

Diurnal migration of passerine birds over South Sweden in relation to wind direction and topography

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The diurnal migration of passerine birds over South Sweden was studied using simultaneous radar and field observations during the autumns 1971 to 1973. Main movements were directed either towards SSW or towards SE/SSE. Radar and visible migration consisted of different bird categories flying at high and low altitudes, respectively. Radar migration was most intensive under NE winds, while visible departures from promontories over the sea were associated with headwinds (SE to W). Visible movements along the east and west coasts took place under offshore winds, while inland visible migration was uncorrelated with wind direction. Compensation for wind drift was achieved, but wind still affected flight directions: radar track directions shifted away from, and visible track directions into, the wind direction.

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INTRODUCTION

The diurnal migration of passerine birds is a highly complicated process owing to, among other things, the birds' reactions to topography and various meteorological factors, their variable flight altitudes, and the simultaneous activity of many species (Rudebeck 1950, van Dobben 1953, Ulfstrand 1960, Gehring 1963, Gruys-Casimir 1965, Evans 1966b).

Field observations of diurnal passerine migration have to be treated with great caution. Only low-flying birds are seen, and large movements at high altitude may pass unnoticed. In addition, considerable errors may affect the estimates of the number of birds involved (Enemar 1964, Källander & Rydén 1974).

Radar exclusively records bird movements at high altitudes and ignores all low-flying birds (Wilcock 1964, Alerstam & Ulfstrand 1972). Consequently, radar and field studies are almost completely supplementary.

This paper reports on studies conducted during the autumns 1971 to 1973 at three radar stations and 16 observation sites in South Sweden. The objective is to describe the passerine migration at sites differing in topography and to analyse its relationship with prevailing wind conditions.

METHODS

Three high power S-band radar stations in Gothenburg, in Skåne, and in Blekinge were filmed with time-lapse technique (2.5 frames/min). The first two stations were filmed from 17 September to 8 October 1972 and from 23 September to 14 October 1973. The latter station was filmed only during the study period in 1973.

Small-sized echoes from passerines migrating in flocks (Alerstam & Ulfstrand 1972) usually moved on a broad front in vast numbers, and the daily magnitude of migration was rated as

low, moderate, or high. Flight paths of individual echoes were plotted on maps and daily mean track directions were estimated over 13 different areas (A to M in Fig. 1).

Daily field observations between 0600 and 1400 hrs took place at a total of 16 different sites (1 to 16 in Fig. 1) during 1971 to 1973. Five observation sites were manned from 21 September to 10 October 1971, and the passerine migration at these sites was compared to the movements of small echoes, as recorded from the Bulltofta radar, by Alerstam & Ulfstrand (1972). The field data from 1971 are included in the present study. Field observa-

tions were conducted at seven and eleven sites in 1972 and 1973, respectively, simultaneously with radar filming.

Observations at sites 1, 10, and 11 refer to departures over the sea. Such departures took place also from site 14, but a considerable part of the birds flew towards a land area visible in the southeast. Oversea departures were scarce at the coastal sites 2, 3, 4, 5, 12, and 15, where movements along the coastlines dominated. Departures over the Kattegatt occurred from site 13, but were usually directed towards about NW, whereas southward migration at this site comprised birds arriving over the sea.

