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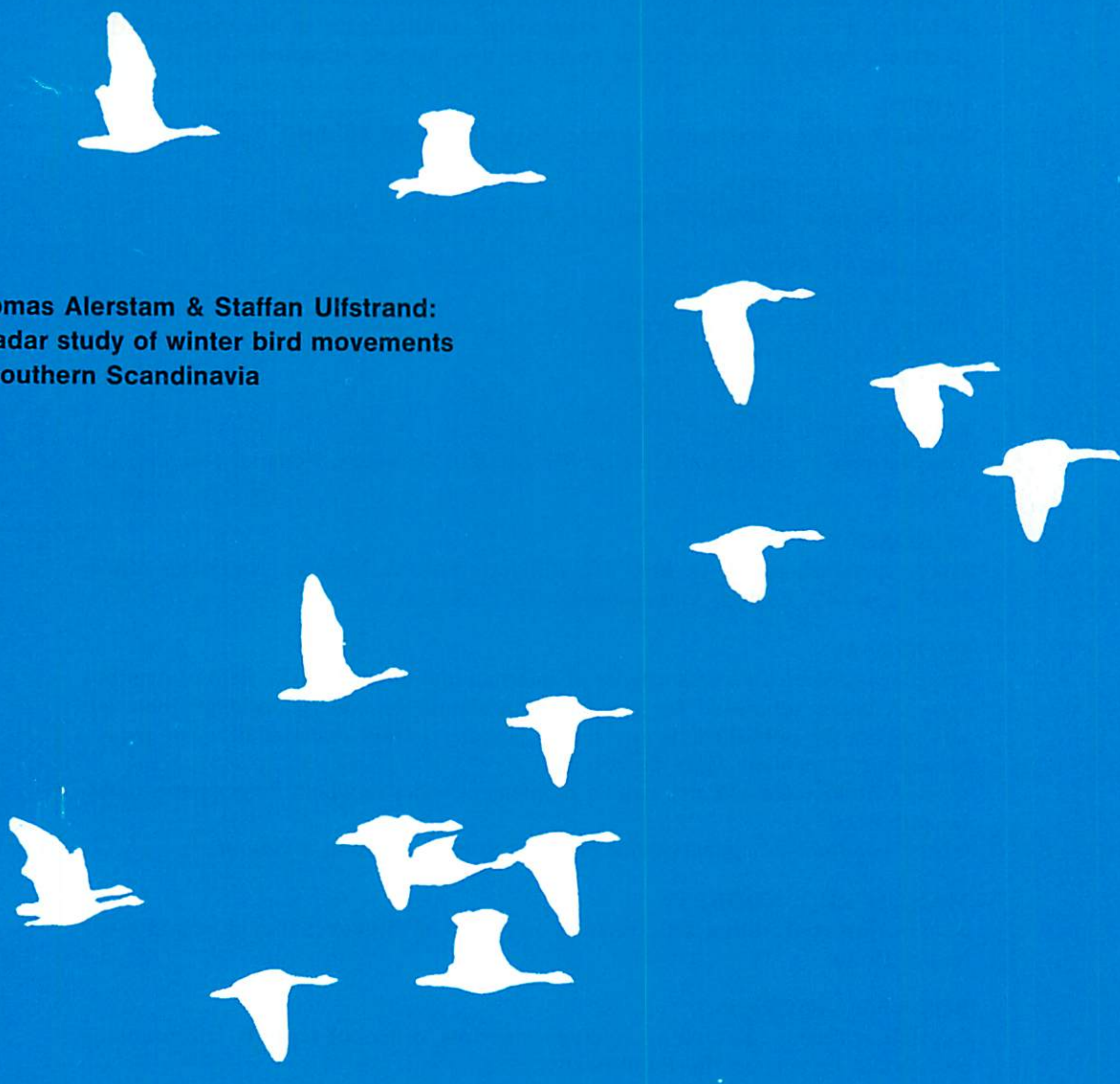

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A radar study of winter bird movements in southern Scandinavia

THOMAS ALERSTAM & STAFFAN ULFSTRAND

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Waterfowl movements in and around southern Scandinavia during the winter 1972/73 were studied by radar filming. Movements took place in all directions, invariably under tailwind conditions. Precipitation, or possibly cloud cover, inhibited movements, whereas temperature influenced frequency of movements only during periods when the frequency and intensity of movements were low. Fog did not influence activity at all. The general effect was that the birds moved from colder to warmer areas. Their behaviour seems ecologically highly advantageous; the birds move out well in advance of ice formation and low temperatures leading to high food requirements that may be difficult or impossible to satisfy.

