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AN ANALYSIS OF THE SPRING MIGRATION OF
THE COMMON SCOTER AND THE LONG-TAILED DUCK
IN SOUTHERN FINLAND

BY

GÖRAN BERGMAN AND KAI OTTO DONNER

ZOOLOGICAL DEPARTMENT OF THE UNIVERSITY, HELSINGFORS

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I. Introduction

As long ago as 1874 and 1876 J. A. PALMÉN described the migratory route of the ducks and geese breeding in NE Europe and NW Siberia (PALMÉN 1876). He classified them as »submarin-litoral» migrants, as on their migration they follow mainly the route of waters formed by the North Sea, the Baltic Sea, the Gulf of Finland, the Karelian lakes Ladoga and Onega, and the White Sea. A number of published observations exists of this northeastern migration of waterbirds (cf. e.g. R. PALMGREN 1913, HORTLING 1930, GRENQUIST 1938 and 1954, PUTKONEN 1942), all of which show the vast number of birds involved, though they represent, however, only a few species. This migration is usually mentioned in the ornithological literature only when it has been par-

ticulatory intense. A detailed study of the spring migration was carried out already during the years 1937—1940 by one of the present authors in the area west of Helsingfors (BERGMAN 1941). These observations have since been continued nearly every spring and thus give the present study a good basis of field-ornithological records and experience.

At the southern coast of Finland two species, the Common Scoter, *Melanitta nigra* (L.), and the Long-tailed Duck, *Clangula hyemalis* (L.), together constitute about 90 % of the ducks and geese that pass along the Gulf of Finland in spring and autumn. Other species represented are the Velvet Scoter, *Melanitta fusca* (L.), the Brent Goose, *Branta bernicla* (L.), and the Barnacle Goose, *Branta leucopsis* (Bechst.). In addition, a much less conspicuous migration of limicoles, Divers and Grebes occurs, as well as of various gulls. In the spring these other migrants are as numerous as the Common Scoter and the Long-tailed Duck only during short spells, of perhaps a few hours, during the approximately 15 days of migration of these two duck species.

The general course of the spring migration of the Common Scoter and the Long-tailed Duck at the southern coast of Finland is the following:

The Common Scoter. This species arrives at the Gulf of Finland in larger numbers after May 10th. The flocks do not rest for any length of time on the sea or in the archipelago, and the migration continues so that maximum intensities of migration are observed close to the date of the first arrival. The migration at the Gulf of Finland culminates 2—4 days earlier than for the Long-tailed Duck, but flocks of Common Scoters are still seen during the last days of the migration of this latter species. In the daytime the migration is strongest between 19.00 and sunset and usually still increases in the late evening. It begins to fade out about an hour after midnight. The short interruption in the migration after sunset, as observed by BERGMAN (1941), is evidently only a local effect caused by topographical factors (see below p. 54).

The Long-tailed Duck. From March to the beginning of May there is a slow and gradual arrival at the southern coast of Finland; during this phase real concentrated migration cannot usually be observed. There is, however, a clear tendency for the flocks to move in a definite direction (NE). During this phase the movements and the rarely occurring migratory flights take place as far as is known only in the daytime. In mild winters with little or no ice, a restricted number of Long-tailed Ducks is seen as far north as the Gulf of Finland during the whole winter season. The state of the ice appears to determine the rate of arrival of the birds at their resting places, in the shallow regions outside the coast and in the outer archipelago (cf. GRENQVIST 1938, 1954, BERGMAN 1941, 1951). Between May 15th and 28th approximately, the Long-tailed Ducks migrate towards their arctic breeding places. This migration has the same daily rhythm as that of the Common Scoter.

Both species migrate in large flocks, with an average of 150–160 birds in each flock, or in groups of smaller flocks. Occasionally small groups of birds belonging to one of the species may be seen in flocks of the other species, but as a rule the flocks are pure. The conditions that release and favour migration appear to be very similar for both species.

The use of radar in the study of bird migration (SUTTER 1957 a, b, HARPER 1957, 1958), has provided entirely new possibilities for analysing the principles involved, but the method has also some considerable limitations. Extensive studies on movements and migration of birds have been carried out in Britain by LACK and his co-workers (LACK 1958, 1959, 1960, 1962 a, b, 1963 a, b, TEDD & LACK 1958, LACK & EASTWOOD 1962, LEE 1963). Further, there are studies of the migration along the eastern coast of the United States (DRURY 1960, DRURY, NISBET & RICHARDSON 1961, RICHARDSON, STACEY, KOHLER & NAKA 1958, DRURY & KEITH 1962, NISBET 1963). In Sweden, spring migration has been studied in the Stockholm area (MASCHER, STOLT & WALLIN 1962) and observations from Cyprus have been published by ADAMS (1962). GEHRING (1963) describes in detail the autumn migration over Switzerland.

One of the main drawbacks of studying migration with the aid of radar is that it records the movements of most if not all birds flying within the area under study. Because a relatively large number of species is frequently involved, an analysis is possible only in rather general terms. DRURY & KEITH (1962) clearly describe the kind of species classification that can be made based on radar observations alone. For instance, small passerines can easily be separated from larger and faster birds, flocks of limicoles show a high speed, gulls are fairly slow etc. This is still a very rough classification and it is conceivable that a good deal of the advantages of radar in the study of bird migration is lost when the species under study cannot be identified.

In the present work this disadvantage is to a great extent eliminated because of the nature of the migration studied, with only two dominating species represented. As stated above, the Common Scoter and the Long-tailed Duck largely outnumber all other migrants during their period of migration, thus the radar records give a fairly homogeneous material presenting a good starting point for an analysis of the factors that influence the intensity and direction of migration. In addition, these duck species are both easy to identify in the field even at a great distance, a further advantage being that their flight calls are very characteristic so that the proportion of each species can be determined even at night. Thus it is possible to check the radar records continuously with field observations.

Although only two dominant species are represented the number of birds is considerable, in spite of the fact that in recent years great numbers of Long-tailed Ducks have become the victims of oil pollution of the sea in the Baltic

region. On the basis of the radar records of 1960 BERGMAN & DONNER (1960) calculated the number of Common Scoters passing the Gulf of Finland in the spring to be about 1 200 000 and the corresponding number of Long-tailed Ducks to be about 300 000. With the experience of the radar technique gained since then we are, however, now inclined to correct these figures to about 1 500 000 and 500 000 respectively. The radar films of the migration in 1961 and 1962 indicate an increase in the number of flocks passing, as compared with 1960. On the other hand the field observations show that this increase is almost wholly due to an increase in the number of Long-tailed Ducks.

KUMARI (1963), reviewing the results obtained by the Baltic Commission for the study of Bird Migration in Estonia, stresses the fact that during recent years the numbers of Long-tailed Ducks have dropped to an exceptionally low level, but still estimates that about 20 000 000 (!) birds of this species have passed the Estonian coast annually in the autumn. Our radar studies show that the total number of passing ducks and geese cannot be higher than about 5 million birds, even on a very optimistic calculation. Because there always has been a clear majority of Common Scoters, the number of Long-tailed Ducks must consequently lie below 2 million and most likely even below 1 million. Although the number of birds in the autumn migration as compared with the spring migration can be assumed to be approximately doubled due to the presence of the juveniles, the number given by KUMARI (20 million) thus appears to be about 10–20 times too high. Since KUMARI does not clearly state how this number has been calculated, it is difficult to find the reasons for this discrepancy. It should be noted that in the spring the Common Scoters and Long-tailed Ducks observed and counted at the NW coast of Estonia are identical with the birds reaching the southern coast of Finland somewhere in the central parts of the Gulf of Finland. In actual fact the number of birds observed at the Estonian coast indicate a migration of the same general intensity as that of the migration reaching the Finnish coast east of Hangö, as recorded by radar.

Observations from western Estonia (Puhtu bird station at the straits between the coast and the islands of Ösel and Dagö (Saaremaa and Hiiumaa), JÕGI 1958, 1961, VEROMAN & JÕGI 1961), however, show a general ratio of 1 : 1 : 1 between the Velvet Scoter, the Common Scoter and the Long-tailed Duck. The disagreement with records from Finland is striking because at the southern coast of Finland the percentage of Velvet Scoters is only 2–8 % of the total number of passing flocks of the three species mentioned, as established by observations in the field. Further, the number of birds in a single flock of Velvet Scoters is on an average only about half of the number of individuals in flocks of Common Scoters and Long-tailed Ducks. Thus only 1–4 % of the diving ducks passing along the northern coast of the Gulf of Finland appear

to be Velvet Scoters. In our preliminary report (BERGMAN & DONNER 1960) on the numbers of Common Scoters and Long-tailed Ducks, it was tentatively assumed, to account for this discrepancy, that the Velvet Scoters observed at Puhtu possibly fly in a more eastern, and the Common Scoters and Long-tailed Ducks on the other hand in a more northeastern direction. In the light of the present evidence, this appears rather unlikely because a corresponding separation in different flight directions has not been established in our radar observations. Possibly the majority of the Velvet Scoters seen at Puhtu are birds breeding in the coastal area of western and southwestern Finland and eastern Sweden.

II. Methods

1. Material and technique of recording

The investigation has been carried out on the spring migration in three consecutive years, 1960—1962. In all, three different radar stations have been used, although not more than two simultaneously. The technique used for recording has been the same as that used by SUTTER and LACK. The plane position display (PPI) of the radar equipment has been recorded on 16 mm negative film with the exposure of a single frame of the film for each revolution of the radar antenna (usually 15 sec). A clock with illuminated hands has been included in each picture. Thus films have been obtained that give the position of different targets, e.g. bird flocks, on a compressed time scale, each frame on the film giving the situation 15 sec before the next. The films so obtained have given the following material for the present analysis (see Fig. 1, p. 8 and map on p. 22):

1960: 17—18.V., 21—25.V., 28.V. Migration has been analysed in the central parts of the Gulf of Finland, approximately between Porkkala and Lovisa, as well as on the adjoining Finnish mainland south of a line Lojo—Hyvinge—Lovisa.

1961: 6—24.V. The same area as above.

