A LONG TERM STUDY ON INITIAL ORIENTATION IN SAND MARTINS (RIPARIA RIPARIA)

by

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Summary

Over a period of 18 years sand martins (*Riparia riparia*) were displaced from their breeding colonies and released to investigate the relationship between distance of displacement and initial orientation. The results show significant homeward orientation at the shortest distances of displacement (7.1-18.2 km, series A), but not over longer distances (49-180 km, series B and C). Birds displaced over 49 km from their breeding colonies only seldom show homeward directedness, while pseudo-pooling and second order analysis of their directional choices seem to indicate the tendency to fly in a given compass direction. Possible causal factors that can induce this behaviour in sand martins are discussed, taking into account not only local biasing factors but also the existence of a so called preferred compass direction. These data show that sand martins are able to determine the correct homing direction inside a probably familiar area. The response over longer distances indicates difficulties in determining the appropriate homing course at takeoff.

Introduction

The sand martin is an holoarctic long distance migrant whose homing performances have been tested by several authors, especially in its nearctic range (see Baldaccini *et al.*, 1986a; Beason *et al.*, 1994). This species has been used due to several factors, *e.g.* colonial breeding, site faithfulness

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and local abundance, that make the experimental work less problematic. Indeed, the study of the homing abilities of free living birds involves a lot of difficulties (Schmidt-Koenig, 1979; Able, 1980), and even though experiments have been carried out since the first half of this century (for references see Matthews, 1968; Schmidt-Koenig, 1979; Papi & Wallraff, 1992), many of them only report homing success, not initial orientation, and the number of birds involved is often very small. For this reason only rarely have researchers obtained sufficient information to characterise the homing behaviour of a particular species or understand its causal factors (see Wiltschko, 1992 for a review). The recent development of recording techniques based on satellite tracking and route recorders has certainly allowed a notable improvement in the quality of collected data (Jouventin & Weimerskirch, 1990; Nowak & Berthold, 1991; Dall'Antonia *et al.*, 1995; Benvenuti *et al.*, 1998), but for the moment the results pertain only to a few species and again to a limited number of individuals. Actually systematic studies are still lacking, although they are essential to thoroughly analyse the effect of variables, like experience (Graue, 1965; Wallraff, 1967, 1974a; Alexander & Keeton, 1972; Wiltschko, 1991), or general environmental conditions (see references in Foà *et al.*, 1984; Dornfeldt, 1991, 1996) on the homing behaviour of birds. Also the understanding of some phenomena associated with the initial orientation, such as 'release site biases' (Keeton, 1973; Grüter *et al.*, 1982; Wiltschko, 1993) or 'nonsense orientation' or 'PCD' (Matthews, 1968, 1984; Wallraff, 1970, 1974b, 1978, 1986), requires long term research programmes, which involve accurate planning of balanced releases (Wallraff, 1974b) and experimental subjects with different breeding sites in a given geographical region. All these conditions are rarely satisfied by the studies carried out so far on free living animals. It is therefore very important to supply further data useful for the interpretation of the above mentioned phenomena.

It is in this context that we present our results on a species whose initial orientation seems to depend on the distance of displacement (Sargent, 1962; Baldaccini *et al.*, 1986a), showing directional preferences uncorrelated with home direction when released from sites farther away from the colony (Baldaccini *et al.*, 1986a, b). The aim of the present work is to provide an enlarged set of data about the connection between initial orientation and distance of displacement in order to have a further look inside the orientational capabilities of sand martins.

Methods

Birds

Sand martins arrive at their breeding colonies usually in April. In our tests only birds incubating or in the parental stage of the breeding cycle were used. Birds were trapped with mist-nets erected in front of the nest entrances or with Morris traps (Morris, 1941). The birds were caught during the last part of the night or, at most, around or just after dawn, when presumably most individuals had not yet left their nest-holes. Immediately after capture the sand martins were ringed, weighed and measured according to Svensson (1984). In each test, sand martins coming from the same colony site and experiencing their first experimental release were used.