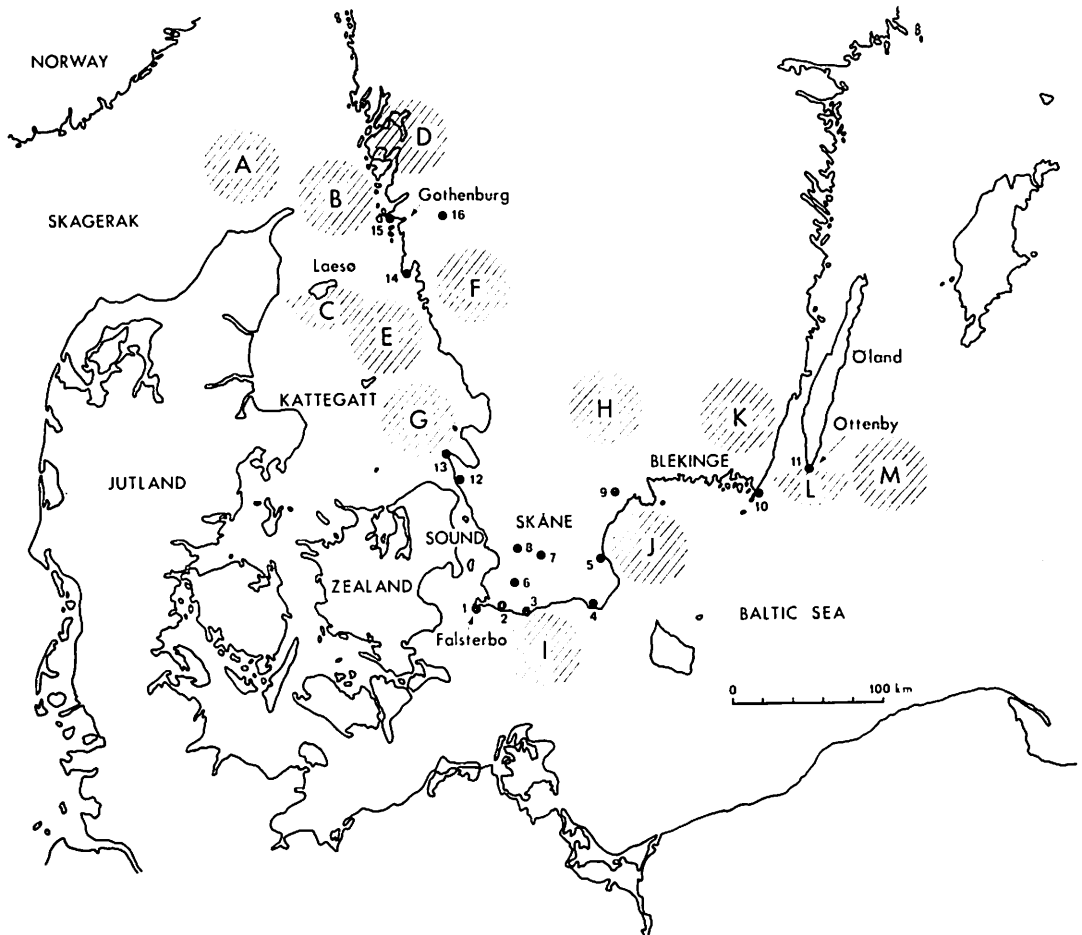


Fig. 1. Study area. Field observations took place at sites 1-16 and track directions were measured on the radars over the areas A-M.

The inland observation sites 8 and 9 were located in open farmland, and sites 6, 7, and 16 were situated within woodland areas.

Wind direction and speed were evaluated from ground-level synoptic maps (at 0700 hrs), assuming wind direction to be parallel to the isobars and wind speed related to the air pressure gradient. These wind conditions prevail at about 500–1000 m altitude. The ground-level wind directions were closely correlated to these directions. High-altitude wind data were used when analysing the radar data, whereas field observations at the different sites were related to ground-level wind measurements (at 0700 hrs) from the nearest weather station (always within 30 km, most often in the immediate vicinity).

RESULTS

Radar (1972, 1973)

Periodicity of passerine migration. Passerine migration usually became visible on the radarscopes between 0500 and 0600 hrs. The start occurred, rather abruptly, on average at 43 min ($SE \pm 1.6$, $n = 34$) before sunrise. On days with 0/8 to 5/8 cloud cover, the start took place at 46 min ($SE \pm 1.6$, $n = 25$) and on days

with 6/8 to 8/8 cloud cover at 36 min ($SE \pm 3.3$, $n = 9$) before sunrise. The difference between days of different degrees of cloudiness is significant ($p < 0.01$). The migratory peak was usually recorded during 1–2 hours following the starting time, and activity most often ceased before 1100 hrs.

SSW- and SE/SSE-bound migration. Migratory movements within the sector WSW to ESE greatly dominated, and most often the main direction was towards SSW or SE/SSE. Normally movements were restricted to either of these directions, but sometimes simultaneous movements in both directions were witnessed. Since movements towards due S were scarce, basically SW- and SE-bound cohorts may be grouped in separate categories with only little overlapping. As shown in Table I, SW-bound movements occurred under wind directions with an easterly component, or in calm weather, while SE-bound movements were confined to days with a westerly wind component. No significant movements were recorded under headwind conditions.

Magnitudes of migratory movements. On five days heavy and widespread rain prevailed, during which no migration was seen either on

Table I. Frequency of SSW- and SE/SSE-bound radar movements in relation to wind direction. Track directions west of 175° were classified as SSW-movements, those east of 175° as SE/SSE-movements. This division was chosen because of the scarcity of movements directed towards about 175° . No differences in frequency of movements were found between NE and SE winds or NW and SW winds. This justifies the classification of wind directions in only two groups, W and E winds, respectively. In A, there were 3 days with no data available, 18 days with SSW-movements, 10 days with SE/SSE-movements and 10 days with simultaneous SSW- and SE/SSE-migration. In B, the corresponding figures were 12, 20, 8 and 1, respectively

	SSW-movements		SE/SSE-movements	
	Days with movements	Days without movements	Days with movements	Days without movements
A. Gothenburg				
Easterly winds	14	1	4	11
Westerly winds	4	9	12	1
Calm	10	0	4	6
B. Skåne				
Easterly winds	5	0	0	5
Westerly winds	5	8	9	4
Calm	11	0	0	11

the radarscopes or by the field observers (two days in 1971, three days in 1973). These days are excluded from all the following analyses.

The magnitudes of radar migration in relation to the wind conditions are presented in Table II. Approximately NE winds were associated with the largest migratory movements. Consequently migratory movements towards SSW are larger, on average, than those towards SE/SSE (Table III).

Track and heading directions. The heading direction (towards which the birds aim, i. e. the direction along the body axis of the flying bird) can be calculated from the track direction (the course recorded on the radar screens or by a field observer), the estimated air speed of the bird, and the wind direction and wind speed. In the subsequent calculations, the true air speed of the migrating passerines has been assumed to be 40 km/hr (Bruderer 1971). Even a considerable error in this estimate will not affect the conclusions appreciably.

