Migratory orientation of free-flying Robins *Erithacus rubecula* and Pied Flycatchers *Ficedula hypoleuca*: Release experiments

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Release experiments were conducted to examine a number of questions concerning the orientation behaviour of free-flying birds. (1) We found distinct differences in the orientation performance of Robins released under clear and overcast skies, respectively, during autumn migration. While Robins oriented in a seasonally appropriate direction under clear skies, they selected a northwesterly mean direction under overcast, pointing to the importance of visual celestial cues during autumn migration. There was no significant difference in orientation under clear and overcast skies in releases performed during spring migration. Pied Flycatchers failed to orient in their expected migratory direction when released under clear autumn skies, probably because of strong winds. (2) The amount of stored fuel reserves had a pronounced influence on the decision to take off on migratory flights, both for Robins and Pied Flycatchers. (3) Autumn releases of Robins and Pied Flycatchers under clear skies revealed a significantly larger angular dispersion in orientation for migratorily naive (first-year) birds as compared to adults. This suggests that adult birds orient with higher precision due to experience and/or that strong selection among young migrants operates to maintain orientation within narrow limits. (4) Pied Flycatchers (long-distance migrants) vanished from view significantly faster than did Robins (short-distance migrants) when released under clear autumn skies. (5) Displacement experiments with Robins and Pied Flycatchers, captured at two different sites and then transported to a common release site, yielded inconsistent results which, in only one case out of four, could be interpreted as compensatory orientation towards the capture sites.

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Introduction

Orientation research during the past decades has demonstrated that migratory birds do not rely on a single directional cue for their orientation, but rather on a complex array of stimuli including the sun, skylight polarization, stars and the geomagnetic field (reviewed by Able 1980a, Baker 1984). Thus, to disentangle the complicated web of orientation behaviours shown by migrants, a multifaceted approach is required.

The most commonly used approaches in studies of migratory orientation of birds are orientation cage experiments, and radar and visual observations of free-flying migrants. Our present knowledge about migratory orientation is based largely on the results of cage experiments with night-migrating passerines as test subjects (Keeton 1981, Baker 1984). Although orientation cage experiments allow rigorous control of cue information presented to the test subjects, they are performed in a confined and unnatural environment. Only under free-flying circumstances may we be certain to study the full orientation capabilities of migratory birds. Consequently, the results of cage studies should be interpreted in the light of field observations of migratory
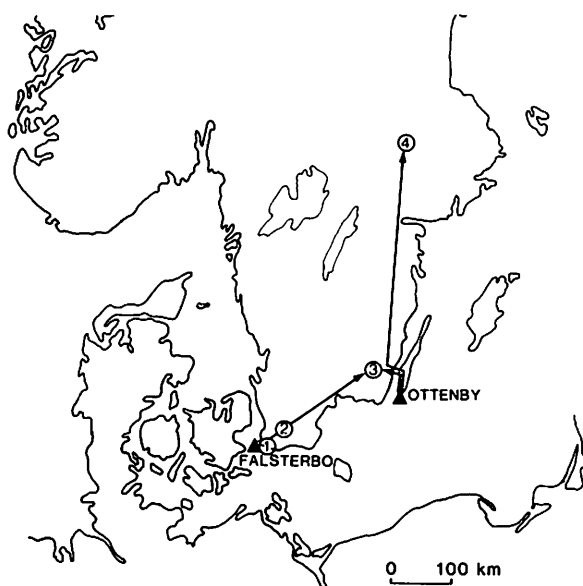
Fig. 1. Location of capture sites (closed triangles) and release sites (circles with numerals). For more detailed information on geographical coordinates of the different sites, see Table 1. Arrows show the approximate displacement routes and distances (cf. inset scale).

behaviour, including experiments with free-flying migrants as recently stressed by Able and Cherry (1985) and Moore (1987).

Radar and ceilometer studies demonstrate that fewer birds initiate migration under solid overcast than under clear skies (Griffin 1973, Richardson 1978a). In addition, under clear skies with access to sunset and/or stellar information, birds orient in the expected direction for the season, even with opposing winds, whereas migrants seem to have difficulties in selecting a seasonally appropriate direction under solid overcast, and instead frequently select downwind headings (Able 1978, 1980b, 1982a,b). Migrants seem to respond to long-term overcast conditions ($\geq$ 24 h) by becoming increasingly disoriented (Tinbergen 1956, Hebrard 1972, Emlen 1980). This effect of overcast skies on orientation has been confirmed in experimental release and telemetry studies (Cochran et al. 1967, Emlen and Demong 1978, Able et al. 1982). However, if the sun reappears only a short while during such a period of overcast, the concentration of tracks observed on radar screens and in the field increases significantly (Tinbergen 1956, Emlen 1980, Able 1982b).

Emlen and Demong (1978) released White-throated Sparrows Zonotrichia albicollis singly at migratory altitudes, using helium-filled weather balloons that carried the birds to the desired altitude inside a cardboard box equipped with a fuse-operated opening device. After release, experimental birds were radar-tracked under both clear and overcast skies. The authors found that birds released under overcast hesitated more before they selected a heading, circled frequently or engaged in 'zigzag' (sinusoidal) flights, and were less well oriented than under clear skies. Able et al. (1982) used the same release technique, and equipped an experimental group of White-throated Sparrows with frosted contact lenses that deprived the birds of detailed form vision. These birds were released together with a control group (untreated) under clear skies, with light winds that were opposed to the normal migration direction for the season. The results corroborated earlier radar observations, i.e. control birds headed in the predicted migratory direction whereas the experimental category chose downwind bearings.