Thomas Alerstam and Staffan Ulfstrand, Dept. of Animal Ecology, Ecology Building, Helgonavägen 5, S-223 62 Lund, Sweden.

INTRODUCTION

Previous information about mid-winter bird movements in Europe as well as elsewhere is very limited. However, certain species have been described to react to weather changes in winter by moving away from cold areas, returning as soon as the weather ameliorates. Such movements were noted by Gätke (1895) on Heligoland, and have been studied by several German ornithologists as summarized in Schüz (1971), and by Lack (1963, see also Eastwood 1967). The birds have been called 'Wetterpendler' ('weather commuters'), and the phenomenon 'hard-weather movements'. Lack's study is the only radar study of winter bird movements. In southern Sweden, winter movements of various species have been described by Roos (1962) and of Bean Geese *Anser fabalis* by Markgren (1963). Indirectly, the existence of considerable winter movements may be deduced from the rapid fluctuations in local distribution and abundance of several waterbird species during the winter months (Joensen 1968, Nilsson 1968, 1970a).

Within the frame of a project aiming at a fuller understanding of the patterns of bird movements in and around Sweden we have analysed radar films obtained at a station in central Skåne and covering about three months in the winter 1972/73. A large quantity of echoes reflecting non-passerine movements were recorded in these films. Already at this stage it has to be pointed out that the winter in question was exceptionally mild with no or very little ice in the Baltic Sea and in the lakes of southern and central Sweden.

METHODS

An L-band radar station described in a prior paper (Alerstam & Ulfstrand 1972) was continuously filmed with time-lapse technique (2.5 frames/min.) Large-scale autumn migration was still recorded on 24 November and heavy spring migration had started on 9 March. Thus,

Report No. 58 from Falsterbo Bird Station

in the present study, winter is defined as the period between 25 November and 1 March; no radar data are available from 2 to 8 March. The radar is equipped with an MTI-system preventing slow and weak echoes from being registered. The echoes studied were distinct and moved fast and could be quantified by direct counting. Their identification will be discussed below.

Weather data have been extracted from the daily reports of the Swedish Meteorological and Hydrological Institute.

Wind data have been obtained using measurements at Copenhagen at about 1500 m altitude, estimations from synoptic maps reflecting conditions at about 500 m altitude, and finally measurements of surface winds at several weather stations in the province of Skåne. Wind directions at 1500 and 500 m, respectively, were very similar. In this paper wind directions will always refer to upper winds and have been determined to the nearest ten degrees. When no wind direction could be defined from synoptic maps and wind at ground stations was weak and very variable, calm weather was said to prevail. On such occasions surface wind speed was less than 5 km/h and upper wind speed reported from Copenhagen less than 18 km/h.

The radar surveyed Zealand and surrounding waters, the southern Baltic Sea including the East German coast, and the southern part of the Scandinavian peninsula.

RESULTS

Table I presents in condensed form the information obtained. Although impressive the winter movements were of modest size when compared to spring and autumn migratory movements. Maximal echo intensity in winter was only about one tenth of what may be seen in autumn and spring.

Much the largest proportion (approx. 70 %) of the echoes were recorded during the dark hours. The activity usually increased at about sunset and showed a peak a couple of hours

Table I. Number of echoes and nights with movements towards N, S, W and E, respectively. Mean directions on different nights were between 350° and 10°, 170° and 190°, 220° and 290°, 40° and 150° for movements towards N, S, W and E, respectively. Wind directions within the following sectors are regarded as tailwinds, viz. for movements towards S: 280° – 40°, N: 120° – 260°, W: 000° – 180°, E: 200° – 350°. December = 25 November to 31 December.