The angle between track and heading directions corresponds (A) to the amount of wind drift, if birds fly on fixed headings, and (B) to the amount of compensation, if they fly on fixed track directions. If the daily mean track directions are plotted against this angle (track direction minus heading direction) and the

corresponding equation using the linear least square method is determined, the regression coefficient in case (A) will be 1 and in case (B) zero. A negative regression coefficient would indicate over-compensation.

Table IV presents the coefficients calculated separately for each of 13 different areas (Fig. 1) and for echo cohorts moving towards SSW and SE/SSE, respectively.

When SSW- and SE/SSE-bound movements were treated together, the regression coefficients in all cases were significantly larger than zero and in many cases quite close to one. This result might be interpreted as an indication that the birds did not compensate for wind deflection (cf. Alerstam & Ulfstrand 1972).

However, if the regression analysis was carried out for the SSW- and SE/SSE-bound cohorts separately, then regression coefficients closer to zero were obtained. In 19 out of 23 cases they were significantly lower than 1; at the same time, excluding cases with scarce data, they were significantly greater than zero (between + 0.18 and + 0.70). The different result when all data were pooled and when each direction category was treated separately provides additional justification for our division of the migrating cohorts in two separate categories with respect to their track directions. Since different birds were involved in the movements towards east and west of south, respectively, the fact that, when all movements were included, regression coefficients close to 1 were found was purely coincidental.

Table II. Relation between wind direction and occasions of low, medium and high radar migration intensity

Wind direction	Magnitude of migration (number of days)		
	Low	Medium	High
A. Gothenburg			
NE	—	2	5
SE	1	3	3
SW	—	3	—
NW	4	4	3
Calm	—	7	3
B. Skåne			
NE	—	—	6
SE	—	1	—
SW	—	1	1
NW	4	4	1
Calm	—	5	6

Table III. Relation between flight direction and magnitude of radar movements. Days with simultaneous migration towards both SSW and SE/SSE are excluded from this table. See Table I.

Flight direction	Magnitude of migration (number of days)		
	Low	Medium	High
A. Gothenburg			
SSW	1	9	8
SE/SSE	4	5	1
B. Skåne			
SSW	—	6	14
SE/SSE	4	4	—

Table IV. Regression coefficients (\pm S. E.) for the regression of track directions on the angles between track and heading directions in radar observations. Numbers of days are given in brackets. The angle between track and heading directions is calculated as track direction minus heading direction. Thus this angle is positive when track direction is to the right of the heading direction and vice versa. A indicates regression coefficients not significantly different from 0, and B coefficients not significantly different from 1

	Area	All movements	SSW-movements	SE/SSE-movements
Echoes over the sea	A	0.32 ± 0.13 (18)	-0.09 ± 0.09 (10)	A 0.20 ± 0.11 (8)
	B	0.48 ± 0.10 (31)	0.18 ± 0.10 (19)	A 0.19 ± 0.09 (12)
	E	0.33 ± 0.12 (26)	0.11 ± 0.06 (20)	A 0.08 ± 0.15 (6)
	G	0.92 ± 0.17 (24)	0.47 ± 0.19 (18)	-0.06 ± 0.18 (6)
	I	0.96 ± 0.10 (23)	0.57 ± 0.13 (17)	0.25 ± 0.20 (6)
	J	1.11 ± 0.15 (28)	0.42 ± 0.14 (20)	0.25 ± 0.23 (8)
	M	1.15 ± 0.25 (15)	0.70 ± 0.28 (10)	B
Echoes departing from land	C	0.81 ± 0.20 (15)	0.40 ± 0.64 (5)	A,B 0.67 ± 0.44 (10)
	L	0.44 ± 0.13 (12)	0.31 ± 0.13 (11)	
Echoes over the land	D	0.40 ± 0.10 (21)	0.18 ± 0.08 (15)	0.13 ± 0.15 (6)
	F	0.54 ± 0.11 (24)	0.18 ± 0.07 (18)	-0.05 ± 0.11 (6)
	H	1.92 ± 0.32 (28)	0.24 ± 0.33 (20)	-0.12 ± 0.53 (8)
	K	1.21 ± 0.30 (17)	0.40 ± 0.25 (13)	

The regression coefficients for the SSW-moving echo cohorts at the inland areas F, H, and K (Fig. 1) were smaller than those calculated for the same echoes when travelling over the sea areas, G, I, and J (Table IV). The median regression coefficients for all areas pooled were 0.40 ($n = 9$) over the sea and

0.21 ($n = 4$) over the land; the difference, however, is not significant (Mann-Whitney U-test, $p > 0.05$).

Regional differences in track directions. Do birds in the western and eastern parts of the study region differ with respect to their flight directions under comparable wind conditions?