The release experiments described above have the disadvantage of forcing the birds to fly (released in mid-air). Starting in 1985 we have used an alternative technique, similar to the method described by Able and Terrill (1987), whereby the birds are released from the hand, much in the same way as homing pigeons. We have performed several release experiments with nocturnal passerine migrants, to answer a number of questions: (1) Are there any differences in orientation performance under clear and overcast skies? If celestial cues are important for the selection of seasonally appropriate migratory directions, then we would expect distinct differences in orientation between birds released under clear (seasonally appropriate orientation) and overcast (disorientation or seasonally inappropriate orientation), respectively (cf. above). (2) How do the fuel reserves of migratory birds affect orientation and the decision to migrate? Fat birds should be more likely to depart on migration than lean birds (e.g. Gwinner et al. 1985). Furthermore, birds that are not yet fully prepared (insufficient fuel reserves) for migration should either stay at their current position if foraging conditions are benign or, alternatively, reorient in search of more profitable stop-over sites (Alerstam 1978, Biebach 1985, Lindström and Alerstam 1986, Terrill 1988). (3) Do orientation behaviour and accuracy differ between experienced and inexperienced migrants? If birds learn to integrate available orientation cue information more efficiently with increasing age, old birds should display less variation in directional choices than first-year migrants (Rabøl 1978, Moore 1984). (4) Do long- and short-distance migrants behave differently? If long-distance migration is associated with greater risks for orientation errors due to, for example, a higher probability of encountering inclement weather en route, then such migrants can be expected to be more independent of celestial cues than would short-distance migrants (cf. Wiltschko and Wiltschko 1975a,b). (5) Are there any effects of displacements on orientation? If migrants know their current position in relation to a goal (like winter grounds, breeding areas or goal areas along the migration route) they should be able to compensate for experimental displacements and change their directional choices in a predictable way (Rabøl 1972).

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Table 1. Release experiments with Robins (A) and Pied Flycatchers (B). The table shows the location of release sites in geographical coordinates, the dates on which the test birds were transported (Fbo = Falsterbo, Ott = Ottenby, cf. also Methods). It should be noted that the data given for release site 2 concerning displacement direction and distance do not pertain to transportation immediately before the releases were conducted, instead these birds were captured at Falsterbo Bird Observatory and then subjected to orientation cage tests for about two weeks at site 2 before releases took place. D(α) and D(km) denote the rhumbline displacement direction and distance, respectively.

	Release site	Geogr. coord.	Release dates	Year	Exp. cond.	Displacement D(α)	D(km)	Capture site	No. of birds
A. Robins									
	1. Falsterbo	55°23′N, 12°50′E	25 April	1988	C	–	–	Fbo	9
			26 April	1988	C	–	–	Fbo	11
			13 May	1988	C	–	–	Fbo	14
			2 May	1988	O	–	–	Fbo	11
	2. Stensoffa	55°42′N 13°25′E	24 Sept.	1986	C	46°	46	Fbo	3
			25 Sept.	1986	C	46°	46	Fbo	3
			21 Oct.	1986	C	46°	46	Fbo	2
			27 Oct.	1986	C	46°	46	Fbo	2
			2 Nov.	1986	C	46°	46	Fbo	4
			14 Nov.	1988	C	46°	46	Fbo	20
	3. Emmaboda	56°36′N 15°36′E	28 April	1987	C	52°	219	Fbo	27
			28 April	1987	C	312°	66	Ott	35
			24 Sept.	1987	O	52°	219	Fbo	32
			24 Sept.	1987	O	312°	66	Ott	30
			9 Nov.	1987	C	52°	219	Fbo	29
			9 Nov.	1987	C	312°	66	Ott	31
	4. Norberg	60°05′N, 15°55′E	6 May	1987	C	356°	432	Ott	23
			20 May	1987	O	356°	432	Ott	13
			20 Oct.	1987	O	356°	432	Ott	29
			16 Nov.	1989	C	356°	432	Ott	26
B. Pied Flycatchers									
	1. Falsterbo	55°23′N, 12°50′E	23 Aug.	1986	C	–	–	Fbo	3
			29 Aug.	1986	C	–	–	Fbo	5
			30 Aug.	1986	C	–	–	Fbo	3
			20 Aug.	1987	C	–	–	Fbo	8
			1 Sept.	1987	C	–	–	Fbo	5
			26 Aug.	1988	C	–	–	Fbo	11
			6 Sept.	1988	C	–	–	Fbo	17
			13 Sept.	1988	C	–	–	Fbo	4
	2. Emmaboda	56°36′N, 15°36′E	8 Sept.	1987	C	52°	219	Fbo	32
			8 Sept.	1987	C	312°	66	Ott	21

Methods

Experimental birds

Robins *Erithacus rubecula* are short- to medium-distance nocturnal migrants with a breeding range throughout central and northern Europe. They rarely winter further south than the Mediterranean region (Cramp 1988). Pied Flycatchers *Ficedula hypoleuca*, on the other hand, are long-distance migrants with approximately the same breeding distribution, but with wintering grounds in central and western Africa, south of about 11°N (Moreau 1972).

All experimental birds were caught as passage migrants during autumn and spring migration. They were mist-netted at Falsterbo Bird Observatory (55° 23′N, 12° 50′E) and at Ottenby Bird Observatory (56° 12′N, 16° 24′E), by the Baltic Sea in southern Sweden. The birds were released either after about two weeks in captivity (during which time they were subjected to orientation cage experiments), or held in captivity three to five days prior to the release experiments. For details about holding cages and maintenance conditions see Sandberg et al. (1988).