Experimental series

Series A consists of 25 test releases carried out in different years (1983-1998) with birds captured in several colonies located along the banks of Taro River, near Parma (northern Italy). Single colonies changed location over the years according with the changing morphology of the river banks. The farthest colonies were about 18 km apart. The release sites (Fig. 1) were chosen in roughly symmetrical directions with respect to the home colonies at distances which ranged between 7.1 and 18.2 km.

Series B consists of 25 test releases performed in eight years, from 1981 to 1990, with birds captured in the same area as series A. Due to the geomorphology of the region, the
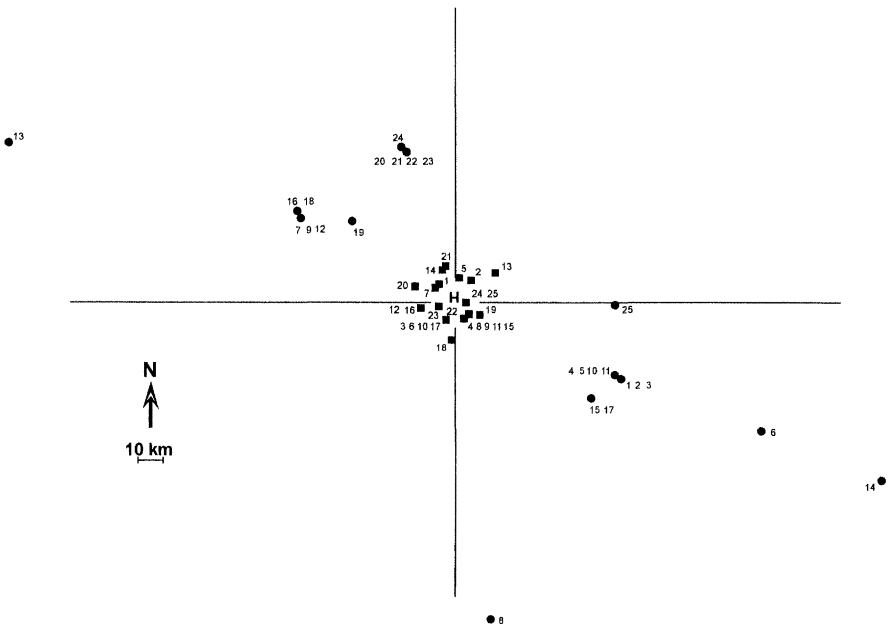

Fig. 1.   Location of release sites in series A (squares) and B (dots) with respect to the home colony (H). Numbers correspond to those indicated in the column 'Test' of Tables 1 and 3.

release sites (Fig. 1) were chosen in two opposite quadrants at distances which varied between 49 and 180 km.

Series C consists of four test releases performed in two years (1983 and 1985) with birds captured in a colony along the Ronco River, near Forlì (northern Italy), as far as about 180 km eastward of the colonies from series A and B. The release sites were chosen in two almost opposite directions at distances which varied between 66 and 102 km.

Release methods

The birds were singly placed in cloth-bags and as soon as possible displaced by car to a given release site. Here they were singly tossed in random directions during the same morning or the early afternoon of the day of capture. Each bird was followed up to vanishing with 10×40 binoculars from a vantage point (top of a van). Birds vanishing from sight too early, disappearing behind vegetation or flying low over the ground, were not included in statistical calculations. Releases took place only on sunny days and with no or only moderate wind (less than 5 m/s).

