The influence of transport conditions on the initial orientation of sand martins (*Riparia riparia*)

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The initial orientation of breeding sand martins (*Riparia riparia*) released at short distances (4.2-12.3 km) from their home colony was significantly affected by treatments that apparently did not interfere with their homing process (transport to the release site in total darkness and/or inside transparent bags). Compared to the behaviour of birds transported in daylight inside semitransparent bags, both treatments worsened the degree of homeward orientation and increased the sand martins' tendency to fly in the preferred compass direction. These results supported previous findings collected on homing pigeons and indicated that emotional components could also play a role in determining the initial orientation in free-living birds. Considering the widespread occurrence of home-independent orientation in the few wild species whose homing behaviour has been rather intensively studied, these data suggested that stress-induced phenomena are a serious obstacle to a proper comparative analysis of the homing mechanism of birds.

KEY WORDS: home-independent orientation, homing, initial orientation, PCD, *Riparia riparia*, sand martin, stress.

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INTRODUCTION

The most recent evidence on the homing mechanisms of avian species leads one to consider the initial orientation as the resultant of home-related and homeindependent components (WALLRAFF 1991, 1996). The first one is the output of a true homing processes, relying on information of the bird's position with regard to home (see PAPI & WALLRAFF 1992; R. WILTSCHKO & W. WILTSCHKO 1999a, 1999b; WALLRAFF 2001 for update reviews on the navigational mechanism of birds). The other component is rather heterogeneous and includes all kinds of orientation not guided by navigational information. This component can turn into an increased scatter of vanishing bearings and/or into a tendency to fly toward a population-specific preferred compass directions or PCD (WALLRAFF 1991, 1996, 2001; BALDAC-CINI et al. 1999).

This model of initial orientation emerges from data collected only on homing pigeons, which show that the loss of navigational information (WALLRAFF 1986) or the lack of homing experience (WALLRAFF 1986, IOALÈ 1995) can cause increased scatter of bearings and/or a full expression of the PCD. Similar effects on initial orientation, but not on the homing performance, have been obtained by subjecting pigeons to a series of treatments, which increase the stress conditions of the animals or reduce the birds' capacity to compensate for stressful factors (PAPI & LUSCHI 1990; PAPI et al. 1992; DEL SEPPIA et al. 1995, 1996; LUSCHI et al. 1996; but see R. WILTSCHKO & W. WILTSCHKO 1998a). As pointed out by DEL SEPPIA et al. (1996), these results lead one to consider home-independent orientation as an expression, at least in part, of an 'emotional' component of the initial orientation.

As previously stated, this model has not been supported by comparative data, probably because of the difficulties involved in the study of homing abilities of free-living birds (SCHMIDT-KOENIG 1979, ABLE 1980). It seems reasonable to assume that stressful factors could deeply affect birds not accustomed to handling. Indeed, although the homing behaviour of free-living birds has only been rarely analysed thoroughly (see R. WILTSCHKO 1992, for a review), the published data show that the initial orientation of wild species is often characterised by a noticeable scatter of bearings and/or by directional preferences not related to the home direction (the 'nonsense' orientation of MATTHEWS 1961, 1984; see also WALLRAFF 1991; BALDACCINI et al. 1999). To what degree these phenomena are related to those observed in pigeons is currently not known, although it could be speculated that they have to be interpreted as home-independent orientation. Considering the broad occurrence of this behaviour and the recent findings that testify to the importance of taking stress-induced side-effects into consideration when the outcomes of the experiments on the homing pigeons have to be evaluated (DEL SEPPIA et al. 1996, LUSCHI et al. 1996, SANDBERG et al. 1999), it seems particularly important to verify the degree to which this analogy could be supported.

In this respect, sand martins (*Riparia riparia*) seem a particularly good model species. On the one hand, this is one of the few wild birds whose homing behaviour has been systematically investigated (see BALDACCINI et al. 1999); on the other hand, its initial orientation depends strongly on the distance of displacement. Indeed, a significant homeward orientation has been observed only at short or moderate displacement distances (7-18 km), inside the home range of this species in its breeding quarters (TURNER & ROSE 1989, ALVES & JOHNSTONE 1994), while at the farther distances tested, homing performance falls off rather abruptly and the birds tend to head toward fixed compass directions (BALDACCINI et al. 1986a, 1986b, 1999). This dichotomy in homing orientation offers an interesting opportunity to verify: (a) if an alteration of birds 'emotional' state could affect the initial orientation of sand martins; (b) if the directional preferences of this species have to be considered as a home-independent component of the initial orientation.