Direction	Month	Echoes	Nights with movements (A)	Echoes/ night	Nights with tailwind or calm (B)	A / B %
N	Dec.	4.900	22	230	26	85
	Jan.	600	11	60	21	52
	Feb.	300	4	70	6	67
	Total	5.800				
S	Dec.	300	2	130	8	25
	Jan.	3.400	10	340	16	63
	Feb.	500	4	130	15	27
	Total	4.200				
W	Dec.	1.900	7	280	8	88
	Jan.	1.500	6	250	16	38
	Feb.	800	4	200	9	44
	Total	4.200				
E	Dec.	1.000	7	140	28	25
	Jan.	1.600	11	150	20	55
	Feb.	2.900	10	290	13	77
	Total	5.500				

later. Movements, however, in various directions sometimes continued throughout several days and nights without interruption. In contrast, eastbound movements in February to a large extent (60 %) took place in daytime, chiefly before noon.

The echoes moved with ground speeds ranging from 70 to 120 km/h. Since the altitude of the echoes is unknown, it is impossible to combine certain narrowly defined wind speeds with certain echo speeds, and thus only estimates of the true air speeds of the echoes are feasible. Usually mean true air speeds fell within the range from 60 to 80 km/h.

The data in Table I show that north- and west-bound movements were most frequent and intense in December, south-bound movements in January, and east-bound movements in February.

The northward movements were recorded over the Baltic Sea south of Skåne. The echoes were most often detected immediately off the East German coast near the island of Rügen and the Bay of Pomerania and vanished from the display when approaching Sweden's south coast. A few echoes veered and moved along the coast-line off-shore towards east or west for a few kilometres. Occasionally echoes were seen over the land, but then only close to the coastline, and there is no evidence of any significant travels over land by these north-bound cohorts. It may be mentioned that the distance from the German to the Swedish coast varies between 70 and 160 km.

Southward movements were clearly made up of at least two different bird categories. One was the exact reverse of the northward movements described above. These echoes appeared off the south coast of Skåne and disappeared off the German Coast. While the northward movements were particularly intense in December, movements towards the south mainly took place in the latter half of January and in February. On a few nights with calm weather in January, north- and south-bound echo cohorts were travelling over the Baltic at the same time.

The second type of south-bound echoes entered the radarscope from the north, crossed Skåne and the Baltic Sea, and proceeded across the coast-line into Germany. These echoes were exceptionally large and distinct, and their manner of progress highly characteristic. Although their velocity was high, their path was erratic, the echoes often veering for 10 to 30°, keeping to a constant bearing only for brief periods. No reactions were seen when they approached the coast-lines. These movements took place in the former half of January, on some days with extensive fog over much of southern Scandinavia. In all probability the birds responsible for these remarkable echoes were cruising above the fog belt.

Westward movements usually crossed Skåne, the Sound and Zealand. Echoes were sometimes seen east of Skåne over the sea, but most often they were not detected until above the coast-line. On many nights, echoes departed inland across Skåne from the Bay of Hanö and across Zealand from the Sound. Most numerous were movements directed towards WSW crossing southern and southwestern Skåne as well as the southern parts of the Sound and Zealand. Movements further north across the Sound were directed towards W/WNW. Due to the large distance from the radar station, echoes usually vanished over Zealand, but some WNW-bound cohorts could still be followed over the Kattegatt.

East-bound movements were almost exactly the opposite of those towards the west. Most echoes appeared over southern Zealand and crossed Skåne on ENE bearings. Echoes also arrived from over central and northern Zealand and the Kattegatt, and these cohorts crossed Skåne on E/ESE bearings. Especially during February SE/SSE-bound movements were also recorded. These echoes entered northwestern Skåne from over the Kattegatt and continued over the southern Baltic still keeping the same course. Usually they were lost on the radar display when over the sea between the islands of Bornholm and Rügen, heading for Pomerania.

