (Fig. 1 and 2). Furthermore, the recoveries of ospreys in North Africa are rather evenly scattered, and do not show any clear tendency to become concentrated after the crossings of

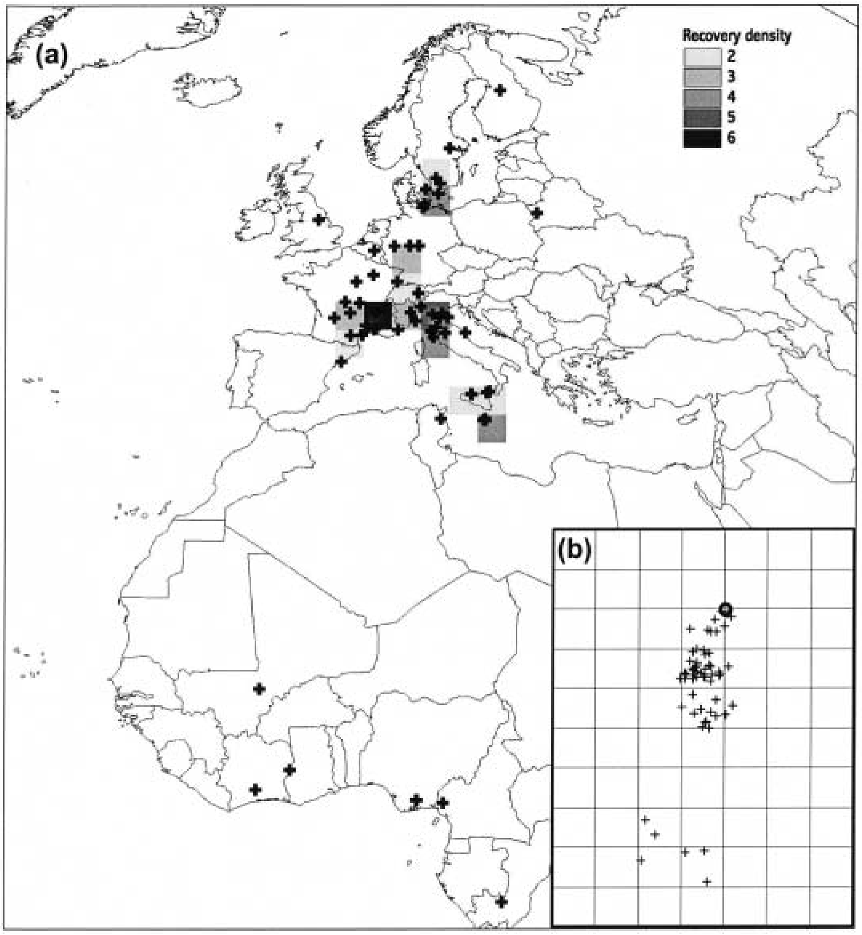

Fig. 2. Ring recoveries (+) of honey buzzards ($N = 61$) ringed as nestlings in Sweden and recovered in their first autumn/winter. (a) Equal-area projection. (b) Distance and direction (circle denotes point of origin; gridcells are 1000 km × 1000 km).

the Mediterranean Sea (Fig. 1). This indicates that the Mediterranean Sea does not exert any important funnelling effects of the ospreys towards the shortest sea crossings.

Vector summation model

The expected directional concentrations along the migration route using different initial values of the directional concentration per step (r_{step}) and step length are given in Table 2.

Only a few of the combinations r_{step}/step length fit the observed ring recovery data reasonably well, as indicated in Table 2. If we use the concentration after 2000 km as a fix point for ospreys, then r_{step} values of 0.5, 0.7 and 0.8 for step lengths of 250, 500 and 750 km, respectively, result in the same concentrations as the ring recoveries (0.95). These combinations of r_{step}/step length equal the values observed for the short distance recoveries of ospreys (< 1000 km). For recoveries in the wintering area, r_{step} values of 0.7, 0.9 and 0.93 with step lengths of 250, 500 and 750 km, respectively, result in the expected concentration of 0.991. The concentrations of ring recoveries after 2000 (0.95) and 6000 km (0.991) are highly unlikely to result from the same directional concentration per step, as the confidence intervals of the corresponding r_{step} values do not overlap ($P < 0.01$, step length = 250, 500 or 750).