Initial orientation in sand martins

We have tested these hypotheses by releasing sand martins subjected to moderately stressful transport conditions, at least partially analogous to those reported in DEL SEPPIA et al. (1996), near their breeding colony (less then 13 km). The expectation is that these treatments could determine a deterioration of the homeward orientation and/or a tendency to fly in fixed compass direction, which normally does not occur at these displacement distances (BALDACCINI et al. 1999).

METHODS

General methods and data analysis

Test birds were adult sand martins caught and ringed during the breeding season at different colonies along the Taro River (Northern Italy). Captures were performed with mist-nets erected in front of the nest entrances during the last part of the night, when most individuals had not yet left their nest-holes. In all tests, sand martins experiencing their first experimental release were used. To control for possible effects of sex on the initial orientation of released birds (see BALDACCINI et al. 1997), comparable numbers of males and females were used in all the experimental series. In all but the last series birds were released from sites chosen in roughly symmetrical directions with respect to the home colonies.

Releases were carried out on the same morning of the day of capture, singly tossing the birds in random directions, and alternating animals transported in different conditions. Each bird was followed up to vanishing with 10×40 binoculars from the top of a van. Birds disappearing behind vegetation or flying low over the ground were not included in statistical calculations. Tests took place only on sunny days and with no or only moderate wind (less than 5 m/sec at 3 m above the ground). Homing times were not recorded, due to the considerable difficulties in verifying the successful return of these small birds on the same day as the release (see GIUNCHI et al. 1999). However, non-systematic observations and repeated capture sessions at the colony sites indicated that the used treatments interfered only temporarily with the homing processes of sand martins and that the return rates were comparable to those reported in previous tests performed at roughly the same distances of displacement (BALDACCINI et al. 1986b).

Mean vector length and direction were calculated from vanishing bearings of each release and the standard circular statistical evaluations were performed (BATSCHELET 1981). The 95% confidence intervals calculated according to BATSCHELET (1981) and only for significantly oriented samples (P < 0.05, Rayleigh or V test) were used to test if the mean direction of a distribution was significantly different from the expected direction. As pointed out by WALLRAFF (1991), a proper method to test the occurrence of a home-independent orientation is to summarise data collected at a number of release sites symmetrically distributed around home. For this reason, vanishing bearings of each experimental group in each series were pooled with respect to the North (P_N) or home directions (P_H) set to 0°. Circular distributions were compared using the Watson U^2 test (BATSCHELET 1981). Specific hypotheses were tested using the 'nonparametric test for dispersion' (WALLRAFF 1979, BATSCHELET 1981). In detail, from individual bearings we calculated the angular distances (see BATSCHELET 1981) from the home direction (AD_H) and from the mean direction of the P_N distribution (AD_M) . The AD_H was a measure of the degree of homeward orientation of a series, while the AD_M was a measure of the degree of concentration of directional choices with respect to North (see WALLRAFF 1979 for a detailed explanation). The AD_H and AD_M were compared using the Mann-Whitney U test.

Due to the small sample sizes of each release and to the variability in directional choices that characterises homing experiment on sand martins (see BALDACCINI et al. 1999), statistical tests were used to compare only pooled data of each group within each experimental series. Limiting the number of comparisons reduced the amount of statistical tests used to address the same null hypothesis, thus avoiding the problems associated with adjusting the overall significance level of dependent tests (RICE 1989, SOKAL & ROHLF 1995), and also increasing the statistical power of each test, due to the larger sample sizes considered in the calculations.

All the non-circular statistical analyses were according to SOKAL & ROHLF (1995). Since we were testing explicit hypotheses, all tests were one-tailed.