17—20.V. and 22—26.V. Area analysed: the western part of the Gulf of Finland, approximately between Jussarö and Bengtskär, the archipelago north of the Hangö peninsula and the adjoining parts of the mainland.

1962: 7—14.V. and 16—20.V. Area same as 1960.

9—11.V., 13—18.V., 21.V. and 24—25.V. Area analysed: region around Lake Saimaa, approximately from Jyväskylä to Kuopio and Villmanstrand (Lappeenranta).

In a number of cases separate measurements of the altitude of flight have been carried out in addition to the ordinary PPI recording (cf. p. 15).

2. Film analysis

Direction of flight. For each time interval chosen the film was projected on to a screen of paper numerous times, during which the paths of individual flocks were followed with a pencil. With a high intensity of migration it was not always possible to trace in this way all the flocks, because in some places the density was so high that the points representing

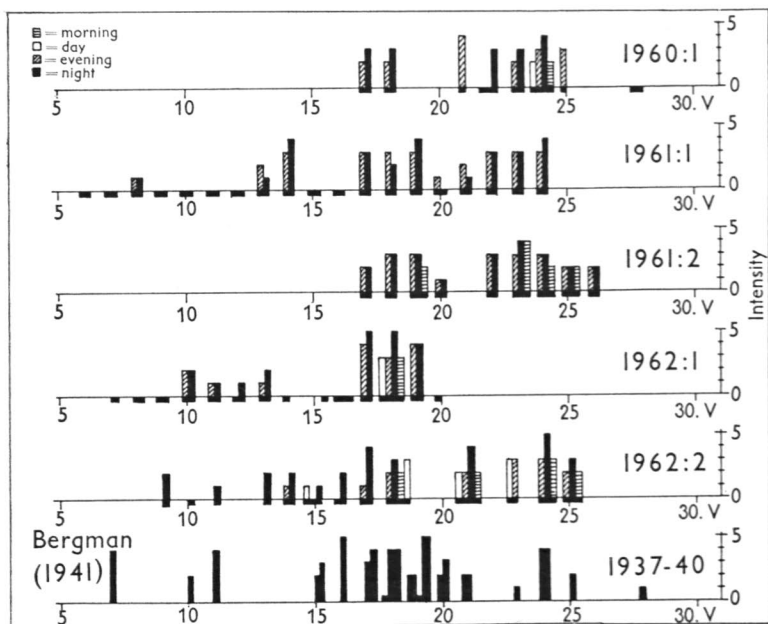


FIG. 1. The intensity of migration in the years 1960—62 in different parts of the investigation area. 1960, 1961, 1962: 1 = central parts of the Gulf of Finland and the Finnish mainland between Porkkala and Lovisa. 1961: 2 = the western part of the Gulf of Finland and the archipelago north of Hangö peninsula. 1962: 3 = SE Finland, region around Lake Saimaa and area west of the lake. Thick horizontal bars below the lines indicate periods for which radar observations have been carried out. Lowermost line: intensities recorded by BERGMAN (1941) for the years 1937—40 (field observations).

individual flocks merged together. The actual direction of movement could, however, always be determined. The tracings on paper so obtained were later used to measure the direction of flight in any part of the area of investigation. Data on direction have been used either as giving the average direction of the stream of migrants during a restricted period or as directions of individual flocks (see p. 21).

The flight speed (ground speed). When the time for a full revolution of the radar antenna and the displacement of a single spot (flock) between two subsequent frames on the film is known the ground speed can be calculated. Such measurements of the speed were generally carried out using the movement of a flock during 11 subsequent frames (= 10 time intervals of about 15 sec) as a basis. This movement was traced on paper and the length of the traces measured with an accuracy of 0.1 mm. Considering the scale of projection the flight speeds so obtained should be correct to 2—3 %. — A faster method, giving, however, only the average speed of the stream of migrating flocks, is to follow continuously the general movement on the screen when the film is running during a certain time, for instance corresponding to 30 min, the time being obtained from the clock included in all frames of the films. With this method and with films obtained under conditions giving strong radar echoes from the flocks, the results are comparable in accuracy with those obtained with the former method, but can obviously only give the average speed of all the moving flocks. Thus for a detailed analysis of the speed of flight only the former method has been used.

The intensity of migration. Classification has been done using a scale of 0 to 5, where 0 denotes no migration and 5 the highest intensity observed as given below (the numbers of flocks mentioned are very approximate):

- 0 = no radar echoes of the type most probably due to flocks of Common Scoters or Long-tailed Ducks in the area of investigation.
- 1 = within the area studied not more than about 25 such radar echoes visible simultaneously that must probably be attributed to the duck species under study.
- 2 = weak migration. About 100 flocks simultaneously visible.
- 3 = normal migration. Approximately 200—400 flocks.
- 4 = strong migration. About 400—1 000 flocks.
- 5 = very strong migration. The echoes of individual flocks occur over the whole area and very frequently tend to merge together because of the small distance between them. Perhaps 1 000—2 000 flocks.

The intensities according to this scale have not, in individual cases, been determined by actual counting of the flocks but are estimates based on the general impression obtained during projection of the film, as compared with a standard agreed upon according to the above scale. The intensity of migration in the evening and during the night is given by a number that denotes the highest intensity observed between 18.00 and 21.00, and between 23.00 and 24.00. If records were not available for the whole evening and night the highest intensity during the time for which recording was done is given. The very regular and continuous increase in intensity from the onset at about 17.00 to 18.00 and further until midnight, with a slow fading out towards dawn makes the precise time to which the intensity determinations refer rather insignificant. Time of the day is here given in Eastern European Time.

Fig. 1 gives a summary of the present material with reference to the intensity of migration. Schematically the time of the day is given: morning, day, evening, night. Thus at most four separate intensity values for each day can be obtained. The data for which radar observations exist are also indicated by the thick black marks below the line. For comparison BERGMAN's (1941) intensity data for the years 1937—1940 are given. It must, however, be observed that his data are, in the light of the present evidence, to a certain extent misleading (cf. p. 47), giving information on the migration over the archipelago only.

The analysis of the direction and speed of flight has been carried out for periods of 1—3 hours, separately for migration in daylight and after sunset. For long continuous films — the longest comprise 12 hours — 3—4 mappings have been made. When a change in the direction, intensity or distribution of migration has been observed, a new analytical map with directions and speeds has been made, even if the preceding one covered a period of less than an hour.

3. The meteorological data

The data used have been obtained from the weather maps of the Finnish Meteorological Office and from the weather statistics of the meteorological stations at the coast of the Gulf of Finland. Because the records generally cover the time from 19.00 to midnight, the reports from the coastal stations at 20.00 and 23.00 have been used. The analysis of the migration in the central parts of the Gulf of Finland has been carried out based on the data from the station Skanslandet (Vallisaari) just outside Helsingfors, and from the station Enskär (Katajaluoto) about 8 km to the SW of the southernmost part of Helsingfors. In addition, the data from Bågaskär 20 km W of Porkkala, Russarö 5 km SE of Hangö.

and Utö between Hangö and Kõkar as well as own (G.B.) observations between Helsingfors and Porkala have been used. Further, the data from Tallinn (Reval) and from Ristna on the island Dagö (Hiiumaa) have been taken into consideration when the prevailing wind on the central parts of the Gulf of Finland has been estimated.

The wind. Since migration over sea proceeds at low altitude (100—300 m) the direction and strength of the wind has been taken as that reported by the nearest meteorological station or observation point. Analysis of the migration at greater altitude — mainly that studied in the Lake Saimaa region — has been carried out using the wind data obtained from the weather maps for 2.00 and 14.00. The air pressure gradient at an altitude of 600—1 000 m has been used to derive the direction and strength of the wind. The accuracy of this procedure is not, however, great because the weather maps as such are not sufficiently detailed and because for data on the migration around 20.00 an estimate of the rate of change of the weather between 14.00 and 2.00 must be done. However, a comparison between the strength and direction of the wind as reported at different ground stations during this interval to some extent eliminates the arbitrariness of this procedure. At the coast with wind strengths below 5—7 m/sec the considerable local deviations of the wind due to thermal, vertical air currents over land, constitute a disturbing factor, especially during warm days and evenings. The most marked deviations from the general direction of flow of the air have, however, presumably been eliminated by comparison with the wind data reported by the coastal stations on both sides of the Gulf of Finland and by direct field observations at Porkala in the outer archipelago, and at Helsingfors.

Cloudiness. Because the degree of cloudiness may show great local variations and migrating flocks may thus rapidly pass areas that differ considerably in this respect, the possible relation of the intensity of migration to this factor has been studied using an average of the values reported from the nearest meteorological stations. For the migration over the central parts of the Gulf of Finland the data from Enskär, Tallinn, Bågaskär and Russarö as well as our own observations were used. Only in cases where an unbroken cloud formation, without any patches of clear sky, covered the whole area, has the overcast been considered complete. It has been attempted to attribute to each situation such a percentage of cloudiness that is representative of the area passed by a flock during a preceding flight of approximately an hour.

For the migration over SE Finland the data from Kotka, Lahti, Jyväskylä and St. Michel have been used in a corresponding way.

Visibility. The sources of data and principles of determination have been the same here as concerning cloudiness. The average visibility generally encountered with different kinds of air masses also to some extent served as a guide. Certain areas with local reductions of visibility due to fog did not generally appear in the material from the meteorological stations. In this respect observations of local inhabitants have been taken into account.

III. The identification of the migrants

It is essential to be able to state with a high degree of probability that the migration observed and studied really consists of the two bird species mentioned, the Common Scoter and the Long-tailed Duck. Some facts about the migration have been presented above (p. 4), based on evidence from field-

ornithological studies, showing that these two species strongly dominate the NE migration occurring at the Finnish coast between May 10th and 28th. As such, these facts suggest that any radar observations of birds during this time should generally refer to Common Scoters and Long-tailed Ducks. An examination of the present film material gives the following additional clues for their identification:

1. The migration observed in the field simultaneously with the radar records has been found on all occasions, to consist almost solely of Common Scoters and Long-tailed Ducks.

2. When no migration of the type studied here has been recorded by radar, no migration of Common Scoters and Long-tailed Ducks has been seen in the field.