For honey buzzards, the combinations r_{step}/step length of 0.90/250 km, 0.95/500 km and 0.95/750 km fit the observed concentrations of ring recoveries rather close (Table 2). The small difference between estimated ($\hat{\rho}$) and modelled concentrations after 6000 km is likely to be caused by the small number of recoveries of honey buzzards in the winter quarters.

The geographic widths of the 95% bands in the winter quarters (including 95% of the simulated tracks at a distance of 6000 km), resulting from simulations using different combinations of directional concentration per step (r_{step}) and step length, are given in Table 3.

The combinations of r_{step}/step length which agree with the observed concentration of ring recoveries at 2000 km (Table 2) can be used for estimating the width (95%) of the winter range at a distance of 6000 km

Table 2. Vector summation simulation using von Mises distributions. Best agreements with estimated concentrations ($\hat{\rho}$) from ring recovery data (Table 1) at the selected distances 2000 and 6000 km, respectively, are indicated by O for ospreys and H for honey buzzards.

		Concentration at distance	
Step length (km)	r_{step}	2000 km	6000 km
250	0.4	0.929	0.976
	0.5	0.948 O	0.982
	0.6	0.959	0.986
	0.7	0.970	0.990 OH
	0.8	0.979	0.993
	0.9	0.989 H	0.996
	0.95	0.994	0.998
500	0.4	0.855	0.952
	0.5	0.895	0.965
	0.6	0.922	0.973
	0.7	0.942 O	0.980
	0.8	0.960	0.986
	0.9	0.980	0.992 OH
	0.95	0.990 H	0.996
750	0.4	0.805	0.929
	0.5	0.864	0.948
	0.6	0.898	0.960
	0.7	0.925	0.970
	0.8	0.949 O	0.979
	0.9	0.974	0.989 OH
	0.95	0.987 H	0.994
Osprey, $\hat{\rho}$ (ring rec.)		0.95 O	0.991 O
honey buzzard, $\hat{\rho}$ (ring rec.)		0.99 H	0.991 H

Table 3. Simulated width (km) of 95% band at 6000 km.

Step length (km)	$r_{step} = 0.40$	0.50	0.60	0.70	0.80	0.90	0.95
250	5200	4400	4000	3400	2800	2000	1500
500	7400	6400	5600	4800	4000	3000	2100
750	9000	8000	7000	6000	5000	3600	2500

Table 4. Directional concentration $r_{segment}$ and corresponding $\hat{\rho}$ and average distance (km) travelled per segment, number of individuals (indiv.) and number of segments (N) available from satellite tracking. The proportion of high quality positions (1, 2, 3) used is also given. (−B) indicates that category B positions were not included. (3rd) indicates individuals tracked every third day and (1) individuals tracked continuously. Significance of $r_{segment}$ is given according to the Rayleigh test (*: $P<0.05$; ***: $P<0.001$).

	age		Indiv.	N	$r_{segment}$	$\hat{\rho}$	Aver. dist.	Qual. prop.
Osprey	juv.	First steps > 500 km (3rd)	5	5	0.773*	0.532	714	0.80
		Full tracks (3rd)	2	15	0.915***	0.893	836	0.58
			2	11	0.921***	0.892	1118	(−B)
	ad.	First steps > 500 km (3rd)	11	11	0.862***	0.805	891	0.50
		Full tracks (3rd)	6	44	0.914***	0.907	912	0.28
			6	40	0.913***	0.905	1004	(−B)
		Full tracks (1)	5	94	0.821***	0.813	359	0.36
			5	81	0.848***	0.840	409	(−B)
Honey buzzard	juv.	Full tracks (3rd)	3	38	0.899***	0.890	482	0.59
			3	27	0.936***	0.928	648	(−B)

according to the principle of vector summation. Such calculations give estimates of 4400–5000 km for the osprey, as seen from Table 3. The observed width (95%) of the winter range as reflected by the concentration of osprey recoveries at 6000 km is, however, smaller than this; 3000–3400 km (Table 3; for the combinations of r_{step}/step length which agree with the observed concentration at 6000 km see Table 2).