The experimental plan

Series 1 and 2: transport in total darkness inside transparent bags. These two series were designed to replicate, at least partially, the experiments reported in DEL SEPPIA et al. (1996). Among the different stressful treatments used in that paper, we chose to keep birds in total darkness during transport, since this treatment had been widely used in pigeon homing experiments (e.g., W. WILTSCHKO & R. WILTSCHKO 1981; R. WILTSCHKO & W. WILTSCHKO 1985, 1998b) and it seemed the most readily adaptable to sand martins. After capture, control (L_T) and experimental (D_T) birds were placed singularly inside transparent bags (20 \times 30 cm). Unlike pigeon experiments (see DEL SEPPIA et al. 1996), bags were used to avoid possible damage to the birds during transport. These bags were comparable in size to those used in previous experiments on sand martins (BALDACCINI et al. 1986a, 1986b, 1999; GIUNCHI et al. 1999) and allowed the birds to move their wings and their legs quite freely, thus avoiding possible side-effects due to immobilisation (e.g., stress-induced responses: see DEL SEPPIA et al. 1996). The fabric of these bags (tulle) was different from that used in previous experiments (cotton) and was chosen to allow proper ventilation of the animals, while simulating, at least partially, the condition of control pigeons in DEL SEPPIA et al. (1996), which were transported in baskets inside a box made of transparent Plexiglas. L_T-birds were transported inside a strong cardboard box without cover, fixed on the top of (series 1) or put inside (series 2) a car. Both internal and external transports were used to control for possible side effects caused by the different locations of the boxes during displacement (i.e., exposure to the turbulence caused by airflow over the car in series 1, and reduced ventilation inside the boxes in series 2). During transport, L_T -birds (especially in series 1) could see only the sky and the higher elements of the surrounding landscape; at the release site, they were also exposed to the view of the experimenters during the release procedures. The D_T -birds were treated similarly to the L_{T} -birds, but the box was provided with a light proof cover, that allowed an adequate ventilation trough an S-shaped opening. Depending on local traffic and distance of displacement, the driving time was 30-45 min. At the release site, all the animals were kept inside the boxes up to the moment of release. Bags of D_T -birds were extracted from the box immediately before release through an opening, which was closed during transport and at the release site, connected with a long sleeve of opaque cloth. Though not measured, the amount of light that entered the box during this procedure was probably negligible. Apart from the use of bags, the treatment was not completely analogous to that reported in DEL SEPPIA et al. (1996). We prevented the L_{T} -birds from seeing most of the surrounding landscape, as in previous experiments performed by our research group, while the D_T -birds were kept in total darkness also at the release site to increase the (potential) effect of the treatment. In series 1, four experimental releases were performed in 1997 from four different sites, arranged almost symmetrically with respect to the home colony. In series 2, four tests were performed in 1998 from two different sites, located almost symmetrically with respect to a different colonial site, about 6 km from that used in series 1. Considering the outcomes of experiments with pigeons (DEL SEPPIA et al. 1996), the expected result of these two series was that the light deprivation would produce an increased scatter of bearings and/or an increased tendency to fly in fixed compass directions.

Series 3: transport inside transparent vs semitransparent bags. This series was designed to test if different bag fabrics could affect the orientation of sand martins and it was essentially suggested by the unexpected outcome of series 1 and 2 (see below). As previously mentioned, the bags used in the foregoing two series were transparent, while those used in previ-

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ous experiments (BALDACCINI et al. 1986a, 1986b, 1999; GIUNCHI et al. 1999) did not allow the birds to see the surroundings, although they permitted the light to filter inside. Two experimental groups were used in this series. One group (L_T) was treated in the same way as L_T -birds of the previous series. Subjects of the other group $(L_S$ -birds) were placed inside semi-transparent, cotton fabric bags of the same size as the transparent ones. Both groups had therefore free access to the daylight, but only L_T -group could see distinctly outside the bag. Other aspects of the birds' treatment in this series were analogous to those of L_T -groups of series 1 and 2. Four tests were performed in 1998 from three different sites located almost symmetrically with respect to the home colony. Birds were captured at a single colonial site, a few tens of metres from the colony used in series 2. The expected result was that the use of transparent bags would significantly affect the initial orientation of the sand martins, increasing the scatter of bearings and/or the tendency to fly in fixed compass directions.

Series 4: transport in total darkness inside semitransparent bags. This series was designed to replicate the experiments of series 2 using semitransparent bags. Three tests were performed in 1999 with birds captured in a colony located about 6 km from that used in series 3. Due to difficulties in finding open sites symmetrically distributed with respect to the colony, we used only one release site, chosen so that the home direction was opposite to the PCD revealed in previous series and also in BALDACCINI et al. (1999). Considering the use of only one release site, our expectation was that the vanishing bearings of birds transported in total darkness inside semitransparent bags ($D_{\rm S}$ -birds) would be more scattered and less polarised toward the home direction than those of $L_{\rm S}$ -birds, as reported for homing pigeons (DEL SEPPIA et al. 1996).