Table V. Normal directions (in degrees) of radar movements over different areas (A to M, Fig. 1). Directions (\pm S. D.) for SSW movements were corrected for wind influence using the regression equations on which the coefficients in Table IV were based. n = number of days

Area	SSW-movements					SE/SSE-movements		
	Median direction	Range	Corrected for wind influence	S. D.	n	Median direction	Range	n
A	187	180–198	188	6	10	157	127–169	9
B	194.5	180–223	193	9	20	159	129–173	14
C	181	176–218	171	19	5	156.5	100–173	10
D	192	180–210	191	7	15	158	138–171	6
E	190	180–214	190	7	20	151	128–161	7
F	200	188–217	198	6	18	151	144–161	6
G	184	176–230	199	11	18	145	128–173	7
H	206	179–223	205	11	21	138	115–150	9
I	200	190–238	202	8	17	155	145–162	7
J	204	189–239	207	10	20	142	138–158	9
K	228	192–304	224	27	13	121.5	98–140	4
L	209	187–236	210	13	12	159		1
M	224	186–275	215	24	10	134	95–170	5

Table VI. Total numbers of migrating birds recorded at different observation sites. The study periods covered 21 Sept.–10 Oct. 1971, 17 Sept.–8 Oct. 1972 and 23 Sept.–14 Oct. 1973

Observation site	Approximate direction	Year	<i>Fringilla</i> sp.	<i>Carduelis spinus</i>	<i>Carduelis cannabina</i>	<i>Anthus pratensis</i>	<i>Alauda arvensis</i>	<i>Sturnus vulgaris</i>	<i>Hirundo rustica</i>	<i>Motacilla alba</i>	<i>Parus caeruleus</i>
1	W/SW	1971	518,046*					38,071			
		1972	156,470	4,263	8,694	1,087	978	25,558	3,237	25	3,323
		1973	403,716	7,144	20,824	2,842	794	69,960	9,382	22	4,008
2	W	1971	561,395	80	4,521	1,229	877	13,474	1,954		
		1971	81,526	257	82	27	73	121	190		
3	W	1972	97,383	10,886	20,087	1,959	1,658	6,812	6,292	638	1,333
		1973	170,847	16,850	7,554	1,818	1,096	17,768	3,908	119	488
	E	1972	4,503	3,625	2,067	219	379	15	1,746	143	1
		1973	763	1,098	779	631	1,194	65	472	40	242
4	W	1972	20,138	4,138	7,109	1,481	1,474	1,689	3,122	1,061	532
		1972	1,648	270	1,316	123	42	27	110	898	
5	S	1972	17,237	417	262	38	211	20	1,584	273	
		1973	4,193	55	85	12	54	113	244	47	21**
	N	1972	78,906	2,317	776	281	173	12,528	3,027	150	
		1973	2,485	215	111	21	11	667		1	68
	S	1971	23,798	3,091	880	476	732	2,077	1,356	24	
		1972	13,633	20	886	640	2,980	1,120	293	159	
6	N	1973	15,280	143	772	509	1,933	3,930	894	20	4
		1971	9,848	1,599	7		45	32	215		
	S	1972	1,437	197	86	294	837	67	107	52	
		1973	18,547	163	70	30	1,173	70	70		
	S	1971	20,558	1,938	172	151	134	1,336	1,821	380	
		1971	2,420	632		10	36		154	7	
8	S	1972	984	149	114	575	740	1,683	408	54	10
		1972	9,784	445	1,066	458	89	139	149	45	318
9	S	1973	5,065	1,305	238	497	1,542	4,071	1,753	224	118
		1973	29	271	47		28		3		252
10	SW	1973	954	1,469	376	1,498	391	1,206	1,592	855	647

11	SW	1973	21,085	41	13,668	3,092	5,860	6,333	3,091	4,748	10
12	S	1973	46,083	1,328	1,692	2,633	2,494	16,596	1,107	81	2,508
	N	1973	1,690	115	15			2,385	86		
13	S	1972	1,556	188		472	346	2,009	112		905
	N	1972	4,370	61	373	1	40	8,319	322	8	11,116***
14	S	1973	40,990	2,649	2,539	3,092	1,525	13,732	420	241	773
	N	1973	2,863	193							
15	S	1973	11,445	996	228	5,733	331	11,449	303	93	128
	N	1973	132	64	16	15				2	
16	S	1973	11,965	1,907	266	3,332	632	45	104	241	17
	N	1973	89	48	1	117	17		18		

* This figure includes all passerines except *Sturnus vulgaris* and *Parus caeruleus*.

** 549 inds. migrated towards W.

*** A large proportion of *Parus ater* is included.

To examine this question all the 13 measuring areas (Fig. 1) were arranged from WNW to ESE, that is, along a line perpendicular to the main direction of the dominating SSW-bound echo category. Table V presents the hypothetical track directions under no wind influence determined from the regression equations (Table IV), as well as the median track directions, for each of the areas. For SE/SSE-bound movements only the latter value is given, since data do not permit the calculation of the hypothetical direction.

Tracks of cohorts belonging to the SSW-bound category over the western part of the study region were directed more to the south (about 190°) than over the eastern part (about 210°). When the hypothetical directions were compared with the position of the measuring area on the WNW/ESE axis, a highly significant ($p < 0.001$) Spearman rank correlation coefficient ($r_s = 0.93$) was obtained, and also when the median track directions were used ($r_s = 0.82$, $p < 0.001$).