Release sites and test procedure

Locations of release and capture sites of the test birds are given in Fig. 1 and Table 1. The birds were released under clear skies (median cloud cover = 2/8, range: 0/8 – 4/8), and under solid or close to solid overcast (median cloud cover = 8/8, range: 7/8 – 8/8). Releases at sites 3 and 4 involved transportation of the birds by car or trailer on the day of release. During transportation, the birds had no access to visual cues. Soon after arrival at

A) ROBINS, Autumn

B) ROBINS, Spring
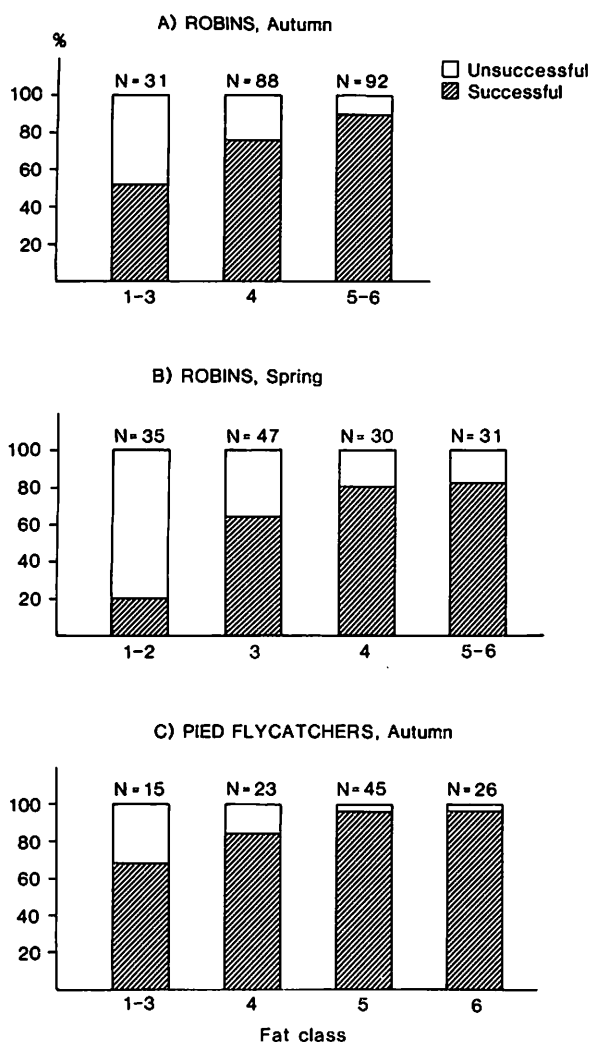

C) PIED FLYCATCHERS, Autumn

Fat class

Fig. 2. Relationship between body condition of released birds, as indicated by visually estimated fat loads (estimated according to a seven class scale, cf. Methods), and the motivation to migrate. A) Robins released during autumn migration under both clear and overcast skies. The number of individuals in each fat class (F) was: F0 – 0, F1 – 0, F2 – 3, F3 – 28, F4 – 88, F5 – 78 and F6 – 14. B) Robins released during spring migration under both clear and overcast skies (no. of individuals in each fat class: F0 – 0, F1 – 7, F2 – 28, F3 – 47, F4 – 30, F5 – 26 and F6 – 5). C) Pied Flycatchers released under clear autumn skies (no. of individuals in each fat class: F0 – 0, F1 – 1, F2 – 4, F3 – 10, F4 – 23, F5 – 45 and F6 – 26). The proportions of successful and unsuccessful releases, respectively, are shown for different fat class categories (fat classes with few data have been pooled).

the test sites (about 1 – 2 hours before local sunset), holding cages were placed on the ground, and all birds were weighed to the nearest 0.1 g with a Pesola spring balance, and fat deposits were estimated visually on their bellies and tracheal pits, according to a seven-class scale (cf. Pettersson and Hasselquist 1985). The estimates of fat levels were made by three different persons

(the authors) with frequent calibrations to minimize inter-observer variability (site 1: Persson, site 2: Sandberg, site 3 and 4: Pettersson). Afterwards the birds were allowed to see the sunset sky (clear skies only) and the surroundings. The same overall procedure was used at release sites 1 and 2 (no transportation involved), with the exception that, at site 2, the birds were held indoors until the onset of experiments (until approx. 1 h after local sunset), and thus were prevented from seeing the twilight sky. Local characteristics of the geomagnetic field at the release sites were checked on geographical and aeromagnetic maps, and with a fluxgate magnetometer to ensure that tests were performed at sites with normal magnetic conditions.

All releases started at the earliest 1 – 2 h after local sunset to avoid that the birds landed prematurely, which is more likely when nearby vegetation is readily visible. Consequently, during the time of releases (clear skies) most or all traces of the sunset sky glow had vanished. The birds were released singly as they were lightly tossed straight up into the air. When test birds were transported from both Falsterbo and Ottenby to be released during the same night and at the same site (releases at site 3, cf. Table 1), individuals from the two capture sites were released in an alternating sequence. This was done to ascertain that environmental conditions were equal for the two experimental categories. A small chemiluminescent plastic container (Cyalume Lightstick, 0.15 g, 95281-17, American Cyanamid Company) was attached to two tailfeathers with transparent adhesive tape. When such a lightstick is bent, a small enclosed glass container is broken and two chemical components will mix. The subsequent chemical reaction produces a clear green light that, under weather conditions with good visibility, is perceivable at distances up to 1 km. The birds get rid of the light capsule as soon as the tape gets wet.