In contrast, the distribution of ring recoveries for the honey buzzard conforms better to the predicted pattern according to orientation by vector summation since the data at 2000 and 6000 km can be reconciled rather well with a common set of r_{step}/step length throughout the journey (Table 2). Relying on the larger sample size after 2000 km results in a winter range width (95%) of about 2000 km.

Satellite tracking

A summary of the data from the satellite tracking is given in Table 4. The distribution of initial directions for juvenile ospreys having migrated more than 500 km (first step) showed a rather large scatter ($r = 0.773$, $\hat{\rho} = 0.5$), but still differed significantly from random. The two juveniles that were tracked all the way to the winter quarters showed a mean combination $\hat{\rho}_{segment}$/segment length of 0.89/836 km (Table 4). Probably due to the low number of segments, there was an overlap in the 95% confidence intervals for the concentration of simulated tracks, using the combination 0.89/836 km from complete trackings of juvenile ospreys, and for the combinations inferred from medium distance (2000 km) ring recoveries (0.80/750 km) or long distance (6000 km) recoveries (0.90/750 km).

For juvenile honey buzzards there was no difference between the combinations found for satellite tracking (0.89/482 km) and that inferred from medium distance ring recoveries (0.95/500 km, Table 2).

With the combination found for satellite tracking, 95% of the ospreys are expected to be within a 2200 km wide band ($r = 0.963$) after migrating 2000 km and within 3900 km ($r = 0.986$) in the winter quarter (at 6000 km). For honey buzzards, the corresponding figures are 1700 km ($r = 0.977$) and 3100 km ($r = 0.992$) for 2000 and 6000 km, respectively. However, the differences between the concentrations of ospreys and honey buzzards were not significant (95% confidence intervals overlap), though segment lengths of juvenile ospreys were significantly longer than for honey buzzards.

When considering only segments not influenced by ospreys following the coast of west Africa, there was no difference in concentration of directional choices between adult and juvenile ospreys – the directional concentration of juveniles being $\hat{\rho} = 0.89$ ($r = 0.915$) and that of adults $\hat{\rho} = 0.91$ ($r = 0.914$) (Table 4). Furthermore, no differences were found in segment lengths between adults and juveniles ($P = 0.42$; two-tailed t-test). Satellite tracks of adult ospreys showed a rather large scatter of initial directions ($r = 0.862$, $\hat{\rho} = 0.81$) compared to tracks all the way to the winter quartes ($r = 0.914$, $\hat{\rho} = 0.91$), similar to the tendency found in juveniles.

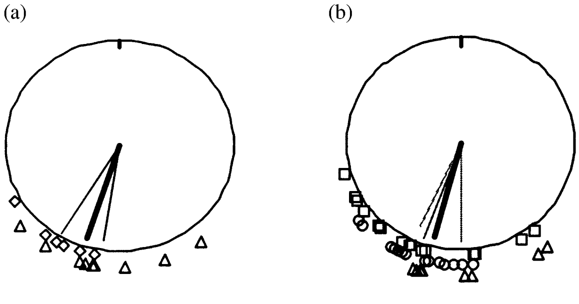

Fig. 3. Directions of different migratory segments, as recorded by satellite tracking of (a) the two juvenile ospreys and (b) the three juvenile honey buzzards completing their migration to the wintering area. Different symbols indicate different individuals. Thin lines indicate the mean vectors of different individuals. Thick lines are sample mean vectors.