3. The general course of the migration, starting gradually between May 8th and 13th and ending normally about May 28th, fully agrees with the results of earlier field observations (BERGMAN 1941) (Fig. 1).

4. The diurnal rhythm of the migration observed on the radar screen is identical with that observed in the field.

5. The geographical distribution is the same as that observed in the field, as far as it has been possible to determine visually or on the basis of the flight calls of the flocks at night. Migration over the archipelago and over land occurs according to the radar records at exactly the same conditions as indicated by the field observations of 1937–1940 (BERGMAN 1941).

6. The agreement between field and radar records is very good regarding the number of flocks passing a certain observation point during a given time, the differences being explicable as due to the fact that flocks flying close together tend to merge to a single point on the radar screen. Also, it should be borne in mind that even in the field it is often difficult to decide what should be regarded as a separate flock if migration is intense.

7. The direction of flight as seen on the radar films also fully agrees with the directions observed in the field.

It must not be denied, however, that other species of migrants occur at this time of the year. The flocks of arctic limicoles migrating along the Gulf of Finland and over southern Finland, should most likely be recorded on the radar screen. According to many field observations, e.g. at Porkkala bird station, the migration of waders culminates at approximately the same date in May as the migration of the Common Scoter and the Long-tailed Duck. The flocks are, however, as a rule very much smaller than those of the present duck species and furthermore the individual birds, with a few exceptions, are much smaller in size and should accordingly give considerably fainter radar echoes than flocks of ducks. For a few days during the migratory period of the Common Scoter and Long-tailed Duck some 10–20 greater flocks of limicoles can be

seen, for instance, at Porkala. But the intensity of this migration of limicoles never reaches the strength even of a weak migration of the ducks.

The species of the genus *Calidris* are generally observed to fly at a very low altitude, and hence a considerable part of these flocks are presumably not recorded with radar except very close to the station used. Of other limicoles only *Limosa lapponica* and *Charadrius squatarola* regularly migrate at considerable altitude and in flocks, which, due to their size (> 50 ind.), may be thought to give radar echoes comparable to those of the flocks of ducks. The number of *Limosa lapponica* is, however, according to observations at Porkala less than 3 000 and thus quite insignificant in comparison to the number of ducks. *Charadrius squatarola* is even less numerous — at Porkala not more than 1 500 each season (these figures were kindly given to us by cand.rer.nat. PERTTI SAUROLA). Reference may also be made to the data on the migration of limicoles at Ottenby bird station on southern Öland (SVÄRDSON 1953). A great number of calls made by limicoles may occasionally be heard, but apparently only from single birds or small flocks. These calls refer mainly to the species *Calidris alpina*, *Charadrius hiaticula* and a few *Tringa*, or *Numenius phaeopus*. The more noticeable radar echoes can hardly be expected to arise from such a migration. It is thus very unlikely that any kind of migration of limicoles can have changed the picture obtained of the duck migration in the present investigation. — The number of migrating geese (the Brent Goose, *Branta bernicla*, and the Barnacle Goose, *B. leucopsis*) does not exceed 10 000, according to field observations. These birds migrate in flocks of generally less than 100 ind. Their migration period coincides approximately with the migration of the Common Scoter and the Long-tailed Duck but the geese show a different diurnal rhythm, migrating especially in daytime and mainly in the morning.

To some extent a certain migration of flocks giving the same kind of radar echoes as the duck flocks has been observed moving towards the NNW before May 15th, both over the Gulf of Finland and in SE Finland. The type of echoes and the speed of flight indicate rapidly flying flock migrants. Because no field observations are available on this migration the identification is very uncertain. It seems likely that some goose (*Anser erythropus*?) or duck species is involved, possibly Pintails (*Anas acuta*). Being common in northern Fennoscandia, this species is not, however, seen in southern Finland in any considerable numbers on daytime migration. Marked SSE-NNW night migration might possibly give an explanation to the fact that this species is not seen very frequently in the field. The absence of a strong specific flight call would also explain why this duck has not been reported as a night migrant either.

The radar films also demonstrate the movements of presumably single birds of various species in the vicinity of the radar stations, especially on the Gulf of Finland. For instance, Herring Gulls (*Larus argentatus*) can regularly be identified in their flights between ships outside the coast and their breeding habitats in the outer archipelago SW of Helsingfors. Other irregular movements of birds are also observed in all the films, but differ markedly from the characteristic nearly rectilinear movements of truly migrating birds or bird flocks.

IV. The speed and direction of migration

1. The speed of flight and its dependence on various external and internal factors

The radar films provide a good opportunity to determine with a fair accuracy the *ground speed* of the migrating flocks, i.e. the speed of the birds in relation to the ground. Such measurements have been carried out by two different methods as described above (p. 8). Both methods have been found to give the flight velocities within $\pm 2-3\%$ of the correct value as judged from results with repeated measurements on the same film. It is obvious that on the assumption that the moving flocks all have the same speed it is sufficient to determine only the speed of the whole stream of flocks as seen when the radar film is projected. With a very homogeneous migration as in the present case this assumption may come near the truth. But it may also be argued that even when only a single species is considered, variations in altitude of flight, motivation to migrate etc. produce large variations in the velocity of flight. This makes it necessary to study also the speed of individual flocks.

When the ground speed is known the *air speed* of the flocks can be calculated if in each case the direction of flight is known as well as the direction and strength of the prevailing wind. This calculation has been carried out graphically which gives an accuracy sufficient for the present purpose.

Considering first the average speed of the whole stream of migrants, more extensive measurements of this kind have been carried out on the migration crossing obliquely the Gulf of Finland in the area roughly about 25 km S of Helsingfors. Here ground speed values between 60 and 120 km/hr have been recorded. On the other hand measurements on the migration over land in the area around Helsingfors and also in SE Finland have given ground speeds between 75 and 190 km/hr. From these data the corresponding air speeds, i.e. the speeds actually resulting from the active flight of the birds, have been determined with a correction for the drift caused by the prevailing wind, the result being summarized in Fig. 2. The variation between the individual values is seen to be very large, the flight velocities over the sea covering the range between 65 and 102.5 km/hr, the variation being marked for migration over land too. Two clear features, however, emerge from Fig. 2. Firstly, the air speed for migration over sea is lower than for migration over land, the corresponding mean values being 82.2 km/hr (sea) and 92.7 km/hr (land). Secondly, the distribution of the data for migration over the sea appears inconsistent with the notion of a homogeneous material, but strongly indicates the presence of two separate components with average air speeds of about 73-74 and 83-84 km/hr respectively.

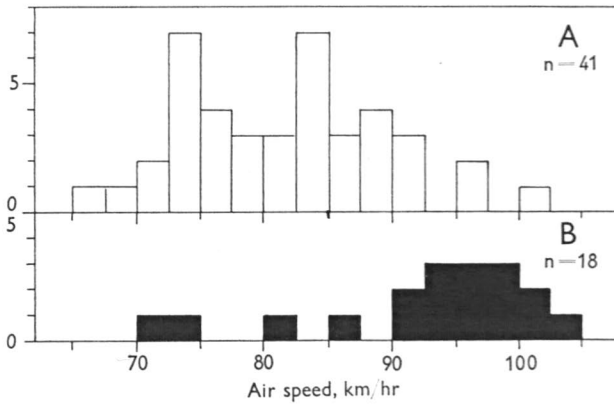


FIG. 2. Average air speed of the stream of migrants. A: Migration over the sea. B: Migration over land.

As mentioned above the actual measurements have individually taken an accuracy of $\pm 2-3\%$. The inaccuracy of the available wind data introduces additional errors. Wind velocity has originally been obtained in whole m/sec and since 1 m/sec corresponds to 3.6 km/hr the accuracy here is not greater than ± 1.8 km/hr, even if the data are otherwise completely correct. Local wind variations as well as errors in the actual weather data may well add to this an uncertainty of about $\pm 3-4$ km/hr. But it should be kept in mind that wind directions nearly perpendicular to the direction of flight affect the flying speed only to a very small extent with the wind strengths usually observed. It then seems safe to assume that the calculated air speeds are correct to ± 5 km/hr in each individual case.

It is not, however, *a priori* to be assumed that migrating birds of a certain species always fly with the same air speed, although normal migratory flight can be expected to be carried out at a speed requiring a minimum output of energy per unit distance. Even this may be questioned because earlier measurements of the speed of flight (HARRISSON 1931, ROBERTS 1932, MEINERTZHAGEN 1955) show that the speed of migratory flight apparently is about 20% higher than that of normal flight in a number of birds. Generally it may, however, be stated that variation in the speed of migratory flight may occur because:

1. The air speed is different at different altitudes, or
2. the speed is correlated with the strength of motivation to migrate, being higher with a strong motivation.

Considering the accuracy of the individual values for the air speed it is clear that the data of Fig. 2 for migration over the sea are well consistent with the notion of two speed components with an uncertainty in the individual values for each of the magnitude ± 5 km/hr. This condition, is not, however,

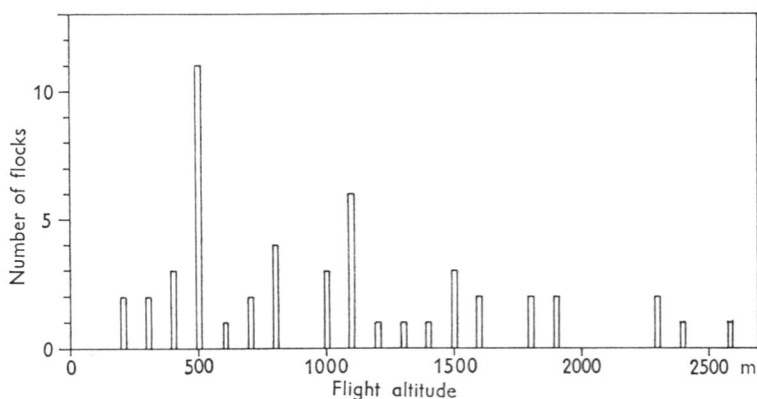


FIG. 3. The altitude of flight of individual flocks over SE Finland.

realized when migration over land is considered, where the two peaks are absent and in addition the average speed is about 10 km/hr higher than over the sea. The possibility that some other bird species flying faster is involved over land can safely be excluded because it is clearly seen on the radar films that the same flocks that pass over the Gulf of Finland, under those conditions when migration over land occurs, continue their flight directly when they reach the Finnish coast. There is, however, a striking difference in the behaviour of the Common Scoter and the Long-tailed Duck when migrating over the sea or over land. BERGMAN (1941) found that the flight altitude over the sea was 100–250 m, while the flocks passing over the inner parts of the archipelago along the Finnish coast flew considerably higher, at about 500–900 m. Measurements with radar during the present investigation have given flight altitudes over land between 200 and 4 200 m, the average being 1 050 m. These data refer to the area in SE Finland and are summarized in Fig. 3. The altitudes 500–1 500 m seem to be preferred by the majority of flocks, the result being in good agreement with BERGMAN's earlier figures for migration over the inner archipelago, quoted above. So far, and with this relatively small material, it is impossible to say whether there is a general preference for a certain altitude during a certain type of weather. There is, however, some evidence that the average flight altitude varies during different nights.