RESULTS AND DISCUSSION

Series 1 and 2: transport in total darkness inside transparent bags

The results of series 1 and 2 are quite comparable (Tables 1 and 2). The directional preferences appear poorly homogeneous: indeed only 8 out of 16 tests performed in both series (independent of the treatments) are significantly oriented (Rayleigh or V test). Considering P_N distributions, D_T - and L_T -birds in both series show a significant directional preference toward S-SW and no significant difference emerges between the two treatments. P_H distributions also are not different. All groups are significantly homeward oriented, as indicated by the confidence interval analysis.

The results of these two series do not confirm our expectation: no significant difference are recorded between the initial orientation of the two experimental groups. It is important to notice, however, that the behaviour of the D_{T^-} and particularly L_T -birds (the supposed control group) are rather anomalous, both considering the relatively poor performance revealed by the P_H distributions, and, particularly, the appearance of a significant directional preference in the P_N distributions, which is normally absent at these displacement distances (see BALDACCINI et al. 1999). Actually, both groups behave as expected if stressful factors affect their initial orientation, determining the appearance of home-independent phenomena (poor homeward orientation and increased tendency to fly in the PCD). A reasonable hypothesis that could explain these results is that the bag fabric used in these tests, which is different from that previously used by our research group (see Methods), could alter the birds' behaviour, thus masking the effect of the treatment. This hypothesis was tested in series 3.

Table 1.

Initial orientation in series 1: transport in total darkness inside transparent bags. Abbreviations: N (*n*), animals released (number of bearings); α , mean direction; r, vector length; Hc, homeward component = r × cos(α – home direction); CI, 95% confidence interval of the mean direction (in = home direction falls inside the confidence interval); vanishing time, median of vanishing time.

Test	Date	Distance (km)	Home direction	Treat- ment	N (n)	α	r	Нс	CI	Vanishing time (sec)
1	14.05	4.2	2420	\mathbf{D}_{T}	20 (12)	242°	0.82***	+0.82***	in	263
1	16.05	4.2	242°	L_{T}	21 (12)	216°	0.93***	+0.84***	out	316
				D _T	16 (10)	126°	0.50	+0.29		206
2	19.05	9.4	071°	L_{T}	16 (10)	107°	0.35	+0.28		277
3	27.05	11.5	126°	D _T	16 (12)	173°	0.42	+0.29		224
				L_{T}	16 (11)	205°	0.26	+0.05		237
		12.3	296°	D _T	16 (13)	226°	0.46	+0.16		260
4	30.05			L_{T}	16 (12)	188°	0.72***	-0.22	out	224
Pool	ing									
	No	rth direct	$tion = 0^{\circ}$	D_{T}	68 (47)	207°	0.40***			227
	North unection = 0				69 (45)	195°	0.49***			262
					68 (47)	007°	0.39***	+0.39***	in	227
	Home direction = 0°			L_{T}	69 (45)	323°	0.30*	+0.24*	in	262

Probability according to the Rayleigh ('r' column) or the V test ('Hc' column): *, P < 0.05; **, P < 0.01; ***, P < 0.001; no symbol, P > 0.05.

Series 3: transport inside transparent vs semitransparent bags

The results of this series are reported in Table 3 and in Fig. 1. L_S-birds show rather homogeneous directional preferences: three out of four tests are significantly and homeward oriented. On the other hand, two out of four L_T-tests are significantly oriented, and only one toward the home direction. Considering the P_H distributions, L_S-birds are significantly homeward oriented, while the vanishing bearings of L_T-birds are randomly distributed. The two distributions are not homogeneous (U^2 = 0.304, P < 0.005, Watson U^2 test) and the L_S- and L_T-groups differed also in the degree of homeward orientation (AD_H median (interquartile range): L_S = 47.0 (18.8-68.8), L_T = 81.5 (43.5-132.0), T = 1255.0, P < 0.005, Mann-Whitney U test). An opposite outcome emerges when considering the P_N distributions: L_T-birds are significantly oriented toward S-SW, while the vanishing bearings of L_S-birds are randomly distributed. These two distribution are not significantly different (Watson U^2

Table	2.
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Initial orientation in series 2: transport in total darkness inside transparent bags (explanations as in Table 1).