The experimental birds were tossed into the air much in the same way as homing pigeons. Released birds were subsequently followed in 10x40 binoculars, until they vanished from sight. Flight behaviour of each individual was observed and vanishing times were registered by a stop-watch. Vanishing bearings were measured to the nearest 1° with a compass.

Data evaluation and statistics

The released birds were considered as successfully taking off on migratory flights if they gained considerable height and vanished from view without descending or landing. Unsuccessful releases were birds that either landed close to the release point, or flew at low altitudes (at the level of tree tops or below). The vanishing bearings of individual birds were pooled for the different experimental categories to obtain a sample mean direction, according to standard procedures given in Batschelet (1981).

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Table 2. Orientation results at the different release sites. Release site numbers refer to the corresponding numbers on the map in Fig. 1 (cf. also Table 1 for geographical coordinates). Wind velocities are given in m s^{-1} and the direction towards which the wind blew are shown under Wind(α). Wind data for each release were collected at the nearest possible weather station, complemented by visual observations of flags and industrial smoke, close to the release sites. The downwind component (h) and the probability of a significant cluster of headings (V) in the wind direction, calculated according to the V-test with the expected direction = downwind, are also given.

|	Exp. condition	Release site	α	r	N	P	Wind ms^{-1}	Wind(α)	h	V
A. Robins										
	Clear skies, autumn	2. Stensoffa	222°	0.51	32	≤0.001	0	–	–	–
		3. Emmaboda	210°	0.73	50	<0.001	0	–	–	–
		4. Norberg	176°	0.59	12	< 0.05	0	–	–	–
	Overcast, autumn	3. Emmaboda	339°	0.34	46	≤0.005	3	30°	0.31	< 0.05
		4. Norberg	277°	0.32	23	<0.1	3	290°	0.31	< 0.05
	Clear skies, spring	1. Falsterbo	296°	0.74	26	<0.001	2.6	238°	0.39	<0.005
		3. Emmaboda	44°	0.53	33	<0.001	2	70°	0.48	<0.005
		4. Norberg	124°	0.43	9	<0.2	6	165°	0.32	N.S.
	Overcast, spring	1. Falsterbo	345°	0.84	8	≤0.001	1	68°	0.10	N.S.
		4. Norberg	318°	0.83	9	≤0.002	3	180°	−0.62	N.S.
B. Pied Flycatchers										
	Clear skies, autumn	1. Falsterbo	190°	0.49	51	<0.001	3	160°	0.42	<0.001
		3. Emmaboda	109°	0.60	46	<0.001	8	60°	0.39	<0.001
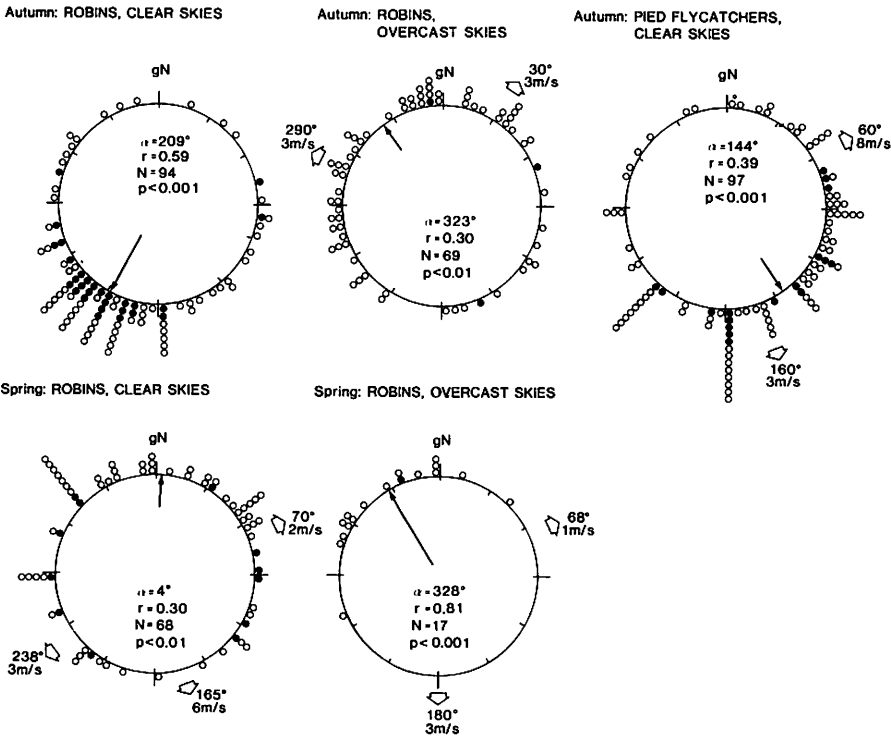
Fig. 3. Vanishing directions of birds released at different sites and during different seasons. Upper left: Robins released under clear autumn skies (calm nights, cf. Table 2) at three different sites; upper middle: corresponding releases under overcast skies (2 sites); upper right: Autumn orientation of released Pied Flycatchers on clear nights at two sites. Lower diagrams show the orientation performance of Robins during spring migration, released under clear starry skies (3 sites) and under overcast skies (2 sites). The mean direction of each sample (α) is represented by an arrow whose length (r) is proportional to the radius of the circle = 1. Furthermore, information on the number of successfully released individuals (N), and significance levels according to the Rayleigh test (P, cf. Batschelet 1981) are given inside the circular diagrams. Filled dots denote old birds and open dots represent first-year birds. Wind directions (towards which the wind was blowing) and velocities during the releases, are shown outside the diagrams, where relevant (cf. Table 2). The location of geographic north (gN) is marked on the outside of each diagram.