The difference observed in Fig. 2 between the air speed over land and over the sea is also evident in measurements on single flocks as described above (p. 8). An analysis of this kind, referring to the period 21.40–22.30 on 24.V.60, is presented in Fig. 4. On that night migration was very intense and apparently due to the low ground visibility (cf. p. 39) the flocks crossed the coast and continued inland already much before sunset. The wind was from the east

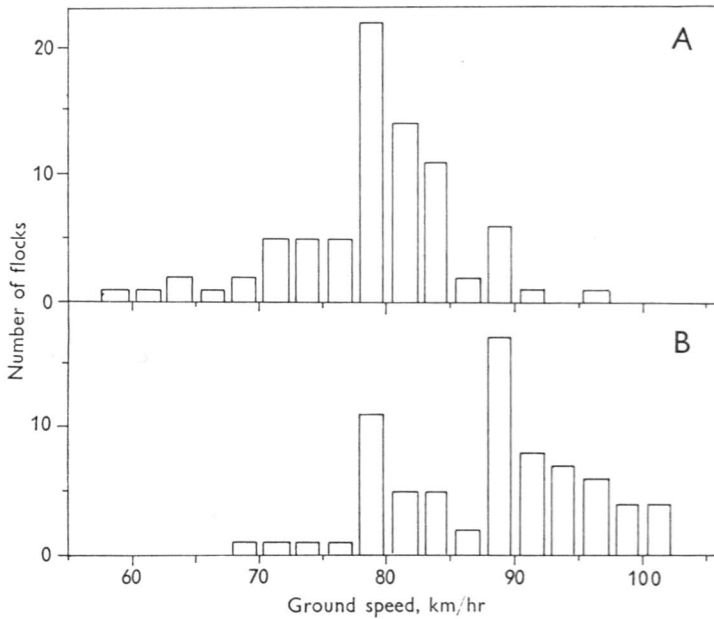


FIG. 4. Ground speed distribution of individual flocks 24.V.1960 21.40—22.30. A: Flocks over the central parts of the Gulf of Finland. B: Flocks over land, N and NW of Helsingfors. A 80 flocks, B 99 flocks.

and fairly weak (3 m/sec) and did thus only slightly reduce the ground speed (which is given in Fig. 4) in comparison to the air speed. According to field observations on this particular evening in Porkkala (Sommarö) by P. SAUROLA the majority of the birds seen or heard were Common Scoters with only very few flocks of Long-tailed Ducks. Considering migration over the sea it is noted that the distribution of speeds in Fig. 4 shows only a single peak around 80 km/hr, the second peak as seen in Fig. 2 being only weakly indicated. These circumstances suggest that the speed component between 80 and 85 km/hr in Fig. 2 should be attributed to flocks of Common Scoters and the slower component to the Long-tailed Ducks. This point will be further discussed below, for the present question about the reason why flying speed is different over land and over the sea the relevant point is that in the case presented in Fig. 4, the vast majority of the migrating birds belong to the same species, the Common Scoter. When the flocks of this species fly over land a different speed distribution is obtained with a stronger representation of higher speeds, the largest group flying with speeds around 90 km/hr. A smaller fraction of the flocks seem to fly with the same speed as used by the majority of flocks over the sea. As described above, flying altitude is 100–250 m over the sea and around 1 000 m over land. On the other hand the Common Scoters, as

shown in Fig. 4 flew on that particular evening about 80 km/hr over the sea and about 90 km/hr over land. A weather analysis shows that this difference in ground speeds cannot have been caused by a different wind velocity at higher altitudes.

These findings thus show that a higher air speed is correlated with a higher altitude of flight, and that the magnitude of this gain of speed is about 10 % for an increase in flight altitude of 800—1 000 m. The following factors may be thought to cause this effect:

1. With the same constant output of energy the reduction of the density of the air at higher altitudes results in a faster flight.

2. Flight at high altitudes is connected with a high motivation to migrate and this strong motivation also results in a faster flight than under other circumstances.

An idea of the effect of altitude on air speed can be obtained from the normal aerodynamical expressions for lift and drag (cf. e.g. BROWN 1961) although it is not clear if these apply as such during conditions of flapping flight. These expressions show that under otherwise unchanged conditions, with the same lift and drag and with unchanged effective power for flight, velocity will be proportional to the square root of the inverse value of the mass density of the air (g/cm^3). Thus

$$v = k \sqrt{\frac{1}{\rho}}$$

where v = velocity, ρ = density of the air and k a proportionality constant. Now Fig. 2 considered together with the data in Fig. 4 suggests that the air speed of the Common Scoter over the sea, which means flight at a low altitude, is on an average about 84 km/hr and over land at high altitude 95—96 km/hr. Taking 1 000 m as the difference in flight altitude between these two cases gives a calculated speed increase according to the above expression of about 6 %. It thus predicts a speed of about 89 km/hr at 1 000 m which value appears to be inconsistent with the actual air speeds measured. The relation between flight velocity and density of the air is according to the observed values much better described by assuming a direct proportionality between speed and the inverse value of air density. In this case 84 km/hr at ground level will correspond to 94 km/hr at 1 000 m. The implication is that in the present case the nondimensional coefficients C_l and C_d in the expressions for lift (L) and drag (D)

$$L = C_l \frac{v^2 \cdot \rho}{2} S; \quad D = C_d \frac{v^2 \cdot \rho}{2} S$$

where v = velocity, ρ = density of the air and S the surface area of the wing, are not constant but are inversely proportional to the velocity v . These con-

siderations, however, apply only if the reduction of the density of the air is the only factor that promotes air speed when the birds are flying at a higher altitude. It must also be observed that the altitude of flight is here taken only as an average on a fairly restricted material.

In this context it is interesting to note that if the speed of flight increases in the way described with altitude because of the aerodynamic properties of the birds, migration at a fairly high altitude may offer a significant advantage due to the greater speed attained. This would be further enhanced if there is a tendency to migrate with tailwinds and to utilize the higher velocity of the wind in the higher layers, as indeed seems to be the case with the two species studied here (p. 45).

The question of the possible influence of the strength of motivation to migrate on the air speed can be studied using the values for the intensity of migration. It can be concluded that the motivation to migrate is high when the intensity of migration is high, and it may then be asked if there exists any correlation between the air speed and the corresponding intensity of migration. The material on air speed for migration over the sea, as given in Fig. 2, does not when analysed in this respect give any indication whatsoever of a correlation of this kind. But it must be observed that this material refers to determinations of the average speed, in addition showing a frequency distribution indicating the presence of two speed components. For these reasons the variation in the material due to other causes may be too large to show any minor differences in the true air speed.

Another factor that may influence the motivation to migrate and thus possibly the air speed is the direction of the prevailing wind. As will be shown below (p. 45) the intensity of migration is generally lower with winds between north and east and with these winds the present material gives a slightly lower air speed. The difference is, however, too small to be considered significant. Now observations in the field by one of the authors (G.B.) show that on an average migration on days with these winds (headwinds) is carried out at a slightly lower altitude than usual. Since it can be inferred that the wind generally increases in strength with increasing altitude, it is obvious that the values derived for the air speed with the aid of wind data for a certain altitude will show a systematic deviation of the kind observed if the flight altitude depends to some extent on the direction of the wind. Another possibility is that with winds between north and east the lower altitude of flight results in a slightly lower air speed due to the increased density of the air. With the present material it is impossible to decide which of these two possibilities give rise to the difference observed, but there appears at any rate to be sufficient reason to exclude changes in motivation as an explanation of the slight reduction of air speed with headwinds.

The possibility that flight at high altitude is connected with a high motivation to migrate and that this strong motivation also results in a faster flight can be excluded because of the fact that migration over the sea, however intense, is not carried out at high altitudes. Furthermore, crossing the coast from sea to land is not related to the intensity of migration but is determined by other factors, as is generally also the deflection in flight direction when the flocks are approaching the Finnish coast. Finally the data presented in Fig. 4 show that at a certain moment, when the general weather conditions etc., that is to say factors which may affect the motivation to migrate, are the same to all birds, migration over land proceeds at a higher air speed. The only remaining possibility, except the physical effect of reduced air density, is then that flight at high altitude as such stimulates the birds to a greater effort in migration, for instance, because the apparent movement of the ground as seen by a flying bird is slower when seen from a higher altitude. This argument is, however, contradicted by the fact stated above that the air speed of birds flying in a headwind is the same or slightly less than of birds flying in tailwinds. This although the ground speed is lower with a headwind and thus also the apparent movement of the ground as seen by the birds is slower.