Test	Date	Distance (km)	Home direction	Treat- ment	N (n)	α	r	Нс	CI	Vanishing time (sec)
		<i>(</i>)		D _T	11 (10)	194°	0.47	-0.22		202
1	12.05	6.3	075°	L_{T}	10 (8)	230°	0.29	-0.26		312
2	14.05	()	0759	\mathbf{D}_{T}	14 (9)	120°	0.66*	+0.47*	out	155
2	14.05	6.3	075°	L_{T}	14 (11)	142°	0.20	+0.08		123
3	19.05	4.2	273°	\mathbf{D}_{T}	13 (8)	269°	0.85***	+0.85***	in	318
				L_{T}	13 (10)	250°	0.54	+0.50*	in	268
	20.05	4.2	273°	\mathbf{D}_{T}	14 (9)	230°	0.85***	+0.63**	in	245
4				L_{T}	12 (9)	236°	0.53	+0.43*	in	193
Pooli	inσ									
1 001			\mathbf{D}_{T}	52 (36)	215°	0.42**			228	
	North direction = 0°				49 (38)	231°	0.32*			219
					52 (36)	010°	0.41**	+0.40***	in	228
	Home direction = 0°			L_{T}	49 (38)	346°	0.21	+0.20*	in	219

test), but the angular deviation from the mean direction of L_S-birds tends to be higher, although not significantly, than that of L_T-birds (AD_M: L_S = 72 (52.3-111.5), L_T = 62.5 (41.0-85.0), *T* = 1714.5, *P* = 0.065, Mann-Whitney *U* test).

These data substantially confirm the hypothesis that the type of visual information during transport and at the release site can affect the behaviour of sand martins. The directional choices of the L_s-group are comparable to those obtained in previous tests (e.g., BALDACCINI et al. 1999), showing a good homeward orientation and no sign of fixed directional preferences. On the contrary, transport in transparent bags caused a significant worsening in the homeward orientation and a significant tendency to fly toward a PCD. Due to the high scatter of bearings of both experimental groups in P_N , no significant difference emerged between L_T - and L_s -groups, although the pattern is rather clear.

Series 4: transport in total darkness inside semitransparent bags

Table 4 and Fig. 2 report the results of series 4. All tests, excluding the first D_s -release, are significantly oriented. Two out of three L_s -tests are also significantly

Tab	le 3.

Initial orientation in series 3: transport in transparent vs semitransparent bags
(explanations as in Table 1).

Test	Date	Distance (km)	Home direction	Treat- ment	N (n)	α	r	Нс	CI	Vanishing time (sec)
1	21.05	()	0750	Ls	14 (9)	095°	0.84***	+0.78***	in	349
1	21.05	6.3	075°	L_{T}	14 (10)	322°	0.23	-0.09		237
				Ls	14 (10)	251°	0.48	+0.45*	in	232
2	26.05	4.2	273°	L_{T}	14 (10)	205°	0.59*	+0.22	out	214
3	02.06	4.2	273°	Ls	14 (10)	258°	0.81***	+0.78***	in	286
				L_{T}	14 (10)	229°	0.55*	+0.39*	in	204
		7.6	041°	Ls	12 (10)	101°	0.36	+0.18		204
4	10.06			L_{T}	11 (10)	164°	0.41	-0.22		216
Pool	inσ									
1 001				Ls	54 (39)	197°	0.12			251
	North direction = 0°			L_{T}	53 (40)	212°	0.33*			218
				L _S	54 (39)	005°	0.54***	+0.54***	in	251
	Home direction = 0°			L_{T}	53 (40)	291°	0.21	+0.08		218

homeward oriented, while in none of the D_s -tests do the confidence interval include the home direction. Considering the pooled distributions, the two groups are significantly, but not homeward oriented, although L_s -vanishing bearings tend to cluster around the home direction, as revealed by the highly significant results of the V test. Although these two distributions do not differ significantly according to the Watson U^2 test, the degree of homeward orientation of L_s -birds is significantly higher than that of D_s -birds (AD_H: $L_s = 54.0$ (25.5-73.3), $D_s = 84.0$ (52.0-112.0), T = 685.0, P = 0.005, Mann-Whitney U test). No difference between the two groups is found when considering the angular deviation from the respective mean directions.