The satellite telemetry data indicate that variation between individuals may be present (Fig. 3). The probability that all individual directional choices of the two ospreys had the same direction is $P = 0.22$ ($F_{1,13} = 1.7$, $N = 15$; Watson-Williams test, Batschelet 1981) and for the three honey buzzards $P = 0.09$ ($F_{2,35} = 2.6$, $N = 38$). However, low quality position readings could influence the individual variation, and if position readings of category B are excluded, the probability for the honey buzzards becomes significant ($P = 0.04$, $F_{2,24} = 3.6$, $N = 27$). Furthermore, the directional concentrations of segments do not differ significantly between ospreys and honey buzzards, and adding together the two directional distributions centred to their respective means result in $P < 0.05$ ($F_{4,33} = 2.7$, $N = 38$) for the combined sample with category B position readings excluded.

If we assume that variation in mean direction between individuals do occur, the maximum likelihood estimate of this variation in the satellite tracking is $r_{between} = 0.97$ for ospreys and $r_{between} = 0.98$ for honey buzzards. The satellite tracking data (Table 4) then contains both within- and between-individuals variation. Thus, taking into account a variation between individuals of approximately 0.98 and calculating r_{within} ($= r_{step}$) gives as a result r_{step}/step length of 0.93/836 km for ospreys (combination $r_{between}/r_{step}$ used in Table 5 – scenario 4) and 0.93/482 km for honey buzzards.

Discussion

Distribution of ring recoveries in relation to vector summation

The observed concentrations of the ring recoveries of ospreys show a larger scatter in orientation within the first 2000 km than at longer distances. This could not be described well by a model of simple vector summation. The difference in scatter may be caused by (1) an initial phase of pre-migration dispersal, (2) more wind-caused scatter in north and central Europe, (3) the effect of losses of misoriented birds or (4) coastal leading-line responses in west Africa. However, leading-line responses were not apparent in the ring recoveries.

For honey buzzards the ringing data generally showed a reasonable fit to a model of simple vector summation.

Comparison with orientation performance according to satellite tracking

The satellite tracking of both juvenile and adult ospreys show a large scatter of the initial orientation, indicating a phase of pre-migration dispersal which is, however, not random. Long-distance satellite tracks indicate orientation performance at the same level as long-distance ring recoveries, i.e. with less variation than for short/medium-distance ring recoveries. These results strongly indicate that pre-migration dispersal constitutes the most important explanation for the large scatter of osprey recoveries made in Europe in autumn. Furthermore, the satellite tracks of juvenile ospreys and honey buzzards generally did not seem to follow the Atlantic Ocean before arrival in the wintering area (Hake et al. 2001, 2003) making coastal leading-line responses less likely as explanation.

For honey buzzards, satellite telemetry data agree well with ring recovery data (and thus a model of constant vector summation), although the scatter of the segments was somewhat larger than the model values fitting ring recovery data.

The difference between ospreys and honey buzzards

The scatter of ring recoveries differ markedly between the two species, with osprey showing the more scattered pattern, especially at medium distances. This could be due to a lower precision of orientation in ospreys than in honey buzzards. However, satellite tracking data indicate that a more likely explanation is that ospreys, but not honey buzzards, show an important element of pre-migration dispersal.

It is not clear why such a dispersal should occur in ospreys but not in honey buzzards. It could be related to the more restricted habitat for ospreys, and that ospreys need to disperse away to avoid competition. The population of ospreys in Sweden is dense

Table 5. Simulations of the proportion of ospreys misorienting according to different scenarios (see text), using 3000 km goal width at 6000 km.