Fig. 4, referring to migration during wind conditions with a slightly reducing effect on the ground speed as compared with the air speed, indicates that the Common Scoter, which completely dominated the migration on that particular evening, has a normal air speed of more than 80 km/hr over the sea and more than 90 km/hr over land. The data of Fig. 2 show two preferred speeds for migration over the sea, about 74 km/hr and about 84 km/hr. Since only two main species are involved in the migration studied, the speed component 84 km/hr must be attributed to the Common Scoter, as already stated above, i.e. to speed determinations on days or times of the day when this species has been the dominant one. The lower speed component can then be ascribed to the Long-tailed Duck. This interpretation is supported by the following facts: The Common Scoter is generally considered by field-ornithologists to be a faster bird than the Long-tailed Duck, although migration in mixed flocks occasionally occurs. In that case it has been observed that a few Common Scoters in large flocks of Long-tailed Ducks are more frequently seen (G.B.), presumably because they have no difficulty in keeping pace with the Long-tailed Ducks. Further, the present material shows a slightly higher mean for air speeds during the period 13—19.V. than during the period 20—25.V. (84 and 80 km/hr, respectively). Although this difference cannot be proved to be statistically significant it may nevertheless be connected with the fact that the migration period at the Gulf of Finland is about a week earlier for the Common Scoter than for the Long-tailed Duck with, however, a considerable overlap (BERGMAN 1941, see also p. 4). Thus speed determinations on the general stream

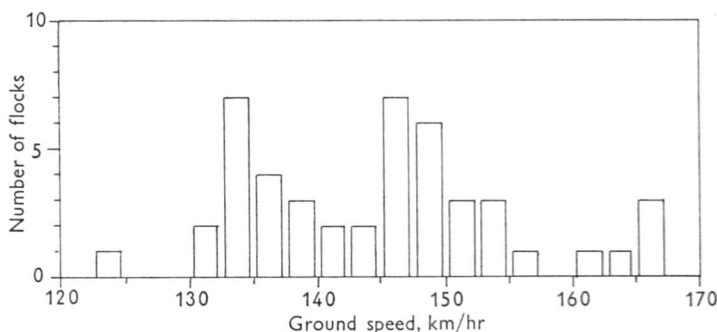


FIG. 5. Ground speed distribution of individual flocks 25.V.1962 01.00 in SE Finland. 46 flocks.

of migrants will in the beginning of the migration period mainly refer to the Common Scoter and later more to the Long-tailed Duck.

MEINERTZHAGEN (1955) gives 54–72 m.p.h. (= 86–115 km/hr) as the speed of the Long-tailed Duck. His figures, however, refer to conditions with a tailwind of unspecified strength and are thus not strictly comparable with the present ones.

Migration over land does not, however, show the presence of two speed components in the material on the average air speed in Fig. 2. This is not surprising, because the number of cases is small and the Common Scoter, according to field-ornithological experience (G.B.), generally to a lesser extent avoids crossing the coast than the Long-tailed Duck, even in daylight. It is then to be expected that most of the speed determinations over land as carried out on the stream of migrating flocks, will give the speed of the Common Scoters and thus not show the two peaks as found in the material on migration over the sea. Analysis of the speeds of single flocks when migrating over land does, however, in many cases reveal the presence of two speed components about 10 km/hr apart. Because in such cases the altitude of each single flock has not been measured the data are more difficult to interpret. An example is, however, shown in Fig. 5, referring to migration on 25.V.62 at 01.00 in the night over an area about 50 km SE of the town St. Michel. Here the two speed components clearly occur with approximately the same speed difference as in Fig. 2. In addition there is a group of very fast flocks, either flocks flying at a very much higher altitude or representing some other species. The high ground speed is due to the fact that there was a strong SW wind at about 600 m altitude with a reported velocity of 46 km/hr. The actual air speeds would then be around 80 and 90 km/hr respectively for the two main groups. The fact that the Long-tailed Duck to a greater extent tends to avoid crossing the coast as observed

in the field (G.B. W of Porkala and N of Hangö peninsula) will naturally lead to a certain separation of the two species at the southern coast of Finland. This difference will result in a more eastward occurrence over land of the Long-tailed Duck. Further, these birds will be observed over land later in the evenings than the Common Scoters.

2. The direction of migration and the factors affecting it

The general direction of the migratory movement studied is NE. The radar films, however, give an opportunity to make more precise statements. Thus the method used, of analysing the films by tracing the flight paths on paper, allows the directions of flight to be measured with accuracy. It is immediately observed that there is a fairly wide variation from day to day, sometimes even from hour to hour, between the directions so determined. In addition, the direction of flight is not the same everywhere in the area studied during a certain moment. As a basis for an analysis of the factors that influence the direction of flight, the *a v e r a g e d i r e c t i o n* of the migration has been measured for each evening and night recorded on film during the years 1960—62 in the following regions (Fig. 6, p. 22):

- A. About 15 km to the south of Pellinge.
- B. About 20 km south of Helsingfors, south of and around the lighthouse Helsinki.
- C. 10—15 km to the south of Porkala peninsula.
- D. The land area to the north and west of Helsingfors.
- E. About 15—20 km to the south of Hangö peninsula.
- F. An area about 50—60 km to the southeast of St. Michel in SE Finland.

These points have been chosen so as to avoid the very clear deflections observed when the birds come close to the Finnish coast when crossing the Gulf of Finland. Such deviations from the general approximately NE direction of flight that are obviously a reaction to the landscape will be discussed in a separate paragraph (p. 36).

In Fig. 7 all the present data on the average direction of flight from areas A—F are presented in relation to the direction of the prevailing wind. The material has been grouped so that those wind directions (NE and SW) that ought to have no effect on the direction of a northeastern migratory movement are given in the centre of the figure. On either side of this have been plotted the wind directions that may be expected to deflect the migrants, on the left hand side of the figure to the north and on the right hand side to the east. Obviously with a NE migration, SE and NW winds will be expected to have the greatest effect on the direction; they have accordingly been placed on each side and the other wind directions between these and the central line in the

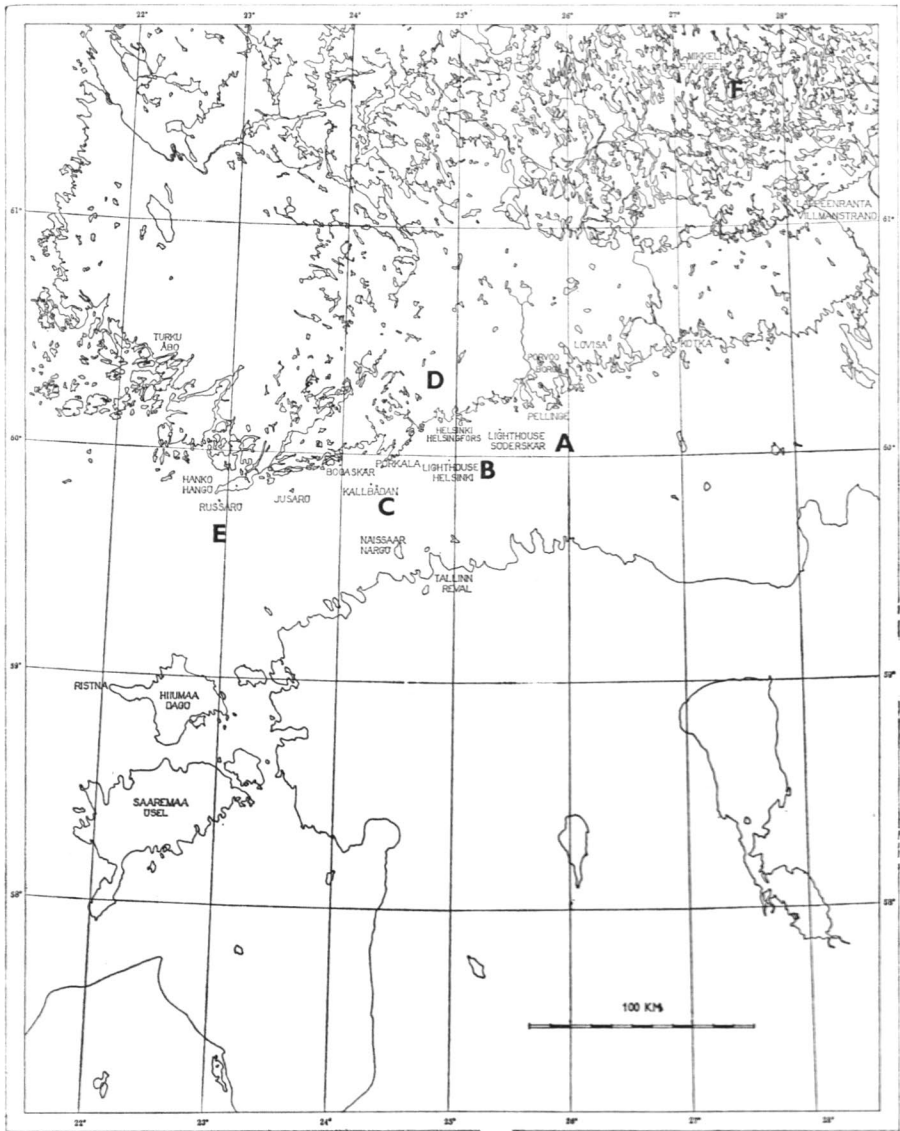


FIG. 6. Map showing the position of the areas A—F for which the direction of migration has been measured and studied as explained in the text.

sequence determined by the magnitude of their expected effect on the direction of flight. The open circles here denote migration before 21.00 and the filled ones after 22.30.

Fig. 7 (p. 24) immediately makes it clear that the direction of flight is by no means a constant, the individual values varying between 80° and 10° . Further,

the figure shows that there is a general tendency towards more northern directions with winds in the sector ENE-SSW ($67.5-202.5^\circ$), and on the other hand a more eastern tendency with winds in the sector WSW-NNE ($247.5-22.5^\circ$). This demonstrates in a qualitative way that the birds are subject to drift by the wind, and is then in agreement with the results obtained in earlier radar work (LACK 1958, 1960, DRURY & KEITH 1962). It is, however, still possible that there is some, although not full compensation for drift.

As stated in the preceding paragraph, the air speed can be determined if the ground speed and the direction of flight as well as the direction and strength of the wind are known. The graphical method used allows a simultaneous determination of the actual heading of the birds, when drift is excluded. This has been worked out in all cases for which corresponding speed measurements exist. In case only the direction of the migration has been measured another procedure has been adopted. Here it has been assumed that the air speed of the birds is equal to the averages obtained (p. 13), 82.2 km/hr over the sea and 92.7 km/hr over land. With these data in combination with the wind data the true direction of flight is found by a simple geometrical construction.