These results confirm the original hypothesis that transport and maintenance in total darkness could significantly affect the initial orientation of the sand martin. Although the pooled distribution of L_s -birds is not homeward oriented, the better performance of L_s -birds is evident both when considering the degree of homeward orientation of P_N distribution and the number of significantly homeward oriented tests (two vs none out of three releases). The observed bias in the initial orientation of L_s -birds with respect to the home direction is rather common when the performances of birds tested from a single release site are evaluated (see BALDACCINI et al.



Fig. 1. — Pooled distributions of vanishing bearings of L_{s} - (left side) and L_{T} -birds (right side) of series 3 with respect to the North (above) or home (H) directions (below) set to 0°. Dashed arrows are used when the Rayleigh test does not reach the significance level. Different symbols are used to indicate different test releases (filled dots = test 1; open dots = test 2; filled triangles = test 3; open triangles = test 4).

1999) and it could have been determined by local factors (WALLRAFF 1991, 1996; R. WILTSCHKO 1993). Thus, this bias does not alter the general conclusion that transport and maintenance in total darkness tends to worsen the orientation of sand martins.

CONCLUSIONS

The presented results show that the initial orientation of sand martins could be significantly affected by treatments that do not interfere with their homing process. Indeed, at the distances tested, the initial orientation of these birds seems to depend quite strongly on the topographical features of the surrounding (Down-HOWER & WINDSOR 1971, BALDACCINI et al. 1989), that are clearly fully accessible to

Table 4

Initial orientation in series 4: transport in total darkness inside semitransparent bags (explanations as in Table 1).

Test	Date	Distance (km)	Home direction	Treat- ment	N (n)	α	r	Нс	CI	Vanishing time (sec)
1	12.05	7.0	0.4.1.9	Ds	12 (10)	106°	0.43	+0.18		220
1	12.05	7.8	041°	Ls	14 (10)	108°	0.80***	+0.32	out	251
2	23.05		041°	D _s	13 (10)	112°	0.66**	+0.21	out	230
		7.8		Ls	13 (9)	074°	0.73**	+0.61**	in	276
_	27.05	5 7.8	041°	D_S	11 (10)	144°	0.78***	-0.17	out	248
3				Ls	11 (10)	067°	0.71**	+0.64**	in	239
Pooling		D _s	36 (30)	124°	0.60***	+0.08	out	243		
North direction = 0°			Ls	38 (29)	084°	0.71***	+0.52***	out	261	



Fig. 2. — Pooled distributions of vanishing bearings of D_{S^-} (left side) and L_{S^-} -birds (right side) of series 4 with respect to the North (above) or home (H) directions (below) set to 0°. Different symbols are used to indicate different test releases (filled dots = test 1; open dots = test 2; filled triangles = test 3).

all tested subjects. It can be hypothesised that transport in total darkness could interfere with the magnetoreception of the birds (see LEASK 1977), thus preventing them from accessing magnetic information during transport, as demonstrated for young homing pigeon (W. WILTSCHKO & R. WILTSCHKO 1981, 1988; R. WILTSCHKO & W. WILTSCHKO 1985, 1988, 1998a, 1998b, 2000; but see WALLRAFF & SINSCH 1988a,

1988b; LUSCHI et al. 1996; WALLRAFF 2000). It is important to note, however, that the tested sand martins were all adult, experienced birds, released very near their home colonies, inside an area that was probably familiar (TURNER & ROSE 1989, ALVES & JOHNSTONE 1994). As demonstrated for homing pigeons, experienced birds, especially when released inside familiar areas, mainly use location-dependent signals to orient, although they can also rely on information picked up en route during the outward journey (see WALLRAFF 1990, 1996, 2001). It thus seems unlikely that sand martins base their homing strategy mainly on 'path-integration' (sensu PAPI 1990). Moreover, the behaviour of D_T -birds, transported and maintained in total darkness, is absolutely comparable to that of L_T -birds, which, following LEASK's model, have full access to magnetic information during transport.