Table 3. A comparison of mean vanishing times (MVT) for Robins (A) and Pied Flycatchers (B) released under different experimental conditions. Only successful releases are considered (cf. Method). Statistical differences between samples were calculated according to the Mann-Whitney U-test.

	Exp. cond.	MVT(s)	±S.D.	Probabilities of statistical difference
A. Robins				
	Clear skies, autumn	120	70	}<0.001 } } }
	Overcast, autumn	176	105	} } <0.001 } <0.001 }
	Clear skies, spring	73	42	} } } } <0.001
	Overcast, spring	64	36	} N.S. } } }
B. Pied Flycatchers				
	Clear skies, autumn	69	51	}

We compared the mean axial (bi-directional) vector length resulting from doubling the angles (r_2) with the corresponding average uni-directional vector length prior to doubling (r), and chose the largest of the two. Differences in mean directions between samples were examined by using the 'one-way classification test', and the concentrations of individual headings around the mean angle were compared between test categories with the 'test for the homogeneity of concentration parameters' (Mardia 1972). Differences in fat loads and vanishing times were investigated by using Mann-Whitney's U-test (Sokal and Rohlf 1981).

Results

Body condition and motivation for migratory flights

As shown in Fig. 2, the fuel reserves of released birds, as indicated by visually estimated fat loads, had a strong effect on the birds' decision to take off on migratory flights or not. Robins with high fat levels were significantly more likely to embark on autumn migration flights than were birds with low fuel reserves (χ^2 = 17.9, df. = 2, P < 0.001, Fig. 2A). The same relationship was evident for Robins released during spring migration (χ^2 = 33.8, df. = 3, P < 0.001), with an even more pronounced difference between birds with high and low fat levels (see Fig. 2B). Pied Flycatchers were similarly influenced by stored reserves of migratory fuel (χ^2 = 6.4, df. = 1, P < 0.025), but were more inclined to migrate in spite of limited fat loads (Fig. 2C), than were Robins.

Orientation under clear and overcast skies

Orientation results at the different release sites are shown in Table 2. In Fig. 3, the total outcome of release experiments is illustrated for both Robins and Pied Flycatchers under clear and overcast skies, during different seasons.

Robins released under clear skies during autumn mi-

gration, selected a well-defined mean direction towards SSW – SW (Fig. 3, upper left diagram). The mean direction was similar at the different release sites (Table 2). Vanishing bearings are in good agreement with expected autumn migration courses, as calculated from ringing recoveries (Falsterbo: mean = 209°, Ottenby: mean = 221°, cf. Sandberg et al. 1988). Average vanishing time under clear autumn skies was 120 s (± 70 s, cf. Table 3).

In contrast, autumn releases with Robins under solid overcast (without access to celestial cues), resulted in strikingly different headings (Fig. 3, upper middle diagram). The northwesterly mean direction was significantly different from the corresponding mean orientation under clear autumn skies (P < 0.01). The V-test revealed a significant cluster of headings in the mean wind direction (μ = 2.74, P < 0.005, cf. Table 2). Moreover, the birds required significantly longer time to select migratory directions under overcast than under clear sky releases (P < 0.001, Table 3). The longer vanishing times were a result of more frequent circling before departure bearings were finally selected. Finally, the angular dispersion of vanishing directions increased significantly under overcast as compared to clear sky tests (P < 0.001).

Release experiments conducted with Robins under clear spring skies, resulted in a mean direction towards almost due north (Fig. 3, lower left diagram). Again the birds selected headings in agreement with ringing data from the two capture sites (Falsterbo: mean = 27°, Ottenby: mean = 19°, cf. Sandberg et al. 1988). The Robins were, however, significantly more scattered in their choices of direction as compared to autumn releases under clear skies (P < 0.001). This wide angular spread was a consequence of differences in mean orientation at the different release sites, possibly caused by the different prevailing winds during releases (cf. Table 2). Vanishing intervals were significantly shorter during spring releases under clear skies than during the corresponding autumn tests (P < 0.001, cf. Table 3).

Under solid overcast during spring migration, Robins chose slightly more westerly directions than under clear skies, albeit not significantly so (P > 0.05). The mean orientation was towards NNW into light opposing winds

Table 4. Visually estimated fat loads for north-heading (vanishing directions: 271°–90°) and south-heading (vanishing directions: 91°–270°) Robins and Pied Flycatchers. The mean fuel reserves are compared between categories released under different experimental conditions. Robins released under overcast during spring migration were too few to permit a meaningful analysis and were therefore excluded. Significance levels (P) are according to the Mann-Whitney U-test.

Species	Experimental condition	Mean fat loads				
		North	(± S.D.)	P	South	(± S.D.)
Robin	Clear skies, autumn	4.4	(1.0)	N.S.	4.6	(0.9)
	Solid overcast, autumn	4.3	(0.6)	N.S.	4.4	(0.5)
Robin	Clear skies, spring	4.1	(1.0)	<0.05	3.4	(1.1)
Pied Flycatcher	Clear skies, autumn	4.3	(1.2)	<0.01	5.0	(0.9)

(Fig. 3, lower middle diagram). Orientation scatter was significantly different between clear and overcast spring tests (P < 0.001). There was no difference in vanishing times between clear and overcast conditions (Table 3).