The directions of the SE/SSE-bound cohorts also changed along the same axis; that is, were directed more to the south (about 160°) in the western part, and more to the east (130 to 140°) in the eastern part of the study area ($r_s = 0.87$, $p < 0.001$).

Field observations (1971, 1972, 1973)

Periodicity. Within the daily period covered by the field observations a peak migratory activity usually occurred within the first three hours after sunrise (cf. Edelstam 1972, Ulfstrand et al. 1974).

Directions and magnitudes. In Table VI the total numbers of migrating birds at each site are shown. The bird categories have been selected so as to encompass the great majority of all passerines. At most sites, finches *Fringilla* sp. were most numerous. Among these the Chaffinch *Fringilla coelebs* generally represented the main portion, the rest being Bramblings *F. montifringilla*. The Blue Tit only migrated in 1972 and 1973. The migration of this species has clear irruptive tendencies (Ulfstrand 1963).

Northbound movements (WNW to ENE)

Table VII. Southbound (E to W, inclusively) migration in relation to wind direction. Preferred wind directions are given

Obs. site	<i>Fringilla</i> sp.				<i>Carduelis spinus</i>				<i>Carduelis cannabina</i>				<i>Anthus pratensis</i>			
1	W p < 0.001	-	S p < 0.10	SW p < 0.001	W p < 0.001	-	S p < 0.10	SW p < 0.001	-	-	S p < 0.01	-	-	-	S p < 0.10	SW p < 0.05
3	W p < 0.01	-	-	SW p < 0.10	W p < 0.05	NW p < 0.10	N p < 0.10	-	-	-	-	-	-	-	-	-
5	-	-	-	SW p < 0.10	-	-	-	-	-	-	-	SW p < 0.05	-	-	-	-
10	-	-	-	-	-	NW p < 0.10	-	-	-	-	-	-	W p < 0.10	-	-	SW p < 0.05
12	E p < 0.05	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13	E p < 0.05	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14	-	-	-	-	-	-	-	-	E p < 0.10	SE p < 0.10	-	-	-	-	-	-

Note: Daily totals comprising more or less than 1 %, respectively, of the annual total (Table VI) were separated. No analysis was carried out based on totals of less than 100 birds.

The frequencies of these two categories under different wind conditions were compared in four tests:

- A) E versus W winds = N-SSE versus S-NNW winds
- B) SE versus NW winds = NE-SSW versus SW-NNE winds
- C) S versus N winds = E-WSW versus W-ENE winds
- D) SW versus NE winds = SE-WNW versus NW-ESE winds

Fisher exact probability or χ^2 (for $N > 50$) tests were used.

The outcomes of the tests A-D are shown for each species and observation site. Preferred wind directions are entered in the table and two-tailed probabilities are given. - = $p > 0.10$.

Tests were carried out also for observation sites 2 (18 observation days), 4 (22), 6 (53), 7 (18), 8 (17), 9 (15), 11 (19), 15 and 16 (15), but no correlation to wind direction was found ($p > 0.10$). The exception was *Carduelis spinus* which preferred NE winds ($p < 0.05$) at site 6. Migratory activity of *Parus caeruleus* at sites 1, 3, 4, 9, 10, 12 and 14 was analysed in relation to wind direction, but no correlation was found ($p > 0.10$).

made up a remarkable proportion at many sites, especially in the inland. Usually these movements culminated later in the day than the southbound movements. In the following discussion we will only treat the southbound movements.

Daily numbers of migrating birds at all sites are related to wind directions in Table VII.

Although data are fairly scarce and allow only a rough analysis, it seems that (A) at sites 1 and 3, on the south coast of Skåne, migration generally was maximal with winds about W, (B) at sites 5 and 10, on the east coast, migration was also most intense with winds about W, and (C) at sites 12 to 14, on the west coast, migration culminated with winds about E. No

<i>Alauda arvensis</i>				<i>Sturnus vulgaris</i>				<i>Hirundo rustica</i>				No. of days
-	-	-	-	-	-	-	-	-	S	SW		<i>Fringilla</i> sp. and <i>Sturnus vulgaris</i> 58
									$p < 0.05$	$p < 0.10$		Others 40
E $p < 0.05$	-	-	-	-	SE $p < 0.10$	-	-	-	-	-	-	39
-	-	-	-	-	-	-	-	-	-	-	-	<i>Fringilla</i> sp. and <i>Hirundo rustica</i> 41
												Others 22
W $p < 0.10$	-	-	-	W $p < 0.10$	-	-	SW $p < 0.05$	-	-	-	-	18
-	SE $p < 0.10$	-	-	-	-	-	-	-	-	-	-	18
-	-	S $p < 0.10$	-	-	-	S $p < 0.10$	-	-	-	-	-	22
-	-	-	-	-	-	-	-	-	-	-	-	19

clear relationship can be detected between wind direction and migratory intensity at the inland localities (sites 6 to 9). This is seen in the data from site 6 from which we have information from all the years (Table VIII).