These considerations lead to the hypothesis that the experimental treatments do not affect the home-related, but the home-independent component of the initial orientation. Indeed, the data collected on D_T -birds are comparable to those reported in DEL SEPPIA et al. (1996) and particularly series 4 demonstrates that, controlling for the effect of transparent bags, the degree of homeward orientation worsens after transport in total darkness. The interpretation of the performances of L_T -birds is more problematic. Indeed, while light deprivation is known to be a stressor (MCCARTY 1989, DEL SEPPIA et al. 1996), any possible explanation of the effect of transparent bags on the birds' behaviour is only speculative. Bearing in mind the known cues used by birds to home (reviewed in PAPI & WALLRAFF 1992; R. WILTSCHKO & W. WILTSCHKO 1999a, 1999b; WALLRAFF 2001), it seems unlikely that the differences in initial orientation of L_{s} - and L_{T} -birds (see series 3) could be attributed to an interference with the homing process. It is most likely that being in transparent bags could affect bird's internal state. The mechanism of this effect is not known. Although a possible stressful effect of the fabric of the bags can not be ruled out, it seems reasonable to hypothesise that L_T -birds might be fully exposed to the stress induced by the entire experimental protocol. They were set into an unfamiliar environment and, moreover, repeatedly exposed to potential predators (the experimenters during the release procedures). Although the general treatment was absolutely the same, L_s-birds could not visually follow the procedures around them, since they had only a vague visual perception of the surroundings, and this condition could determine a less pronounced stressful effect for which the birds could more easily compensate.

Apart from the proximal causes of the observed behaviour, these results shed light on the interpretation of the initial orientation of sand martins outside their familiar area. Indeed, the considered treatments not only produce a worsening of homeward orientation, but also the appearance of a directional preference toward S-SW comparable to that observed at longer displacement distances (see BALDACCINI et al. 1999). This suggests that the 'nonsense' orientation of this species, as the PCD of the homing pigeon (DEL SEPPIA et al. 1996), might be a home-independent component of the initial orientation, thus supporting the model given by WALLRAFF (1991). The adaptive meaning (if any) of these directional preferences is not clear and our data do not add any new insight to this topic. The hypothesis that it could be a normal escape direction facilitating flock cohesion (MATTHEWS 1961, THAKE 1981) substantially lacks experimental evidence, and, moreover, one of the few experiments carried out to test this idea has produced rather contradictory results (MATTHEWS 1962). It is important to note, however, that, excluding series 4, the appearance of 'nonsense' phenomena is not associated with a zeroing of the homerelated component of the initial orientation. On the contrary, no sign of homeward orientation emerges when sand martins are displaced at farther distances (BALDAC-CINI et al. 1999). This indicates that an alteration of the internal state of these birds is probably not sufficient to cancel the homeward orientation inside a familiar area, thus suggesting that sand martins might not be able to navigate during vanishing time when released outside their home range in breeding quarters. This seems however a temporary impairment, since the homing performances reported in other studies (BALDACCINI et al. 1986b, GIUNCHI et al. 1999) do not fully support the use of a random or systematic search for the breeding site.

In summary, the presented results testify to the significant and often unpredictable effect that handling conditions can have on the homing behaviour of freeliving birds. As suggested by WALLRAFF (1991), home-independent orientation might be one of the major sources of confusion in the interpretation of experimental data about the homing mechanism of birds. Considering the difficulties in controlling other potentially confusing variables (see SCHMIDT-KOENIG 1979, ABLE 1980), the weight of this factor on the outcome of tests performed on wild birds could be even larger. Bearing in mind the general lack of systematic studies on the homing behaviour of wild birds, and the widespread occurrence of 'nonsense' behaviour in those species rather intensively studied (MATTHEWS 1984, WALLRAFF 1991, BALDACCINI et al. 1999), it could be inferred that the home-independent orientation could be one of the most important obstacles that prevent a proper comparative analysis of the homing mechanisms of birds. This remark could be extended to migratory orientation. Indeed, the directional choices of birds tested in orientational cages are often quite scattered or polarised toward directions significantly different from the expected migratory direction (e.g., see SANDBERG et al. 1988a, 1988b, 1991; MUHEIM et al. 1999). The causes of these directional choices could be several, but possible effects of handling stress have to be properly evaluated, especially considering that some types of 'non-standard' directional preferences have been interpreted as navigational strategies of migrants displaced from their migratory route (see RABØL 1975, 1985, 1994, 1995).

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