Pied Flycatchers were released in stronger winds blowing towards approximately NE / SE, and they appeared to be influenced by this factor under clear autumn skies (Fig. 3, upper right diagram). The autumn migration of Pied Flycatchers from Sweden, Finland and Norway occurs along a well-defined and narrow southwesterly flight corridor across continental Europe towards the Iberian peninsula (Rendahl and Vestergren 1960, Roos 1984). However, first-year flycatchers display a higher directional variation than do older birds (Rabøl 1978). Pied Flycatchers vanished from view significantly faster than Robins under clear autumn skies (see Table 3). In addition, the flycatchers were significantly more scattered in their directional choices than Robins under the same test condition (P < 0.001).

Effects of body condition on orientation

We examined the possibility that birds which took off on migratory flights, in spite of limited fat reserves, oriented in reverse migratory directions for the season (sensu Alerstam 1978). The total samples of successful releases, were subdivided into north-heading (271°–90°) and south-heading (91°–270°) individuals, respectively. As shown in Table 4, significant differences were found for Robins released under clear skies in spring, and for Pied Flycatchers tested under clear autumn skies (P < 0.05 and P < 0.01, respectively).

Effects of age on orientation

There were sufficient data to allow us to investigate possible differences in orientation performance between old (experienced migrants) and first-year (migratory naive) birds in two cases: (1) Clear sky releases of Robins during autumn migration, and (2) releases of Pied Flycatchers under clear autumn skies. In Figs 3–6, filled symbols represent experienced birds and open symbols denote first-year individuals. Old Robins were significantly more concentrated in their directional choices as compared to young Robins (old: $\alpha = 214°$, r = 0.81, N = 28 vs young: $\alpha = 204°$, r = 0.51, N = 66; P < 0.001). A similar relationship emerged for Pied Flycatchers (experienced: $\alpha = 151°$, r = 0.70, N = 17 vs inexperienced: $\alpha = 140°$, r = 0.39, N = 76; P < 0.025).
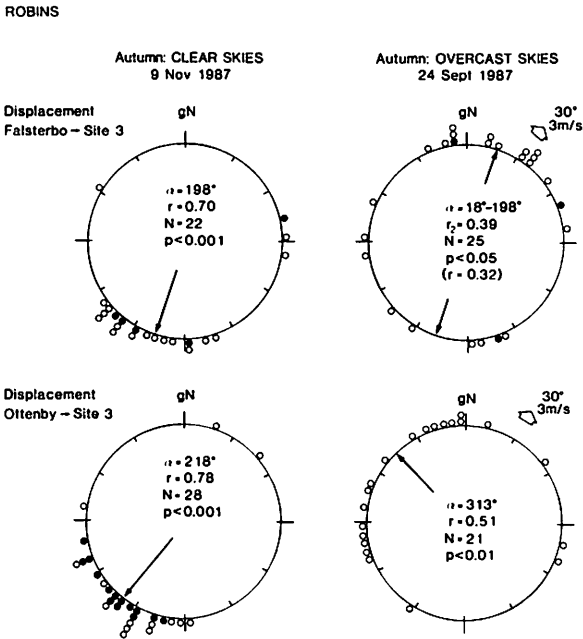

ROBINS

Fig. 4. The results of displacement experiments with Robins during autumn migration. The upper diagrams illustrate the orientation of released Robins after displacement from Falsterbo to site 3 (cf. map in Fig. 1, and Tables 1 and 2), under clear (no wind) and overcast skies, respectively. The corresponding results for Robins transported from Ottenby to site 3 are shown in the lower diagrams. In case of bimodal distributions (cf. Methods), the mean vector length (r₂) is represented by an axis. Other details as in Fig. 3.

Spring: CLEAR SKIES

Displacement
Falsterbo – Site 3   gN

a = 46°
r = 0.52
N = 13
p < 0.05

70°
2m/s

Displacement
Ottenby – Site 3   gN

a = 41°-221°
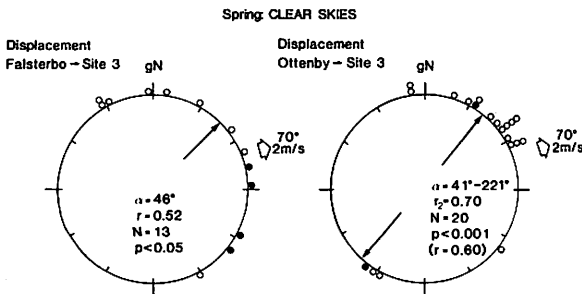r₂ = 0.70
N = 20
p < 0.001
(r = 0.60)

70°
2m/s

Fig. 5. Orientation of Robins displaced from Falsterbo (left diagram) and Ottenby (right diagram) to site 3, and released under clear spring skies. See Figs 3 and 4, and Tables 1 and 2, for further details.

Effects of displacement on orientation

Birds released at site 3 (cf. Fig. 1 and Table 1) were displaced from two different capture sites, thus enabling us to compare the orientation behaviour of two experimental categories that were transported different distances and from different directions. The results are shown in Figs 4, 5 and 6. Note that the birds from the two capture sites were released in an alternating sequence (cf. Methods), and therefore experienced equal environmental test conditions.

The orientation of Robins displaced from Falsterbo and Ottenby, respectively, and released during the autumn migration period under both clear and overcast skies is illustrated in Fig. 4. If the birds recognize the displacement in relation to a goal area (cf. Rabøl 1972), the Falsterbo Robins are expected to be deflected westwards and the Ottenby birds eastwards, compared to their normal migration course (based on ringing recoveries, cf. above). Under clear skies the two groups oriented in good agreement with ringing data from the two capture sites. The two categories did not reveal any significant difference in mean orientation (P > 0.05, cf. Fig. 4, left diagrams). Under solid overcast, Falsterbo Robins displayed an axial distribution of headings with the majority directed towards NNE and downwind, whereas the Ottenby sample showed a unimodal NW orientation at approximately right angles to the wind direction. In spite of the relatively pronounced separation in mean directions, there was no statistically significant difference between Falsterbo and Ottenby birds (P > 0.05, Fig. 4, right diagrams).