Statistical methods

Mean vector length and direction were calculated from vanishing bearings of each release and the standard circular statistical evaluations were performed (Batschelet, 1981). The proportions of oriented ($p < 0.05$, Rayleigh test) *versus* non-oriented distributions in tests of series A and B and the proportions of oriented test of the same two series in which the home direction falls within or outside the 99% confidence interval of the mean direction were compared using the G-test with Williams's correction (Sokal & Rohlf, 1995). The directional preferences of the animals of a given series were calculated by means of two different procedures: (1) pseudo-pooling of all tests of the series, whose use is advised when the number of samples pooled is relatively small and their sizes are different (Wallraff, 1979); (2) true second order analysis, which requires a relatively large number of samples of roughly the same size (Batschelet, 1981). For series A and B both procedures were used, since the number of tests that were pooled was relatively high, but sample sizes were different; the releases of series C were only pseudo-pooled, due to their low number. All these procedures were calculated by setting the North or home direction to $0°$. The results of (1) were statistically evaluated using the Rayleigh test and calculating the 99% confidence intervals of the mean direction. The hypothesis of randomness was tested in (2) by means of the Hotelling's one-sample test (Batschelet, 1981). From the individual bearings of the releases of the first two series we have calculated the angular distances (see Batschelet, 1981) from the home direction (D_h) and from the mean direction of the pseudo-pooled distributions with North direction sets to $0°$ of the respective series (D_m). The D_h are a measure of the degree of homeward orientation of a series, while the D_m are a measure of the degree of concentration of directional choices with respect to the North direction (see Wallraff, 1979 for a detailed explanation). The D_h and D_m of series A and B were compared by means of the modified t-test (Wallraff, 1979). The second order distributions of series A and B were compared using the Hotelling's two-sample test (Batschelet, 1981). To test if the directional preferences of the B and C series with respect to the North were different, we calculated the approximate 95% confidence interval of the difference of the two mean directions of pseudo-pooled distributions (Mardia, 1972, p. 156), using the 'reduced sample sizes' (Wallraff, 1979). If this interval did not include the $0°$, then the mean directions were considered statistically different (Mardia, 1972).

Results

Series A

Table 1 reports the results obtained in the 25 tests of the A series. According to the Rayleigh test 15 trials are significantly oriented. In ten tests the home direction falls within the 99% confidence interval of the mean direction. Table 2 and Fig. 2 report the results of pseudo-pooling. When data are referred to the home direction set to 0°, the resulting distribution is highly significantly oriented and this result is confirmed by the Hotelling's one-

TABLE 1. *Initial orientation data in A series*

Test	Distance (km)	Home direction	N	α	r	CI
1	8.2	135°	26 (23)	178°	0.39*	out
2	9.7	220°	19 (18)	198°	0.63***	in
3	7.8	19°	17 (16)	332°	0.90***	out
4	8.1	315°	40 (34)	280°	0.42**	in
5	9.5	184°	30 (23)	172°	0.87***	in
6	7.8	19°	27 (22)	333°	0.83***	in
7	8.9	128°	28 (22)	134°	0.42*	in
8	8.1	315°	30 (17)	143°	0.17	
9	8.1	315°	26 (19)	249°	0.17	
10	7.8	19°	19 (17)	303°	0.24	
11	8.1	315°	19 (17)	340°	0.15	
12	12.5	78°	14 (11)	109°	0.82***	in
13	18.2	235°	12 (11)	245°	0.42	
14	13.2	160°	11 (9)	129°	0.48	
15	8.1	315°	14 (12)	307°	0.46	
16	12.5	78°	14 (12)	109°	0.90***	out
17	7.8	19°	15 (14)	318°	0.86***	out
18	14.4	2°	17 (14)	326°	0.22	
19	10.8	301°	17 (6)	186°	0.44	
20	15.3	110°	16 (12)	119°	0.59***	in
21	14.8	163°	17 (9)	173°	0.80***	in
22	7.1	327°	18 (11)	264°	0.63***	out
23	6.3	75°	14 (9)	95°	0.83***	in
24	4.2	273°	14 (10)	251°	0.48	
25	4.2	273°	14 (10)	258°	0.81***	in

N = number of birds released (number of bearings evaluated); α, r = direction and length of mean vector; CI = 99% confidence interval of the mean direction (in = home direction falls within the confidence interval). Probability according to the Rayleigh test (r column) are given as asterisks: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; no symbol = $p > 0.05$.