In Table IX the extensive data from the bird stations at Falsterbo (site 1) and Ottenby (site 11) are analysed along the same lines. Generally migration culminated at winds between SE and W. A distinct exception is the White Wag-tail, which at Ottenby was recorded in largest numbers with about E winds. At both sites Swallows showed little relationship to wind directions.

Track directions and wind. In Table X the course of the migrating birds as recorded by the observers at sites 6 and 7 is related to prevailing wind directions; data from other inland sites are inadequate for this analysis. In all species except the Swallow, movements were directed more towards S/SE with E winds,

and more towards SW with W winds. This trend was significant for the finches, Starling, and Siskin.

SE-travelling birds over the inland, when approaching the south coast of Skåne, ought to be deflected towards E along the coastline, while SW-bound birds ought to be linked towards W. This is examined in Table XI, from which may be seen that E-bound movements along the south coast of Skåne were associated with E winds.

DISCUSSION

Track directions: radar and visible

Mean daily track directions of radar movements shifted towards the left when winds were blowing from the right and conversely (Table IV). Such a relationship may be interpreted as wind drift of birds flying on fixed headings, as seems reasonable as long as all movements in

Table VIII. Average number of migrating birds seen per day at observation site 6 (Sturup 1971–1973) in relation to wind direction

Wind direction	No. of days	<i>Fringilla</i> sp.	<i>Carduelis spinus</i>	<i>Carduelis cannabina</i>	<i>Anthus pratensis</i>	<i>Alauda arvensis</i>	<i>Sturnus vulgaris</i>	<i>Hirundo rustica</i>	<i>Motacilla alba</i>
NNE-NE	5	392	5	140	7	47	32	—	—
ENE-ESE	19	911	53	58	36	125	151	81	4
SSE-SSW	2	42	—	2	26	22	—	13	6
SW-W	19	1,554	74	39	21	48	126	28	2
NW-N	8	347	92	36	57	87	53	36	2

the ESE to WSW sector are combined (cf. Alerstam & Ulfstrand 1972). However, after splitting the movements into two groups, ESE-S and S-WSW, respectively, the relationship does not hold, and the drift effect was significantly less than expected assuming fixed headings of the birds. This effect may be interpreted as due to either incomplete wind compensation or 'pseudodrift' (Evans 1966a, Nisbet & Drury 1967).

Wood Pigeons *Columba palumbus* (Alerstam & Ulfstrand 1974a) and Cranes *Grus grus* (Alerstam in press) were found to compensate incompletely over the sea. Probably the same holds for the passerines, since the effects of wind appeared greater over the sea than over the land. This may be due to less accurate orientation in the absence of landmarks.

The relation between wind direction and track direction of low altitude inland migration was opposite to that described above for the radar movements. As shown in Table X, winds from the right were combined with tracks towards the right, and conversely.

A possible explanation is the existence, within a restricted area, of bird cohorts – different species and/or different subpopulations of the same species – with different preferred track directions. All these directions in autumn lie between approx. ESE and WSW. Under winds with an E component, birds with preferred track directions to the W of S would fly with following winds at high altitudes and thus become registered by radar, while cohorts with preferred track directions towards E of S would travel at low altitudes and become visible to field observers. Under W winds, the converse relationships would hold.

As pointed out above, track directions of radar echo cohorts moving W of S shifted along a gradient running from WNW to ESE (Table V). This fits in with Perdeck's (1970) model of the standard direction of the Chaffinch, the most abundant diurnal migrant in southern Scandinavia. He showed that Scandinavian Chaffinches had a standard direction about S/SSW around the Skagerak and the Kattegatt, about SSW/SW in Skåne and Denmark, and more to the W in the Netherlands, Belgium, and northern France.

A similar shift in the opposite direction was established for the birds moving towards E of S (Table V). While the gradual shift in flight directions described for the Chaffinches may be viewed as an adaptation to avoid crossing the North Sea, the explanation is hard to find for the SE-migrants.

The SE-bound cohorts

The bird migration in southern Scandinavia generally is directed towards W of S (Rudebeck 1950). However, the data presented in this paper demonstrate that a larger proportion than expected of the diurnally migrating passerines fly towards E of S. These birds were not victims of wind drift but were flying on preferred tracks.

Which birds are involved in the SE-bound movements? The following alternatives are conceivable:

(A) The winterquarters are situated to the SE of Scandinavia. Few diurnally migrating passerines breeding in Scandinavia, however, are known to winter in a southeasterly direction. One of the few examples is the White

Table IX. Average number of migrating birds seen per day at Falsterbo and Ottenby in relation to wind direction. Number of days are shown in brackets. The analyses are based on daily numbers of migrating birds during the main migration periods (see below) in eleven years (1949–1960, except 1951) at Falsterbo, except for *Anthus pratensis*, *Alauda arvensis* and *Motacilla alba*, for which data were available from only four years (1949, 1950, 1952, 1953, Ulfstrand et al. 1974). At Ottenby data were collected during ten years (1947–1956) (Edelstam 1972). Days with extensive rain were omitted

Falsterbo – site 1:

Wind direction	<i>Fringilla</i> sp.	<i>Carduelis</i> <i>spinus</i>	<i>Carduelis</i> <i>cannabina</i>	<i>Anthus</i> <i>pratensis</i>	<i>Alauda</i> <i>arvensis</i>	<i>Sturnus</i> <i>vulgaris</i>	<i>Hirundo</i> <i>rustica</i>	<i>Motacilla</i> <i>alba</i>
010°–060°	404 (14)	61 (22)	171 (14)	6 (1)	5 (7)	844 (16)	549 (25)	15 (5)
070°–120°	1,570 (26)	48 (45)	409 (26)	25 (2)	15 (9)	1,950 (30)	570 (63)	21 (21)
130°–180°	16,005 (41)	435 (58)	2,129 (41)	542 (9)	51 (16)	3,432 (39)	812 (67)	80 (13)
190°–240°	20,614 (32)	396 (42)	2,336 (32)	574 (12)	6 (18)	2,845 (28)	581 (50)	104 (6)
250°–300°	22,225 (61)	411 (81)	1,925 (61)	1,323 (22)	14 (27)	2,512 (47)	245 (117)	35 (38)
310°–360°	8,723 (33)	219 (41)	1,016 (33)	64 (11)	15 (13)	2,059 (28)	350 (62)	46 (8)
Main migration period	24/9–13/10	19/9–17/10	24/9–13/10	24/9–8/10	24/9–17/10	29/9–17/10	1/9–8/10	25/8–18/9

Ottenby – site 11:

Wind direction	<i>Fringilla</i> <i>coelebs</i>	<i>Fringilla</i> <i>montifri.</i>	<i>Carduelis</i> <i>spinus</i>	<i>Carduelis</i> <i>cannabina</i>	<i>Anthus</i> <i>pratensis</i>	<i>Alauda</i> <i>arvensis</i>	<i>Sturnus</i> <i>vulgaris</i>	<i>Hirundo</i> <i>rustica</i>	<i>Motacilla</i> <i>alba</i>	<i>Parus</i> <i>caeruleus</i>
010°–060°	58 (26)	120 (14)	53 (26)	581 (26)	14 (31)	52 (23)	219 (27)	50 (29)	1,102 (29)	2 (12)
070°–120°	88 (22)	118 (16)	29 (21)	373 (22)	13 (27)	69 (24)	611 (27)	117 (23)	1,245 (23)	8 (12)
130°–180°	455 (61)	628 (36)	129 (52)	602 (61)	49 (71)	168 (63)	1,226 (65)	127 (55)	836 (55)	29 (21)
190°–240°	516 (43)	397 (24)	92 (37)	454 (43)	54 (49)	146 (43)	1,442 (38)	109 (37)	484 (37)	24 (14)
250°–300°	377 (85)	342 (41)	128 (75)	627 (85)	89 (97)	63 (86)	1,024 (72)	199 (99)	473 (99)	25 (23)
310°–360°	33 (62)	100 (40)	53 (56)	209 (62)	13 (69)	29 (57)	311 (62)	83 (42)	795 (42)	2 (22)
Main migration period	20/9–20/10	1/10–20/10	20/9–20/10	20/9–20/10	20/9–25/10	25/9–25/10	1/10–31/10	1/9–30/9	1/9–30/9	20/9–25/10

Table XII. Percent visible migration directed to the E along the south coast of Skåne. Combined data from sites 2 to 4 (1971–1973)

<i>Fringilla</i> sp.	9.4
<i>Carduelis spinus</i>	14.1
<i>Carduelis cannabina</i>	9.8
<i>Anthus pratensis</i>	13.4
<i>Alauda arvensis</i>	24.8
<i>Sturnus vulgaris</i>	0.6
<i>Hirundo rustica</i>	14.2
<i>Motacilla alba</i>	37.3
<i>Parus caeruleus</i>	9.4

Wagtail, whose Scandinavian population travels S/SE, while Danish birds move SW (Edelstam & Österlöf 1969).

Also the Swallow and House Martin *Delichon urbica* may in part move E of S (Salomonsen 1972). In addition scattered ringing recoveries of numerous species have been obtained from the SE, but in all these cases the great majority of the population obviously migrates towards the SW. Probably the populations of the species known to winter to the SE are too small to account for all the S/SE-bound cohorts.

(B) Populations from east of the Baltic are redirecting themselves over Scandinavia to a southeasterly course.

(C) Populations of Scandinavian birds with winter quarters towards the S/SW set out on southeasterly directions, later to change towards the southwest. This may be seen as an adaptation to the frequent occurrence of W/NW winds over NW Europe (Evans 1966a).

(D) Birds prefer different track directions in relation to prevailing wind conditions. Such a relationship was probably found in the waterfowl wintering in the Baltic (Alerstam & Ulfstrand 1974b). However, for the ducks nomadic habits may be advantageous, but not for long-range migrants.

Alternatives (B), (C), and (D) require that birds generally regarded as SW migrants to some extent are involved in SE-bound move-

ments over southern Scandinavia. This calls for a closer examination of the relative abundance of the different species in different parts of the study area.