During spring releases under clear skies, at site 3, the Robins from Falsterbo and Ottenby chose closely similar mean directions towards NE, in spite of their dissimilar displacement routes (Fig. 5).

Pied Flycatchers that were transported to release site 3 from the two abovementioned capture sites, and subsequently released under clear autumn skies, in relatively strong winds, showed mean orientations that deviated from the expected southwesterly autumn migration direction (Fig. 6, cf. above). The mean directions of the two categories were significantly different from each other (P < 0.05). If we consider the deflecting influence of the relatively strong wind assuming an airspeed of 8 – 10 m⁻¹ for the flycatchers, the calculated mean heading of Falsterbo birds would be approximately towards south, whereas the Ottenby birds headed more or less downwind in easterly directions. There was a significant difference in average fat loads between Falsterbo (mean = 4.9, S.D. = 0.7) and Ottenby (mean = 4.3, S.D. = 0.9) birds (P < 0.05).

Displacements of Robins from Ottenby to release site 4, resulted in two statistically significant mean directions: (1) Autumn releases under clear skies and (2) spring releases under solid overcast (cf. Table 2). In the former case, the birds oriented 45 to the left of the normal autumn migration direction typical for Ottenby Robins (α = 176°, 95% confidence interval = 40° vs mean direction of ringing recoveries = 221°, P < 0.05, cf. Table 2 and above). In the second case, the Robins selected a mean direction towards NNW (α = 338°, 95% conf. int. = 28° vs mean recovery direction = 19°, P < 0.05).

Discussion

When we planned the release experiments presented in this paper, we posed a number of questions:

(1) Are there any differences in orientation performance under clear and overcast skies? The results indicate the importance of celestial directional cues for seasonally appropriate orientation of Robins during autumn migration. While Robins that were released under clear autumn skies oriented in a seasonally correct migratory direction, a distinctly different pattern was obtained when the birds were tested under overcast skies. The northwesterly mean direction under overcast skies confirms the results of earlier radar and field studies as

PIED FLYCATCHERS

Autumn: CLEAR SKIES

Displacement
Falsterbo – Site 3   gN

a = 122°
r = 0.67
N = 32
p < 0.001

60°
8m/s

Displacement
Ottenby – Site 3   gN

a = 68°
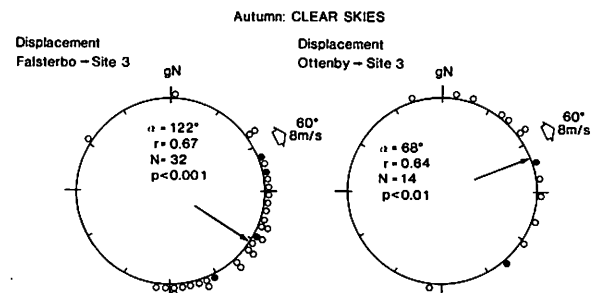r = 0.64
N = 14
p < 0.01

60°
8m/s

Fig. 6. The orientation of released Pied Flycatchers after displacement from two different capture sites during autumn migration. Release tests were performed under clear skies. See Fig. 3, and Tables 1 and 2, for details.

well as release experiments, which have shown that a limited or nonexistent access to celestial cues leads either to disorientation, or more commonly, to downwind orientation in seasonally inappropriate directions (Tinbergen 1956, Hebrard 1972, Emlen 1980, Emlen and Demong 1978, Able 1978, 1980b, 1982a,b).

There were no differences in either mean fat load (clear skies: 4.5 ± 0.9 vs overcast: 4.3 ± 0.6, $P > 0.05$), or in motivation to take off on migratory flights (successful departures: 78% vs 76%), between birds released under clear and overcast skies, respectively. Hence, the observed differences probably reflect difficulties for the birds to determine the appropriate direction without access to visual celestial cues. That the Robins have such difficulties is also suggested by the significantly longer time required for selecting vanishing bearings under overcast as opposed to clear sky releases (cf. Table 3).

This highlights a sharp distinction between field observations and radar studies of experimentally released free-flying birds on the one hand (but see Keeton 1971), and orientation cage experiments on the other hand. Cage tests have shown that most, if not all, migratory birds possess a magnetic compass which should enable them to select appropriate migratory directions without access to celestial orientation cues (cf. Wiltschko and Wiltschko 1988). Why would free-flying migrating birds disregard the possibility of using their magnetic compass to determine a seasonally appropriate migratory direction under overcast conditions? In this context, release experiments at strong geomagnetic anomalies could provide valuable information about the relationship between celestial and magnetic cues for the orientation of free-flying birds.

The absence of a similar effect (i.e. orientation in seasonally inappropriate directions under overcast conditions) during spring migration may indicate a difference in cue integration between experienced (spring) and inexperienced (autumn) Robins. Adult birds may have learnt to integrate directional cues, including geomagnetic information, in a more flexible way than migratory naive birds (cf. below). Alternatively, the observed difference may reflect a distinction between long- and short-distance migration, respectively. Assuming that vernal migration is more rapid than autumnal migration (King et al. 1963), with longer migration legs, allowing spring migrants to arrive as early as possible at the breeding grounds, a backup system based on geomagnetic information could be relatively more profitable for Robins during spring migration. Perhaps experienced birds are more adept at using geomagnetic information as a control device, enabling them to continually check their course, and to ensure that inclement weather en route does not result in fatal deviations from the intended migratory direction (cf. Alerstam 1988).