TABLE 2. *Pseudo-pooled data*

Series	N_{tot}	N_b	N_{red}	αN	rN	αH	rH	CI
A	488	378	150	207°	0.11	344°	0.44***	in
B	464	331	150	233°	0.32***	0°	0.07	
C	86	46	36	128°	0.58***	58°	0.28	

N_{tot} = total number of released animals; N_b = number of pooled bearings; N_{red} = reduced sample size; αN, rN = direction and length of mean vector of pseudo-pooled distributions with North direction sets to 0°; αH, rH = direction and length of mean vector of pseudo-pooled distributions with home direction sets to 0°. Other explanations as in Table 1.
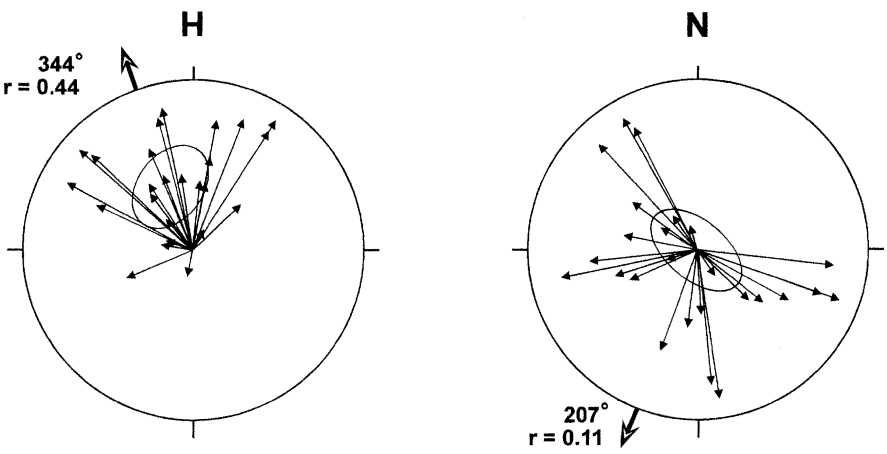

Fig. 2.   Mean vector distribution of releases of series A with home direction (left side) or North direction (right side) set to 0°. Ellipses are Hotelling's 99% confidence ellipses. Length (r) and mean direction (arrows outside the circle) of second-order mean vectors are also reported.

sample test ($T^2 = 65.9$; $p < 0.001$); the home direction falls within the 99% confidence intervals of mean direction. When the same is done with respect to the North, a random distribution is obtained.

Series B

Table 3 reports the results obtained in the 25 tests of the B series, 19 of which are significantly oriented according to the Rayleigh test. In six tests, four of which located westward of the colony, the home direction falls within the 99% confidence interval of the mean direction. Table 2 reports

TABLE 3. *Initial orientation data in B series*

Test	Distance (km)	Home direction	N	α	r	CI
1	70	295°	18 (14)	236°	0.79***	out
2	70	295°	6 (6)	253°	0.76*	out
3	70	295°	16 (13)	220°	0.67***	out
4	67	295°	28 (22)	260°	0.60***	in
5	67	295°	13 (9)	267°	0.55	
6	126	293°	24 (14)	276°	0.80***	in
7	67	119°	24 (18)	241°	0.80***	out
8	119	357°	18 (11)	281°	0.56*	out
9	67	119°	27 (15)	131°	0.84***	in
10	67	295°	16 (11)	124°	0.91***	out
11	67	295°	19 (14)	149°	0.92***	out
12	67	119°	13 (10)	143°	0.86***	in
13	180	109°	26 (18)	294°	0.17	
14	176	293°	24 (15)	268°	0.74***	in
15	63.5	305°	18 (13)	82°	0.49*	out
16	68.5	120°	19 (12)	197°	0.84***	out
17	63.5	305°	20 (9)	158°	0.66*	out
18	68.5	120°	20 (15)	55°	0.19	
19	49	129°	22 (18)	236°	0.62***	out
20	60.5	162°	18 (15)	284°	0.49*	out
21	60.5	162°	13 (10)	286°	0.52	
22	60.5	162°	12 (10)	283°	0.35	
23	60.5	162°	12 (9)	269°	0.22	
24	61	162°	18 (15)	304°	0.65***	out
25	61	271°	20 (15)	272°	0.91***	in