On two occasions in January with calm weather, simultaneous movements directed towards the east and west, respectively, were witnessed.

DISCUSSION

Identification

The distinctiveness and speed of the echoes provide complete evidence that the birds responsible were not passerines. Before the start of our study period, all waders had left Sweden, except, at certain localities, flocks of Lapwings *Vanellus vanellus*. Such flocks may have produced a small number of echoes departing in December, but apart from these we can discount waders as elements of the echo cohorts. This leaves us with waterfowl (Anseriformes) and gulls *Larus* spp. Several types of positive evidence strongly support the assumption that waterfowl were primarily responsible for the vast majority of the echoes recorded. Thus, the echoes commuting across the Baltic Sea between the Swedish and German coasts usually stopped at the shore-lines, sometimes performing a short veering along the coast before vanishing from the display. Also, echoes approaching the east coast of Skåne sometimes gathered in the innermost part of the bay of Hanö, thus showing a behaviour strongly indicative of aquatic birds.

Gulls, particularly Herring Gull *Larus argentatus*, occur in considerable numbers along the coasts and, in smaller quantities, at various inland localities. They produce echoes, ignored in this study, during their flights to and from their roosts, and, judging from the speed and paths of most echoes, gulls probably made up a very minor portion of the birds involved in the movements with which this report is concerned.

A particularly remarkable behaviour was demonstrated by some echo cohorts, already referred to above, moving due south from the inland of southern Sweden, crossing the Baltic and proceeding into the continent. It seems to us that the species most likely to behave in such a fashion are Whooper Swan *Cygnus cygnus*, Mute Swan *C. olor*, Bean Goose *Anser fabalis*, and Canada Goose *Branta canadensis*.

Most waterfowl echoes unfortunately did not allow specific identification, but a good approximation of the probable species composition may be derived from published information about the waterfowl wintering in southern Scandinavia and surrounding waters (Nilsson 1968).

The species roaming most freely over the open Baltic Sea is undoubtedly the Long-tailed Duck *Clangula hyemalis* (cf. Mathiasson 1970); this species was probably responsible for the echoes commuting between Skåne and East Germany. These birds, however, probably do not fly across land regularly. The only other duck species occurring in considerable numbers along the south coast is the Goldeneye *Bucephala clangula*, which, however, occurs much less frequently far away from the coast.

Echoes moving across the land (Skåne and Zealand) may represent several species known to be abundant in marine and freshwater localities in this area, such as Mallard *Anas platyrhynchos*, Tufted Duck *Aythya fuligula*, Goosander *Mergus merganser*, Coot *Fulica atra*, both *Cygnus* spp., and Bean Goose.

Wind effects

Because movements were generally much more intense and frequent at night, we shall restrict our attention to a comparison of nocturnal movements with nocturnal weather.

As pointed out already, large echo cohorts were watched moving in all directions, which we have grouped in four major categories (east-, west-, south- and north-bound). We shall now relate these movements to the prevailing wind conditions.

All movements, irrespective of their direction, took place under following winds (Figure 1, A–D). The relationship is analysed in some detail in Table II, A–D. Within each category of directions, the mean echo direction changed with the wind, so that the tail-wind component became enforced. At least two explanations can be suggested, viz. pseudodrift and incompletely compensated wind drift.

(1) Bird cohorts with a given preferred track direction choose to move under the most favourable wind conditions (i.e. tail-wind) in relation to their goals. Cohorts with different preferred directions thus take part in the movements in different proportions with different wind directions. This has been named pseudodrift or