		% Misorienting
(1)	Simulation by extrapolating the r_{step}/step length of 0.8/750 km (2000 km) as variation within individuals to 6000 km	23
(2)	Starting with observed scatter (ring recoveries) after 2000 km and adding simulation using within-individuals variation of 0.915/750 km	10
(3)	Extrapolation of $r = 0.95$ (2000 km) as variation between individuals	43
(4)	Starting with observed scatter (ring recoveries) after 2000 km and adding simulation using between-individuals ($r_{between} = 0.98$) and within-individuals (0.93/750 km) variation	21

(Svensson et al. 1999) and most pairs breed in areas with oligotrophic lakes. Satellite tracked adult ospreys made post-breeding/pre-migration movements to staging areas different from the breeding area where they prepared for migration (Hake et al. 2001). Most likely they were familiar with these areas that were probably found during post-fledging dispersal (Hake et al. 2001). Similar to the dispersal pattern in ospreys, grey herons (*Ardea cinerea*) were found to disperse in a non-random direction away from colonies before migration, whereas common buzzards (*Buteo buteo*) showed much less dispersal (Olsson 1958). However, the occurrence of such dispersal in adult non-colonial birds is still surprising unless suitable staging areas do not commonly contain suitable breeding sites.

Consequences of different orientation principles for rates of misorientation

Table 5 gives the expected proportion of misoriented birds (that is birds orienting outside the width of their winter range) associated with different scenarios for the osprey. Simulating the migration of ospreys using a combination of r_{step} and step length indicated by ring recoveries in Europe, gives a very high proportion (23%) of misoriented individuals (Table 5 – scenario 1).

Assuming the observed concentration at 2000 km to be partly caused by pre-migration dispersal and extrapolating from there using a combination of r_{step}/step length according to satellite data, results in a more reasonable modelled rate of misorientation of 10% (Table 5 – scenario 2). A close fit to data (at distances greater than 1000 km only) can also be achieved by adding an initial random dispersal step ($r_{first\ step} = 0$) of 750 km and then using a combination r_{step}/step length of 0.95/750 km. However, the rather low number of short-distance recoveries do not indicate that the initial phase of dispersal is fully random. Furthermore, the satellite telemetry data show that the sample of initial directions of ospreys, though showing a rather low concentration, differs from random (Table 4).

So far we have assumed that there is no variation between individuals. Assuming that all variation observed for short-distance ring recoveries (< 2000 km) reflects variation between individuals, the rate of misorientation becomes very high (Table 5 – scenario 3) for both ospreys and honey buzzards. Hence, we can be sure that variation between individuals cannot account for a very large part of the total directional variation observed. Still, it could be important, and the satellite results indicate possible levels of $r_{between}$ of 0.97 and 0.98 for the ospreys and honey buzzards, respectively. Furthermore, as these estimates are based on full trackings from a single year they are likely to underestimate the true amount of variation between individuals caused by the possible loss of misoriented individuals and by variation in wind regimes between years. Variation between individuals is also indicated in data on British ospreys followed by satellite telemetry (Anglian Water Osprey Project 2002), where the directional concentration of long and rather straight segments (unaffected by the sea) of different individuals correspond approximately to a von Mises distribution with a directional concentration of 0.98. Combining an initial phase of pre-migration dispersal according to the ring recoveries (up to 2000 km: $r = 0.95$) with between-individuals variation of 0.98 for the later part of the migration, in addition to r_{step}/step length of 0.93/750 km for the within-individuals variation (cf. satellite data in Table 4), gives a proportion of misoriented birds of 21% (Table 5 – scenario 4).

Satellite tracking data on Swedish ospreys and honey buzzards as well as British juvenile ospreys (Anglian Water Osprey Project 2002) indicate a lower mortality due to misorientation than the values associated with simple compass orientation according to the scenarios assumed for the calculations in Table 5.

Conclusion

For honey buzzards, the model of simple vector summation is in close agreement with migration patterns of the species revealed by ring recoveries and satellite tracking. For ospreys, the simple model of constant vector summation must be extended to include an initial phase with less concentrated orientation in order to provide a reasonable fit to observed patterns. However, it may still be premature to accept the model of simple vector summation because of the high sensitivity to the amount of variation between individuals ($r_{between}$). It is therefore important to investigate this point further by satellite tracking, allowing the separation of the crucial within- and between-individuals variation in long-distance bird orientation.

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