In either of these ways all the directions presented in Fig. 7 have been corrected and the values so obtained have been plotted in a similar diagram (Fig. 8). The large variation between individual values is still present, but the corrected directions appear uninfluenced by the direction of the wind. The material in Fig. 8 has been divided into three groups, as indicated by the vertical broken lines. These groups represent: 1. observations during winds that would deflect the birds to the north, 2. observations referring to winds that would deflect the birds to the east and, 3. observations when the wind has no or very little effect on the direction of flight. For each group the mean has been calculated and the corresponding standard error, the result being:

Group 1	$47.5 \pm 1.55^\circ$
Group 2	$46.4 \pm 1.78^\circ$
Group 3	$51.9 \pm 2.27^\circ$

A comparison of the means for each group gives the following P-values: Group 1 — group 2: $0.7 > P > 0.6$, group 1 — group 3: $0.2 > P > 0.1$, group 2 — group 3: $0.1 > P > 0.05$. There are thus scarcely grounds for assuming that some systematic difference is present. One reason why group 3, referring to winds that have no or little effect on the direction of flight, shows a slightly more eastern direction than the two other groups may be that the measurements from the area in SE Finland are mainly included in this group. And as will be shown below (p. 34) there is some reason to believe that the direction of migration there is slightly more eastern.

The fact then that the true direction of flight, where the effect of wind has been excluded, appears independent of the direction of the wind strongly

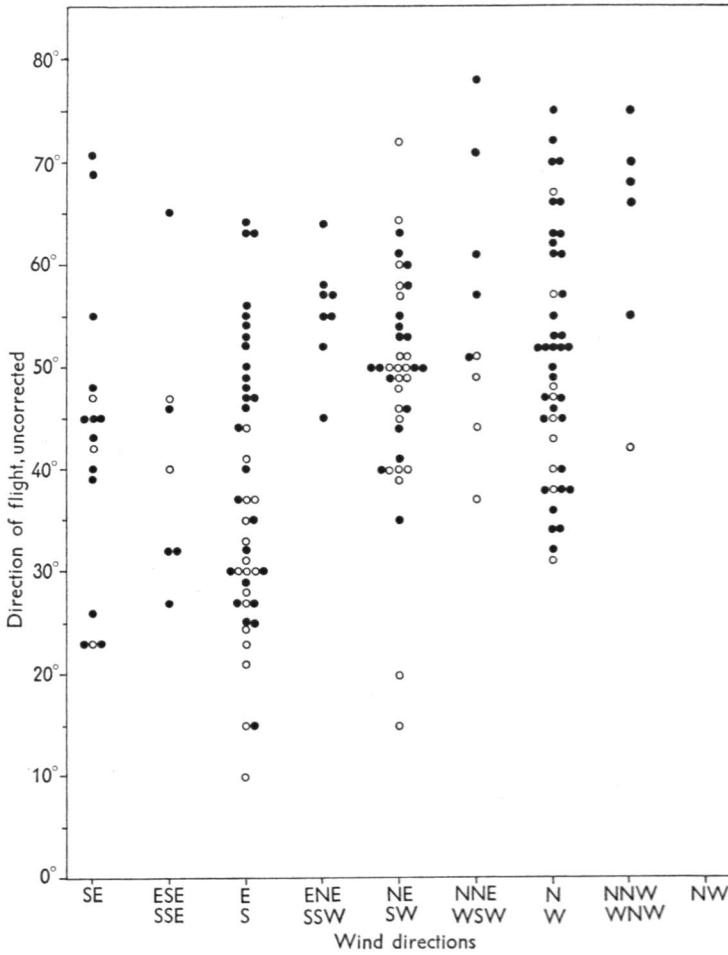


FIG. 7. The distribution of directions in areas A—F in relation to the prevailing wind. Open circles = day migration, filled circles = night migration.

suggests that the birds studied are unable to compensate for drift in any way, but does not of course exclude the possibility of reorientation if they have drifted off their normal migration route.

In the data of Fig. 8 the effect of wind has been eliminated and the values here ought to give the direction in which the birds actively fly. These directions are seen to vary between 70° and 25° . When trying to analyse the factors responsible for this variation the first question naturally is: what is the accuracy of the orientation mechanism that the birds possess? An answer to this question is obtained by studying the variation in the direction of movement of individual flocks during the same external conditions. This is illustrated in Fig. 9, which

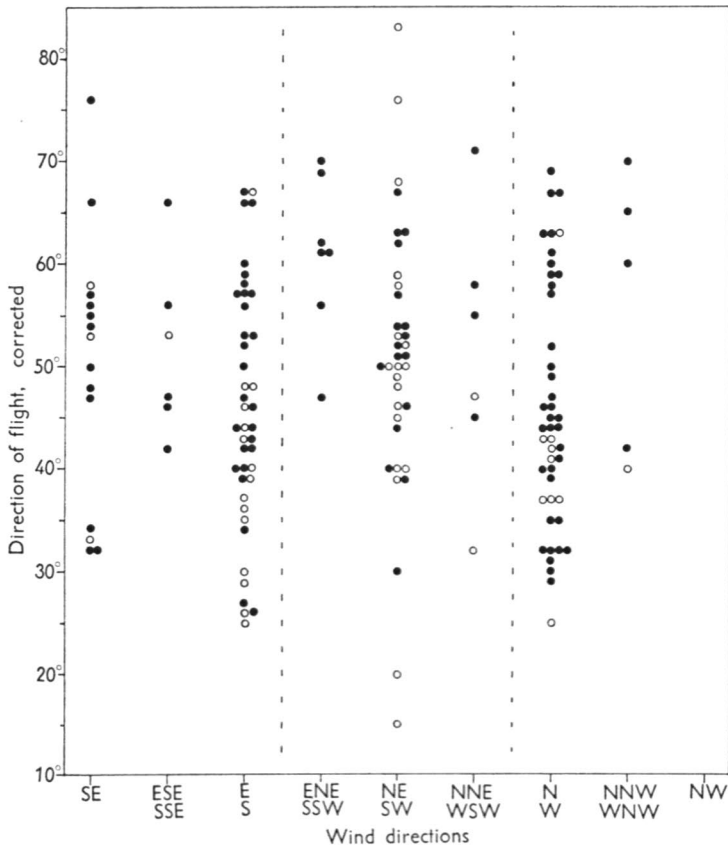


FIG. 8. The directions of flight presented in Fig. 7, corrected for drift. Open circles = day migration, filled circles = night migration.

gives the distribution of directions of single flocks for 24.V.60 at 20.40 in an area about 20×20 km 30 km to the north of Helsingfors. It is seen that the distribution is not a regular one but appears to consist of several groups with slight differences in the preferred directions. Because flight altitude appears to vary considerably over land (Fig. 3), any change in the direction and strength of the wind with altitude must produce an increased variability of the directions measured in the present way, not connected with any property of the innate orientation mechanism. It is then reasonable to assume that the postulated constant external conditions are realized only for groups of the material in Fig. 9, for instance the group showing directions between 25° and 30° . This argument leads to the conclusion that the birds are able to orientate with an accuracy of $\pm 3^\circ$, in other words that the range of variation introduced in the material by this factor is approximately 6° . This is consistent with obser-

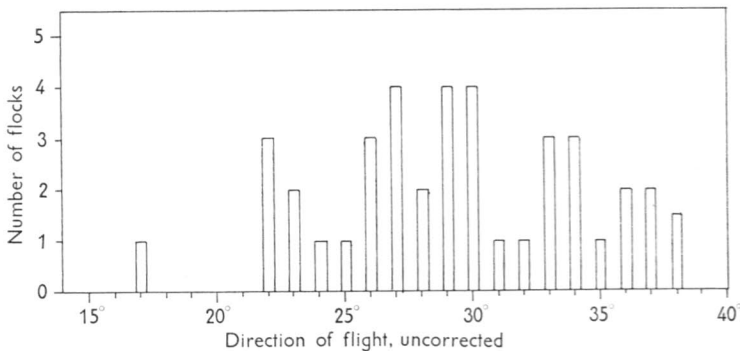


FIG. 9. The distribution of directions of individual flocks 24.V.60 20.40 in an area 20×20 km 30 km to the north of Helsingfors.

vations from other areas and other days. Further, it is often observed that even within a restricted area of the size used here (20×20 km) a systematic variation may occur, indicating a change in conditions from one edge of the area to the opposite one. On the other hand an alternative interpretation may be that a local topographical feature affects orientation. Nevertheless, the orientation mechanism appears most likely to be not at any rate less accurate than stated here; it is possible that the birds are even able to determine their direction of flight so accurately that when they are exposed to the same external conditions their directions do not differ from each other more than $1-2^\circ$.

Consequently, if time-compensated celestial orientation is involved as seems to be the case (p. 29—32), it follows that the internal clock of the birds, whether they orientate according to the sun or the stars, must not give deviations larger than ± 12 min or, if the accuracy is $\pm 1-2^\circ$, not larger than $\pm 4-8$ min. Approximately the same accuracy ($\pm 5-10$ min) in the timing of the diurnal activity rhythm is evident from P. PALMGREN'S (1944, 1949 and personal communication) results on different passerine birds. On the other hand ADLER (1963), discussing the psychophysical limits of celestial navigation hypotheses, states that for single Starlings the error of the internal clock may amount to 15—20 min (ADLER & GIANUTSOS 1962), which corresponds to about $\pm 5^\circ$. Experiments on fish (HASLER & SCHWASSMANN 1960) and on bees (LINDAUER 1957) show that these animals can still use the azimuth of the sun for orientation purposes even when the angle between the sun and zenith is $2-3^\circ$ (bees) or 5° (fish). These findings show that the animals are able to make a discrimination between the directions of two simultaneously presented stimuli of different sensory modalities with about the same accuracy as single birds can use their internal clock for the determination of direction.