Unfortunately, we do not have any data on the orientation behaviour of Pied Flycatchers under solid overcast. There is an interesting possibility that long-distance migrants, like Pied Flycatchers, are more prone towards using their magnetic compass and therefore more independent of access to celestial cues for a successful determination of migratory directions than are short-distance migrants like Robins (cf. Wiltschko and Wiltschko 1975a,b). This is supported by the results of release experiments with Wheatears *Oenanthe oenanthe* conducted under solid overcast in Greenland (Ottosson et al. 1990). The mean direction of these Wheatears was in agreement with ringing data from Greenland, despite the absence of celestial information.

(2) How do the fuel reserves of migratory birds affect orientation and the decision to migrate? As shown in Fig. 2, birds with low fat levels were significantly less likely to embark on migration than were fatter birds. The pronounced effect of the amount of stored fuel on the bird's decision to depart on a migratory flight lends support to a number of earlier stop-over studies (Bairlein 1985, Biebach 1985, Biebach et al. 1986, Moore and Kerlinger 1987) that point to a relationship between fat reserves and the likelihood of resuming migration from stop-over sites. Able (1977) found no correlation between the quantity of migratory activity and the amount of visually estimated fat, but fatter birds were significantly more likely to exhibit oriented movements in cages. If fat deposits are scanty, the birds may decide to stay on their current position to replenish their reserves, or alternatively, to engage in reorientation, probably in search of more profitable resting grounds (Table 4, cf. also Alerstam 1978, Lindström and Alerstam 1986). The choice between these two options may depend on the amount of stored fat and the profitability of the current stop-over site (cf. Biebach 1985, Terrill 1988).

Reorientation of lean birds, as opposed to fat birds, was revealed for Pied Flycatchers released under clear autumn skies, and for spring migrating Robins released under clear skies. In contrast, there was no such relationship between body condition and orientation in autumn releases of Robins (valid for both clear and overcast skies). This difference may be explained by the fact that Pied Flycatchers travel long distances to wintering grounds in central and western Africa and thus may be expected to rely strongly on both favourable weather conditions and sufficient amounts of fuel reserves before deciding to embark on migration. Perhaps this is also relevant for spring migrating Robins, as opposed to autumn migrating Robins (cf. above).

(3) Do orientation behaviour and accuracy differ between experienced and inexperienced migrants? We obtained enough data to answer this question only under clear sky autumn tests for Robins as well as Pied Flycatchers. In both cases, experienced birds were significantly more concentrated in their vanishing directions than were inexperienced birds (cf. Rabøl 1978, Moore 1984). This indicates that old birds are less likely to make orientation errors. It is interesting to note that when orientation errors are mentioned in the literature it is almost exclusively in conjunction with migratory

naive (first-year) birds (Drury and Keith 1962, Able 1977, Ralph 1978, Desante 1983).

The fact that first-year migrants show a higher variability in directional choices than adults, suggests either that stabilizing selection operates to maintain the orientation within narrow limits (cf. Rabøl 1978), or that adults orient with higher precision due to experience. En route experience, including stopover and winter site attachment, may explain why the orientation performance of adult birds differ fundamentally from that of first-year migrants (cf. Alerstam 1990).

(4) Do long- and short-distance migrants behave differently? The only clear difference in orientation performance between Robins and Pied Flycatchers, tested under clear autumn skies, was the significantly shorter mean vanishing interval recorded for the latter species (Table 3). This was probably due to the fact that Pied Flycatchers circled considerably less before they determined their departure direction. The mean vanishing time of spring migrating Robins was, however, of the same order of magnitude as that registered for Pied Flycatchers. One may speculate that the flycatchers (and perhaps spring migrating Robins) have learned to use available directional information, including geomagnetic cues, in a more efficient and accurate way (cf. above) than have young Robins on their first autumn migration.

(5) Are there any displacement effects on orientation? Release experiments conducted at site 3 (cf. Tables 1 and 2) were specifically designed to allow comparisons of birds that were transported in different directions and distances. We performed four different releases at this site and the results are shown in Figs 4, 5 and 6. The only occasion when a significant difference emerged between the two experimental categories (Falsterbo vs Ottenby birds) was in the release of Pied Flycatchers (Fig. 6).

Allowing for the effect of wind deflection, the Falsterbo birds headed towards approx. south and the Ottenby flycatchers towards east. This could be interpreted as a compensatory response towards the two different capture sites (cf. Rabøl 1972). However, since the Ottenby birds carried significantly less fat than the birds from Falsterbo, an alternative explanation could be that the former group headed approximately downwind in reverse directions for the season, presumably to replenish their fuel reserves. In contrast, the Falsterbo birds tried to orient in an appropriate direction, but failed to do so because of the strong winds.

Robins that were transported from Ottenby and released under clear autumn skies at site 4 (cf. Table 2), showed a mean orientation that was significantly different from the expected direction based on ringing data. Again, this could be interpreted as a compensatory *response* towards the capture site. However, when Robins were displaced along the same route during spring migration and released under overcast skies, they showed a mean orientation towards NNW, significantly

different from the recovery direction, but away from the capture site (Table 2).

It must be concluded that the results of the displacement experiments are inconsistent and difficult to interpret in terms of compensatory behaviour, and that alternative explanations for the observed differences may be equally valid. It could be argued, however, that our displacement routes were inadequate for the detection of such effects, and more specifically, that the test birds ought to have been displaced longer distances on an east – west axis.

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