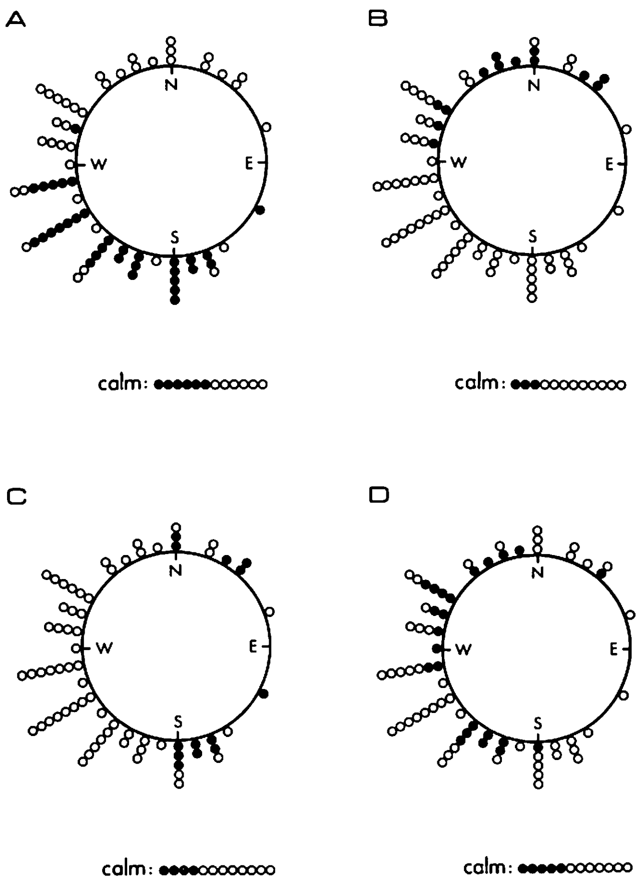

Fig. 1. Movements towards the north (A), south (B), west (C) and east (D) in relation to upper wind direction. Filled circles denote nights with movements and open circles nights without movements.

selective cohort migration (Evans 1966, Nisbet & Drury 1967, Alerstam & Ulfstrand in press).

(2) The birds may be subjected to wind drift, as postulated for night-migrating Long-tailed Ducks and Common Scoters *Melanitta nigra* in Finland by Bergman & Donner (1964, 1971).

The north-bound movements across the Baltic Sea have produced the largest quantity of data. As shown in Table II A, all tracks measured are confined within a narrow sector (350–010°). Winds west of south (200–260°) and east of and including south (160–180°) respectively, were accompanied by significantly different mean track directions (001.7°, S.D. 4.1 and 356.3°, S.D. 4.8, respectively, the total average being 360.0°, S.D. 5.0; $p < 0.01$). This difference, however, was considerably smaller than was to be expected, if uncompensated drift was taking place.

East- and west-bound movements showed a wider scatter than the north-bound movements (Table II, C–D). Again, the birds moved with following winds, and changes of mean directions in relation to wind directions occurred as described for the northward movements.

According to our interpretation echoes will scatter within a limited sector during given wind conditions. If the wind direction changes, the echoes within part of this sector will become less numerous (but normally will not disappear entirely) and in another part more numerous. This will produce a predictable change in mean direction, even though the angle of the scatter will usually remain about the same. Such ef-

Table II. Directions of movements towards the north (A), south (B), west (C) and east (D) in relation to wind direction. Mean track direction and wind direction are given for each night. A: Mean directions were measured to the nearest five degrees. On two nights of calm weather mean directions were 000°. Mean directions could not be properly measured on ten nights due to low migratory activity, and have been excluded. B: Mean directions are approximated to the nearest ten degrees. C: Mean directions are approximated to the nearest 22.5 degrees. D: Mean directions are approximated to the nearest 22.5 degrees. Mean directions could not be properly measured on five nights, and have been excluded. Migration towards SE/SSE was of a special pattern and is perhaps unrelated to other movements towards the east. Thus, it is treated separately and is not included when averaging the total mean directions of easterly movements.

	Wind direction	Direction of movement				
A		350	355	000	005	010
	160 – 180	2	3	2	1	–
	200 – 260	–	2	10	4	2
B		170	180	190		
	280 – 350	5	2	1		
	360 and calm	1	2	2		
	030 – 040	–	1	2		
C		SW	WSW	W	WNW	
	000 – 040	2	3	–	–	
	calm	1	2	1	–	
	120 – 180	–	2	2	4	
D		NE	ENE	E	SE/SSE	
	180 – 220	3	4	–	–	
	260 – 280 and calm	1	6	1	2	
	290 – 350	2	2	4	9	

fects cannot arise, if uncompensated wind drift takes place.