The accuracy of orientation as observed here does not then appear inconsistent with earlier data. Further, a factor that may increase the accuracy is

the fact that the data presented here refer to the movements of relatively large flocks, and never to individual birds. It is clear that flock formation and the stimuli keeping the flocks together will suppress tendencies in individual birds to migrate in slightly different directions. Thus the actual heading of a flock will presumably be an average of the directions individual birds would take when flying alone. This suggests a smaller variation in the headings of individual flocks than in case of individual birds. It is then possible that flock migration in this way increases the accuracy of the orientation mechanism.

It is then clear that the variability of direction as shown in Fig. 8, cannot possibly be considered simply as caused by an inaccuracy of the orientation mechanism itself. The errors introduced by the procedure used here to derive the true directions of flight should naturally next be considered as a source of the variation observed. An estimate can be made from the known accuracy of the data for the wind (speed and direction) as well as for the ground speed and the uncorrected direction of flight. Here by far the greatest error is introduced by the inaccuracy of the wind data, where direction is given with an accuracy of 22.5° and the velocity in full m/sec, thus ± 1.8 km/hr is the accuracy here. With a wind direction perpendicular to the direction of flight and a wind of moderate strength (4–6 m/sec) it is found that with the accuracy stated the value derived for the actual direction of flight should be not more than 2° from the correct value. This figure may perhaps be doubled if one considers that the wind data used may be incorrect due to errors in the wind measurements and that the birds fly at an altitude for which the wind data used do not quite apply, at least not in all cases. Further the birds' own orientation mechanism gives a variation of say $\pm 2^\circ$, and the method of tracing the flight paths may add to this an error of $\pm 2^\circ$. This implies that the present procedure gives the direction of flight after wind correction within at most $\pm 8-10^\circ$ of the correct value. The fact that the standard errors of the mean are about the same as calculated on the present material divided into three groups (Fig. 8), where one of the groups is constituted by those cases where the effect of the wind on the direction of flight is at a minimum, also supports this conclusion. Because if quite considerable errors were introduced by the present correction procedure they would raise the variation of those groups where the wind effect is strongest (groups 1 and 2).

If it is then assumed that all the flocks are heading in the same direction one would expect to obtain all the individual data, such as those in Fig. 8, within $\pm 8-10^\circ$ of the correct value, thus in a $16-20^\circ$ interval, if the above arguments apply. It is immediately clear that the spread of the data is about double this which suggests that the heading of the migrating flocks is variable and may change, for instance, with different modes of orientation.

There are mainly two alternative possibilities to explain orientation, if only such mechanisms are considered for which earlier reliable evidence exists:

1. The birds orientate using the position of the sun or the stars as a guide, compensating for the movement due to the rotation of the earth with the aid of an accurately timed internal clock. This is the kind of orientation discovered by KRAMER (1949), later demonstrated to be possible by the stars too (F. and E. SAUER 1955).

2. The direction of flight is determined by the landscape, as for instance by coastlines, lakes, rivers etc. In this case earlier experience of the migrating birds as well as traditions from previous generations may have a great influence.

It is possible to distinguish between these two modes of orientation, because in case 1 (celestial orientation) the orientation clue should be a constant within a certain, fairly wide area. It follows that the same direction of flight, if wind-corrected values are considered, should in this case be observed in different parts of the investigation area. On the other hand it can be said that case 2 (topographical orientation) must depend on stimuli which vary within the area under study, and that thus orientation by such clues is more likely to result in variable directions of flight determined by the local conditions. Thus if flight directions are found to vary much within the area under study topographical orientation is strongly indicated.

In Fig. 10 the data of Fig. 8 have been plotted separately for each area (A, B, C, D, E, see p. 21), the number of cases being given in each interval of 5° . The mean direction for each area as well as the number of cases are given in the figure. It can be seen that in all areas, except perhaps in E, there is a common direction component around $30-50^\circ$, while on the other hand, as for instance in area B, directions occur that appear to be a characteristic of that special locality. The directions $30-50^\circ$ thus appear to depend on some common orientation factor (case 1) and, for instance, the directions around $55-70^\circ$ in area B on some local effect. It can further be observed in Fig. 10, that only regarding area D, which refers to migration over land, is the distribution of directions approximately symmetrical around the mean. The distributions in areas A, B, C, and E, referring to migration on the Gulf of Finland, are to a greater or lesser extent asymmetrical. When flying over the Gulf of Finland the birds approach the Finnish coast at an angle of about 30° and when reaching the coast change their direction and tend to follow it (cf. below p. 36). Although the present material (areas A, B, C, E) refers to the migration about 15 km south of the coast a certain change in the flight direction is apparently induced already at this distance. The films clearly show a gradual change in direction which, however, is more marked closer to the coast. Thus effects of the topography in areas A, B, C, E should mainly be manifest as

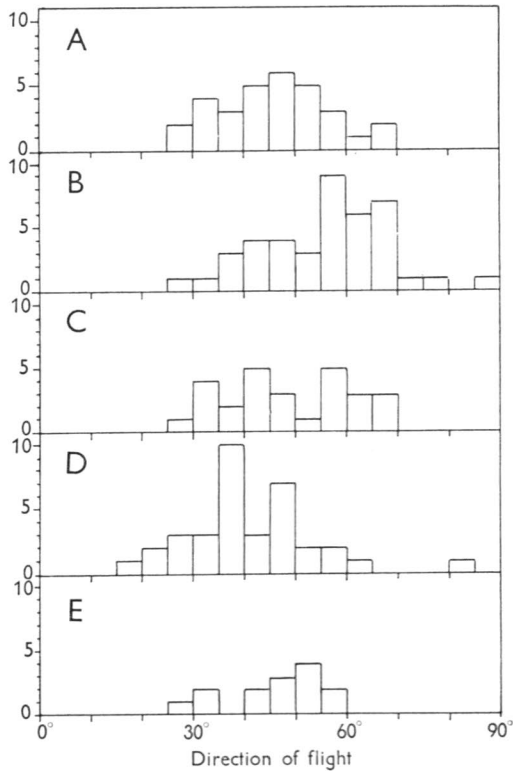


FIG. 10. Distribution of corrected directions of flight for areas A—E (cf. p. 22) 1960—62.

deflections to the east. On the other hand migration over land does not meet with this kind of one-sided deflection, but the effects should be more random and increase the spread on both sides of the mean.

If then the same direction is used by the birds in different parts of the region studied this indicates that presumably the same principle of orientation is used by all birds. The most likely assumption is that they orientate by the sun or the stars (celestial orientation). Because such orientation is excluded with a fully overcast sky, as has been demonstrated both experimentally (KRAMER 1950, 1951, SAUER 1957), in earlier work with radar on migration (LACK 1958, 1960, GEHRING 1963) as well as in case of the «nonsense» orientation discovered by MATTHEWS (cf. MATTHEWS 1955, 1961, BELLROSE 1958, 1963), it is possible to check the present material against the degree of overcast in order to see if this correlates with some special group of directions. In Fig. 11 the present material (corrected directions of flight) has been plotted in relation to the extent of the cloud cover during the time of migration, this being expressed in % of the maximum (full overcast = 100 %). There are only a few observations referring to conditions with a full or nearly full overcast due to

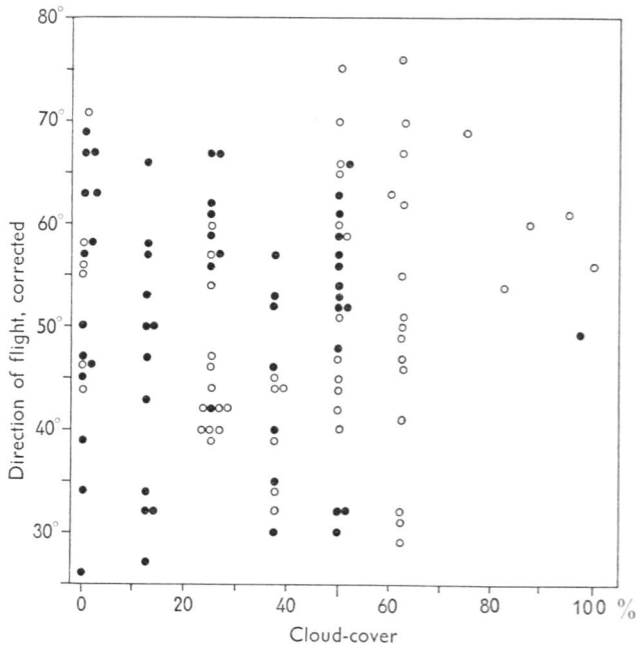


FIG. 11. Corrected directions of flight in relation to the degree of overcast. Open circles = day migration, filled circles = night migration.

the fact that in such weather migration is only weak or completely inhibited, as will be shown below (p. 48). Nevertheless, Fig. 11 shows that when the cloud cover exceeds 60–70 % there are no cases where the birds have flown in directions 30–50°. This group of directions is the one common for the whole area investigated (Fig. 10). It can be inferred that a good view of the clear sky is needed for this kind of orientation to occur. The result is thus consistent with the interpretation that the directions between 30° and 50° are based on celestial orientation. Fig. 11 also suggests that celestial orientation in daylight is still possible when there is a 60 % cloud-cover whereas in the night the limit is slightly lower, about 50 %.

It is, however, evident that although flight in the direction which, according to the above argument, indicates celestial orientation is excluded when cloudiness exceeds a certain limit, the birds still even with a fully overcast sky have some ability to migrate in an approximately correct direction, although they rarely do so. KRAMER (1961) points out that the directional perseverance observed in experiments with caged birds may help them to maintain the correct direction even without a view of the sun or the stars, but stresses that other results with caged birds (MERKEL & FROMME 1958, FROMME 1961, PRECHT 1961) as well as results with homing pigeons give an indication of the existence of still unknown orientation mechanisms. Such

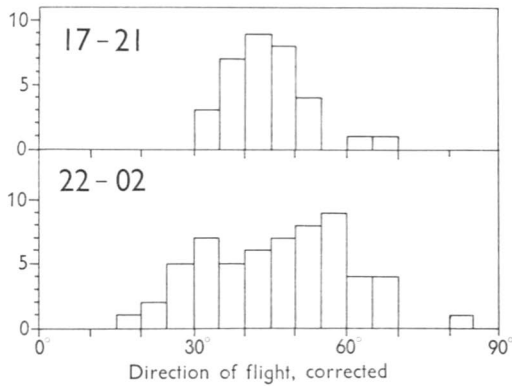


FIG. 12. Distribution of corrected directions of flight 17.00—21.00 and 22.00—02.00.

persistent maintenance of direction if normal orientational clues are lacking appears sufficient to explain migration of the present duck species under an overcast sky, especially considering that generally a fully overcast sky tends to abolish migration completely (p. 48). Further, the direction of flight with a nearly full overcast is always such as to indicate guidance by the coast, which apparently under such conditions gives the immediate orientational clue.