Explanations as in Table 1.

the results of pseudo-pooled distributions with home or North direction set to 0°. The former distribution is not different from random, while the latter is significantly oriented, with the mean vector pointing toward SW. The Hotelling's one-sample test (Fig. 3) confirms the significant tendency to fly towards SW ($T^2 = 27.5$; $p < 0.001$), while it does not offer any significant result with respect to home.

The ratio of tests with a significantly oriented distribution of bearings according to the Rayleigh test is not different in the A and B series ($G_1 = 1.5$, $p > 0.05$), while the proportion of significantly oriented tests in which the home direction falls within or outside the 99% confidence interval of the mean direction is different ($G_1 = 4.0$, $p < 0.05$). The D_h and the
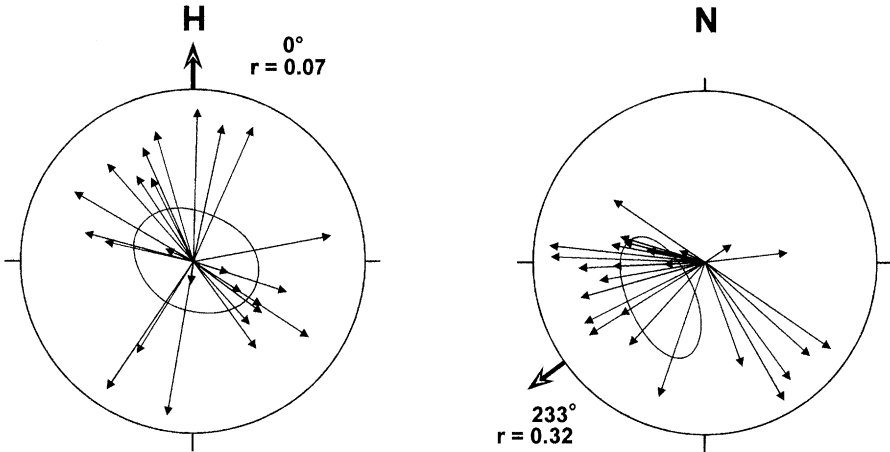
Fig. 3.   Mean vector distribution of releases of series B. Explanations as in Fig. 2.

D_m of the two series are both significantly different ($t_{298} = 5.1$, $p < 0.001$ and $t_{298} = 3.4$, $p < 0.001$ respectively, modified t-test), confirming the better homeward orientation of the birds in the A series and the greater homogeneity of directional choices with respect to the North direction in the B series. Also the second order distributions with respect to the home and North directions were highly significantly different ($T^2 = 161.0$, $p < 0.001$ and $T^2 = 107.0$, $p < 0.001$ respectively, Hotelling's two-sample test), confirming the results obtained from the first order analysis.

Series C

Table 4 reports the results obtained in the four tests of the C series. All trials are significantly oriented according to the Rayleigh test, while in two of them the home direction falls within the 99% confidence interval of the mean direction. The pseudo-pooled distribution with respect to the North direction shows a significant tendency of birds of this series to fly toward SE (Table 2), while the pseudo-pooled bearings with respect to home are randomly distributed.

The flying preferences of the birds of the B and C series are not homogeneous. Indeed, the angular difference between the mean directions of pseudo-pooled distribution with North direction sets to 0° of these two series is 105°. The approximate 95% confidence interval of these difference is 68-142°. Since 0° is not included in this interval, we can conclude that these two mean directions are significantly different.