Evidently wind direction plays a major role for the release of the bird movements discussed in this paper. We have failed to find a single case of significant movements under headwind conditions. This is not caused by the birds flying below radar coverage during head-winds, because the waterbirds involved usually do not fly across land at low altitude, least of all during the night. Moreover the radar coverage also includes low altitude movements over the sea (cf. Alerstam, Bauer & Roos in press). Wind direction also affects the paths of the birds, and this mechanism may operate in more than one way. On these grounds we feel justified to ignore headwind occasions in the ensuing discussion and will restrict our attention to certain tail-wind situations that were not accompanied by significant bird movements.

Precipitation and fog

In Table III we compare the frequency of nights with bird movements during precipitation (usually rain, on a few occasions snow) and dry weather, respectively. In all of the four main categories of movements there was a clear tendency towards fewer movements during rain, and in two categories the difference is significant. When all the data are combined, a highly significant relationship is found. Thus, precipitation may be a factor inhibiting these bird movements in spite of favourable wind conditions. This effect reaches a significant level both during and outside the main periods: December for N- and W-bound movements, January for S-bound movements and February for movements towards E; cf. Table I. It is possible that some factor strongly correlated with precipitation, rather than rain as such, is the direct cause of the inhibition of

Table III. Bird activity in relation to precipitation. Only nights with tailwind or calm are considered. Precipitation was recorded at two weather stations in the province of Skåne (Ljungbyhed and Malmö). As seen in Table I movements towards the north and west tend to be most heavy and frequent in December, towards the south in January and towards the east in February. We have on this basis defined instances of movements as occurring during or outside a main period. Nights with and without movements were compared, using Fisher exact probability or χ^2 tests. Prec. = precipitation, ns = not significant.

Movement towards	Movements		No movements		
	Prec.	No Prec.	Prec.	No Prec.	
N	17	20	14	2	$p < 0.01$
S	10	6	15	8	ns
W	3	14	11	5	$p < 0.01$
E	19	9	25	8	ns
All movements	49	49	65	23	$p < 0.001$
All movements, main period	26	23	11	3	$p < 0.05$
All movements, outside main period	23	26	54	20	$p < 0.01$

flight activity. Compact cloud cover may be such a factor.

Table IV makes the corresponding comparison between nights with and without widespread fog. Surprisingly fog did not seem to interfere with the frequency of the movements. A large number of southward movements took place within a short time interval with much fog in January, and this produced a significant positive correlation between fog and bird activity. This, however, we rate as a spurious correlation. Presumably the birds were cruising above the fog belt.

Temperature

The relationship between temperature and frequency of bird movements is analysed in Table V. In this table we have made use of the temperature difference between the night of actual movement and the preceding night. In each of the four direction categories a tendency to higher activity was found after a temperature drop. The relationship was significant in two cases and for the whole material combined. Alternatively one can use the temperature values as such. When this was done, we found a tendency towards more activity during nights with below-zero temperatures. Thus, either way, the net result is that the birds involved travelled with cold air masses. However, the impact of temperature was statistically significant outside the main period, not during it (Table V).

This, however, is not to say that the tem-

Table IV. Bird activity in relation to occurrence of widespread fog. Only nights with tailwind or calm are considered. Nights with and without movements were compared, using Fisher exact probability or χ^2 tests.

Movement towards	Movements		No movements		
	Fog	No fog	Fog	No fog	
N	4	33	4	12	ns
S	9	7	5	18	$p < 0.05$
W	4	13	4	12	ns
E	7	21	7	26	ns
All movements	24	74	20	68	ns

Table V. Bird activity in relation to changes in temperature. Only nights with tailwind or calm are considered. Temperature was recorded at three weather stations in the province of Skåne (Ljungbyhed, Malmö and Ystad). Main period as defined in Table III. Nights with and without movements were compared using χ^2 tests. ns = not significant.