Table VI shows that different species made up very different proportions of the migrating birds observed at different sites. This indicates specific differences in preferred directions and/or in reactions to environmental factors.

The high percentages of Starlings at the west coast localities suggest a preferred track direction more to the west than in the other species. The local environment probably explains the high percentages at sites 8 and 9 which are situated in open agricultural surroundings.

Finches in proportion to other passerines were clearly concentrated in localities 1, 2, and 3 as well as inland localities 6 and 7 in southwestern Skåne; the latter two sites are located within woodland areas attractive to the finches (cf. Malmberg 1955).

In comparison with the finches, the Siskin, Linnet, and Meadow Pipit occurred in proportionately higher numbers at sites 3 and 4 than at sites 1 and 2. This suggests either a more S-bound preferred direction in part of the population or less reluctance to leave the coast.

The Swallow, Skylark, and especially White Wagtail were relatively more abundant at the more easterly sites in comparison with the more westerly ones. The last-mentioned species was particularly numerous at sites 4, 10, and 11, that is, localities on promontories pointing SE. As earlier pointed out, Scandinavian White Wagtails usually migrate towards the SE (Edelstam & Österlöf 1969).

In Table XII we have calculated the proportions of different species recorded on E-bound movements along the south coast of Skåne. It is in agreement with the above suggestions that the Starling is practically absent from these movements and that relatively large numbers of the White Wagtail and Skylark take part. We regard these percentages as an indication of each population's inclination to move S/SE.

Both the geographical differences in relative abundance and the ratios of W- and E-flying cohorts along the south coast of Skåne probably illustrate specific differences among the re-

puted SW migrants in terms of participation in movements directed more to the S or SE.

Magnitudes of migrating birds: radar and visible

As shown in Table IX, the visible migration of almost all species at both Falsterbo and Ottenby was maximal when winds were between SE and W. This is related to the fact that migration towards the wind tends to take place at low altitude and thus, due to guiding-line effects, to become concentrated to promontories. This is in contrast to the radar results according to which migration usually culminates under N/NE winds, when migration proceeds at high altitude without any influence from topography (Wilcock 1964, Alerstam & Ulfstrand 1972).

The association between headwinds and intense visible migration is much less conspicuous at the inland localities (Tables VII and VIII). Gruys-Casimir (1965) reported that Chaffinch migration over the inland took place on broad front and at least partly at low altitudes (< 100 m) under tail-winds. When approaching the coast the birds were seen to rise to much higher altitudes (up to 1500 m). Under cross- and head-winds they flew at very low altitudes over the inland and proceeded towards the coast line without greatly changing their altitude. Gruys-Casimir, like ourselves, found no obvious correlation between migratory magnitudes and wind directions over the inland.

The explanation of the weak correlation between bird quantities and wind directions over the inland may be that the field observer is able to see part of the tailwind migration, which is also registered by radar. At the coast, however, the tailwind migration takes place completely above visual range.

As indicated in Table VII, at the west coast localities (sites 12 to 14), maximum visible migration took place under approx. E winds, while approx. W winds were associated with high migratory activity at the east coast localities (sites 5 and 10). Note that at these localities birds generally do not have to depart seawards, in contrast to Ottenby and Falsterbo. In view of the finding (Tables VIII and X) that SW/W

winds were associated with low-altitude migration over the inland towards approximately SW, the low numbers of coasting birds under these winds at the west coast are surprising. Similarly, at the east coast localities one would have expected a great deal of visible migration under E winds, when inland observers recorded SE-bound low-altitude migration and birds were coasting eastwards along the south coast of Skåne (Fig. 1, Table XI).

The relationship between quantities of coasting migrants and offshore and onshore winds has been discussed by, amongst others, van Dobben (1953), Gruys-Casimir (1965), Evans (1966b), and Rabøl (1974). All these authors report stronger coasting movements under offshore winds. Evans suggested that wind drift over the inland might explain the absence of coasting birds under onshore winds. However, this does not apply in our case, because birds were recorded flying towards the coast over the inland under onshore winds. An alternative explanation is that birds were flying parallel to the coast but further inland under onshore winds, and so became invisible to the observers.

Two different categories of migrants may produce large quantities of birds along the west coast under E winds and at the east coast under W winds. Firstly, as suggested by Rabøl (op. cit.), high-flying birds migrating under offshore winds may change their direction when approaching the coast because of a presumed hesitation to depart seawards. When following the coast they will encounter crosswinds or headwinds and lower their flight altitude to within visual range. Radar observations indicate, however, that no more than a minority of the birds may perform this manoeuvre. Still, even a small proportion of the birds participating in the high altitude movements may suffice to provide the numbers counted by coastal observers.

Secondly, coastal movements may consist of birds having preferred directions only slightly seawards in relation to the coast line. Thus, birds migrating over the inland at low altitude (Table X) towards S/SSE under E winds would reach the west coast at a very narrow angle

and might follow it towards the south. Similarly cohorts flying S/SSW with W winds at low altitude would concentrate at the east coast.

More detailed network observations in combination with radar monitoring are required to solve these problems (cf. Roos 1974).

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