TABLE 4. *Initial orientation data in C series*

Test	Distance (km)	Home direction	N	α	r	CI
1	66	185°	34 (14)	181°	0.88***	in
2	85	301°	20 (11)	66°	0.62*	out
3	85	301°	18 (12)	103°	0.74***	out
4	102	119°	14 (9)	139°	0.84***	in

Explanations as in Table 1.

Discussion

The results reported here seem to demonstrate that the initial orientation of displaced sand martins is clearly influenced by distance from the home colony, as previously suggested by Sargent (1962) and Baldaccini *et al.* (1986a). Over short distances the pseudo-pooling of individual tests and their second order analysis reveal a home related orientation that fails to emerge over longer distances. Releases of series A and B also show that distance does not influence the degree of concentration of departure bearings: the number of significantly oriented releases using the Rayleigh test is indeed not different in these two series. Some observations (Turner & Rose, 1989), together with radio-tracking data on the home range of sand martins (Alves & Johnstone, 1994), indicate that the area in which these birds show home related orientation is familiar to them.

At the farthest distances tested these birds show a noticeable polarisation of departure bearings, as previously noted by Baldaccini *et al.* (1986a). It is interesting to note that the directional preference apparently varies on a regional basis, as indicated by the difference in the mean direction of the pseudo-pooled distributions of series B and C. However this conclusion should be considered with caution due to the low number of tests involved in series C. In describing this directional preference we may refer to so called 'nonsense orientation' (Matthews, 1968, 1984) or, according to Wallraff (1978, 1986), to 'preferred compass direction' (PCD). Some authors describe such behaviour as common when wild birds are released far from their breeding sites (Matthews, 1984), and it is also evident in homing pigeons (Wallraff, 1978, 1986; Ioalè, 1995). However, the existence of PCDs is still questioned because other authors deny the presence of such directional tendencies (Wiltschko & Wiltschko, 1985a, b; Wiltschko, 1993), preferring the concept of 'release site bias' originally introduced by Keeton (1973).

The behavioural pattern observed in our data is characterised by a high degree of variability, the reasons for which could be of multiple origin, as for instance an influence of landscape features. However the release sites used were quite homogeneous open areas distant from watercourses, that can influence the directional choices at takeoff in this species (Downhover & Windsor, 1971; Baldaccini *et al.*, 1989). Wind can also influence the initial orientation of sand martins, as stated by Sargent (1962). Our experience in releasing these birds generally confirms this observation. However, our releases took place only in moderate or no wind (see Methods) and our study area is not characterised by a constant wind pattern, that could influence the directional preferences that emerge over a long time period. Indeed the long time period over which this study took place could have influenced the variability observed, suggesting temporal variation in the behaviour of this species, as indicated by Wallraff (1986) for pigeons.

All the variables considered do not seem to explain sufficiently the observed directional preferences at longer distances. This indicates the presence of causal factors that are relatively homogeneous over quite a wide area and relatively constant in time. The reasons that prompt the animal to prefer relatively constant directions are, however, unclear. In the homing pigeons the PCD has been identified as a home-independent component of initial orientation, which has little or nothing to do with the homing process (Wallraff, 1986, 1991). The PCD would seem to be determined more by the urgency to get away from a site than by the tendency to reach a goal. It could have a fleeing significance, aiding flock cohesion, as already suggested by Matthews (1962) and by Thake (1981).

Apart from the origin of the directional preferences, the present results seem to demonstrate that sand martins have real difficulties in determine the appropriate homing course when displaced far from their colony; as indicated in Baldaccini *et al.* (1986b) from long distances the homing success can also drop off substantially. This finding contrasts with the high degree of site-fidelity observed over several years in this transequatorial migrant (Mead, 1979). It is important to consider, however, whether some physiological constraint, perhaps linked to the body size or diet of sand martins, could affect their motivation to reach a particular goal. Such factors could complicate the interpretation of the homing behaviour of this species, particularly after a long displacement. In this sense it could be difficult and possibly misleading to directly compare the behaviour of sand martins with that of the homing pigeons.

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