Movements towards	Movements Temperature change +	0	−	No movements Temperature change +	0	−	
N	6	12	19	8	2	6	$p < 0.05$
S	2	8	6	10	2	11	$p < 0.01$
W	2	8	7	4	5	7	ns
E	6	8	14	13	8	12	ns
All movements	16	36	46	35	17	36	$p < 0.001$
All movements, main period	11	19	19	4	4	6	ns
All movements, outside main period	5	17	27	31	13	30	$p < 0.001$

perature factor directly affects the frequency of the bird movements. It is quite conceivable that some other factor coupled with temperature conditions is the most important clue. Precipitation is an obvious possibility. In Table VI both these factors are viewed together, and this yielded the following results.

When there was no precipitation, temperature had no demonstrable effect on the frequency of the bird activity. During the main period for each category of movements, regardless of the temperature, intense movements were recorded on practically every night without precipitation, and since dry weather tends to be associated with falling temperatures, this relationship provides part of the explanation of the temperature dependency established in Table V.

On rainy nights, during the main periods, no temperature effect could be demonstrated. On such nights, however, outside the main periods, falling temperatures seemed to be associated with relatively higher bird activity than rising temperatures.

Thus, during the main periods, the dominant influence of the wind was modifiable by precipitation, but neither fog nor temperature had any effect at all (Table III and V). Outside

Table VI. Bird activity in relation to changes in temperature and precipitation. Only nights with tailwind or calm are considered. Data for all four movements are combined. Temperature, precipitation and main period are defined in Tables III and V. Nights with and without movements were compared using χ^2 tests.

	Movements Temperature change +	0	−	No movements Temperature change +	0	−	
Precipitation							
Main period	7	8	11	4	3	4	ns
Outside main period	3	8	12	27	9	18	$p < 0.01$
Combined	10	16	23	31	12	22	$p < 0.01$
No precipitation							
Main period	4	11	8	–	1	2	
Outside main period	2	9	15	4	4	12	ns
Combined	6	20	23	4	5	14	ns

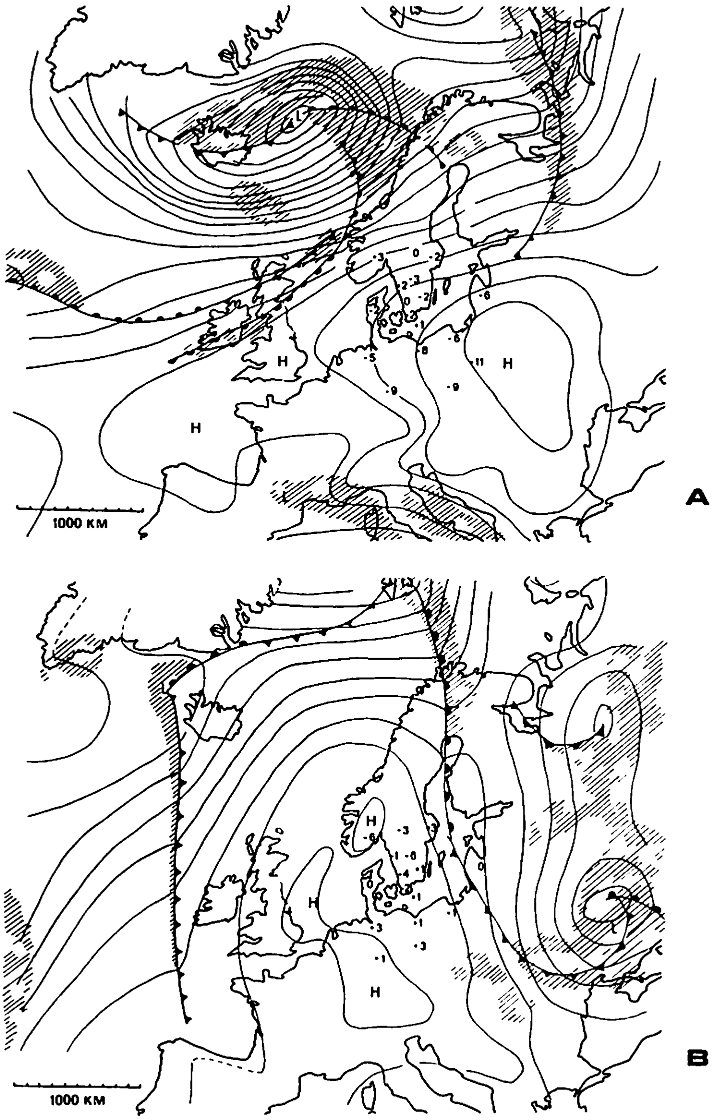

Fig. 2. A: Synoptical situation on 30 December 1972 at 0700 hrs. Heavy movements towards the north over the Baltic took place under SSW/SW winds. B: Synoptical situation on 11 January 1973 at 0700 hrs. Heavy southbound movements took place under northerly winds.

the main periods, by contrast, temperature as well as precipitation seemed to affect the bird activity.

Synoptical situations

The study period was dominated by stable high pressure areas covering most of Scandinavia and the Baltic Sea. Certain recurrent synoptical situations were associated with the major proportion of the bird movements.

(1) A strong high pressure often resided over eastern continental Europe. When this anticyclonic centre drifted from Finland southwards in the direction of the Balkans, winds over the southern Baltic Sea gradually shifted from east to southwest. This transition was accompanied by bird movements, first, when the high pressure centre was over southern Finland, mainly westbound, later, north- or eastbound (Fig. 2 A).

(2) On other occasions the high pressure centre resided to the west of Scandinavia, with

northerly winds and heavy south-bound bird movements over southern Scandinavia (Fig. 2 B).

(3) Near the end of our study period a few cyclones travelled across northern Scandinavia towards the east. After the front passage westerly winds prevailed and were accompanied by considerable east-bound movements.

As exemplified by the maps, flying with the wind under dry weather conditions will carry the birds from colder to milder areas. This important aspect of their travels will be discussed below.

Ecological significance

West-going cohorts were larger and more frequent in December than in later months. They usually travelled across Skåne and Zealand. East-bound movements, by contrast, were largest in February, showing a pattern precisely opposite to the west-bound ones. We regard these movements as consisting largely of bird cohorts performing a late autumn and early spring migration (cf. Lack 1963), respectively, although numbers were much smaller than during the main migration periods. The time-table of the autumn migration in 1972 might well have been delayed due to the exceptionally mild weather.

One should not forget that movements in practically all directions occurred throughout the study period. Most of the movements cannot properly be classified as autumn or spring migration, but are much better described as nomadic or diasporic movements (Wilkinson 1952, quoted from Hochbaum 1955). What is the ecological background to this midwinter nomadism of the waterbirds in southern Scandinavia and the surrounding parts of the Baltic Sea?

The most serious dangers for waterbirds are ice and low temperatures. Ice, of course, prevents these birds from obtaining their food, and even a very partial ice cover will significantly affect their conditions, since ice first covers the shallow sea areas from which waterbirds acquire most of their food. Low temperatures will raise the energy expenditure and thus food requirements of the birds (Nilsson 1970b, 1972). In fact, Nilsson has shown that some species, such as the Goldeneye, and particularly the smaller-sized females of this species, are hard put to obtain enough food under severe temperature conditions. Obviously it is important for the waterbirds to clear out well in advance of the ice formation and preferably also before the advent of really low temperatures. Flying with the wind under dry weather conditions seems to offer an excellent means of evading these hazards, at minimum energy costs. Winter mortality is extremely heavy in many species, as discussed, for example, by Lack (1968), and adaptations to reduce it would have high selective priority. Southern Scandinavia and surrounding waters are close to the limit of what many waterbirds can endure in terms of climatic vicissitudes. The unpredictable climatic conditions require a highly developed alertness to environmental changes and a capacity for long-range and fast movements. The nomadic movements we have seen on the radarscope are an expression of this adaptive strategy.

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