The migration studied here begins in full daylight and is normally quite intense already before sunset. Then it continues nearly all night until dawn. It may now be asked what kind of celestial orientation mechanism the birds use, whether the sun or the stars or possibly both, the sun before sunset and the stars by night. Some information in this respect has been gained by dividing the material from areas A, C, E, and D, but excluding area B where a local effect is marked, into two groups. The first group refers to migration between 17.00 and 21.00 (before sunset) and the other one to the time between 22.00 and 02.00 in the night. Fig. 12 gives the distribution of directions in these two cases. Quite obviously there is a larger variation in the material referring to night migration. The corresponding means are: daylight $43.8 \pm 1.5^\circ$, night $46.1 \pm 2.1^\circ$. These means are very nearly the same without a statistically significant difference. But the standard deviation is 8.8° for day migration and 16.1° for night migration, thus clearly expressing the difference between the two groups.

The interpretation of the result shown in Fig. 12 can proceed along two separate lines:

1. The birds use the sun for orientation during the day and orientate by the stars at night. In that case star orientation is less accurate than orientation by the sun, or star orientation is more easily disturbed by local landmarks such as coastlines, rivers and lakes that may be visible even in the night, as well as by illuminated towns, villages and roads etc. It is also possible that although

the birds possess a mechanism for star orientation, they are unable to use it because of difficulties in seeing the stars in the twilight of the nights at this time of the year.

2. Sun orientation is the only celestial orientation mechanism possessed by these birds and therefore fails after sunset. An assumption of this kind is, however, not supported by what is known for other birds both by experiment (SAINT PAUL 1953) and in the field (LACK 1962 b, cf. also MATTHEWS 1955, 1961, BELLROSE 1958, 1963).

At present it is impossible to decide definitely between these two alternatives. An observation with a likely relevance in this context is, however, that the kind of migration here studied never starts before the date (about 7.V., BERGMAN 1941 and the present material) when a faint glow at the horizon indicates the position of the sun all through the night. If thus the birds determine their direction of flight from the position of the sun they can do so all through the night, although the accuracy with which this can be done must certainly be less in the night than when the sun is directly visible. This would explain the observed variability in night orientation without the need of assuming that the birds possess double orientation mechanisms. As stated above the mean direction between 17.00 and 21.00 as compared with that between 22.00 and 02.00 is practically the same but the standard deviation is about twice as large in the latter case. The weaker adherence to a basic direction is obvious, but it may arise in different ways. It may be said that in the night orientation is less accurate as such, the position of the sun being barely indicated by the evening glow. But it may equally well be said that because the orientation clue is more diffuse and as a stimulus from a sensory point of view not by far so strong as the sun itself when visible, other clues for orientation derived from the topography of the land beneath will be more frequently used. This question has not been studied so far, but an answer should be possible after a detailed study of the radar films in relation to the topography.

In the treatment of the data it has so far been assumed that the mean direction of the migrants as determined by their celestial orientation mechanism is always the same. In order to enable the birds to correct for the movement of the sun they must possess an internal clock, which in case the accuracy of orientation is $1-2^\circ$ as stated above (p. 26), must not be out of phase more than 4-8 min if individual flocks are compared, an hour corresponding approximately to a 15° change in the azimuth position of the sun. As described above, the Long-tailed Ducks gather fairly slowly in the spring at the northern parts of the Baltic Sea and the Gulf of Finland before the rapid and concentrated final migration starts. The Common Scoter, on the other hand, appears to migrate from its wintering area to the nesting area with no marked resting period in between. Depending on the weather conditions there will be differ-

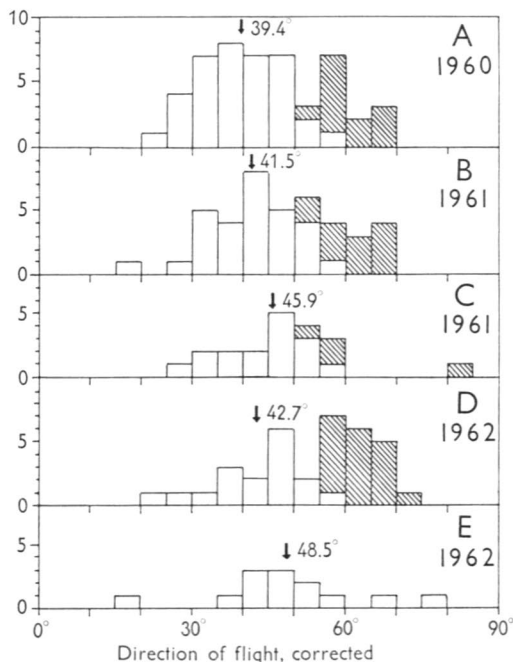


FIG. 13. The distributions of corrected directions of flight during the years 1960—62. A: 1960 (areas A, B, C, D). B: 1961 (areas A, B, C, D). C: 1961 (area E). D: 1962 (areas A, B, C, D). E: 1962 (area F). Full explanation in text.

ences in the time of arrival of the Long-tailed Ducks at the Gulf of Finland between different years, which should not be marked concerning the Common Scoter. Hence it is possible that when the phase of rapid migration starts the internal clocks of these species are not completely in phase with the local day at the starting point, with a possible variation from year to year, this asynchrony, moreover, possibly being different for each species.

Some information on this point is obtained when the direction material is divided according to the year of observation as shown in Fig. 13. The area from which the material has been derived is given in each case. In order to eliminate the directions in the material that, as shown above, (p. 28), most likely represent orientation by other than celestial clues, a slightly arbitrary procedure has been adopted. Of the directions between 50° and 55° thus $\frac{1}{3}$ have been excluded, between 55° and 60° about $\frac{4}{5}$ and of directions $>60^{\circ}$ all. The cases so excluded are shown in the shaded parts of the diagrams. The remaining material shows a fairly symmetrical distribution around a maximum. In each case the mean direction has been calculated and is indicated in the figure by an arrow and the corresponding numerical value. The means for corresponding areas in the years 1960, 1961 and 1962 (Fig. 13 A, B and D) are 39.4° , 41.5° and 42.7° and thus very close to each other considering the

assumptions involved in this procedure. For this reason statistical treatment has not either been carried out. Although conclusive evidence about the variation of the fundamental direction of migration is not obtained in this way, the result suggests that if there are deviations from year to year these are likely to be of small magnitude.

Fig. 13 C refers to the material obtained from the area to the south of the Hangö peninsula. The mean here is 45.9° and thus about 4° different from the general mean for 1961 (Fig. 13 B). But in this case all the individual values have been included, because the restricted material from the Hangö area does not give any clearcut evidence about an eastward deflection of the migrants due to the proximity of the coast. Such an effect may still be there, however, and thus cause the slightly different mean.

In Fig. 13 E the distribution of directions for the area in SE Finland are given separately. In this case migration proceeds completely over land and no coast effect should be present. The mean here is 48.5° as compared with 42.7° for the rest of the material for 1962. Although rather uncertain, being based on a fairly restricted number of observations, this difference in direction of about 6° raises a question of some importance. The observations from SE Finland are mainly if not wholly made on bird flocks that have crossed the southern coast of Finland in the region around Helsingfors sometimes between 21 and 23.00. Their arrival time in the area in SE Finland can be calculated from the observed ground speed and the distance, about 200 km. With a speed of about 100 km/hr the flying time should be about 2 hours, which is consistent with the observations since the wave of migrants reach the area between midnight and an hour after midnight. This migration with its general NE direction results in a rather fast eastward displacement of the birds which will put their internal clocks slightly out of phase even during the migration of a single night. This should result in a change of the fundamental direction of flight, the magnitude of which is predictable on the following argument:

If the migrating birds are assumed to start from the Helsingfors region (long. 25°E) and fly in an approximately NE direction, they have when reaching the St. Michel region moved eastward 2.5° . If their internal clocks are synchronous with local time in Helsingfors, they will be 2.5:15 hours = 10 min slow in the area in SE Finland under study. In other words, according to the internal timing of the birds the sun will have a position 2.5° more to the east than at their starting point at the corresponding moment, and due to this the basic direction of flight should be 2.5° more to the east if a constant angle to the sun is assumed. The actually observed difference here is 5.8° , but considering the restricted material and its variability much stress cannot be laid on the absolute magnitude. Obviously a much larger, and with regard to the wind data more accurate, material is needed in order to allow any definite

conclusion to be made. A similar effect should also be observed at any single point, because flocks passing at different times of the day must be considered to have started from quite different resting localities, provided that migration is started approximately at the same time of the day. The presence of such an effect is possibly suggested by the data of Fig. 11, where the average flight direction at night is found to be 2.3° more eastern than in the evening.

In the case of the present birds it does not seem unrealistic to assume a total flying time of 5–6 hours per day giving a displacement of 500–600 km and thus a change in the basic direction of about $7-8^\circ$ according to the above argument. If migration is continued on the following day it may also be asked whether a resting period of 12–14 hours is sufficient to synchronize the internal clock with local time. Experimental evidence on this point exists for other birds, thus HOFFMANN (1954) found for the Starling 4–6 days to be required for a phase shift of 6 hours, which corresponds to about 1 hour/day. The results of ASCHOFF & WEVER (1963) on Chaffinches suggest ca 1.5 hours/day. The phase shift mechanism then appears to be sufficiently rapid to allow both resynchronization during a half day rest of phase differences of the present magnitude, as well as to explain the relative constancy of direction from year to year.

The accuracy of the wind-corrected directions of flight was stated above (p. 27) to be $\pm 8-10^\circ$. This accuracy is too low to give an opportunity for an analysis of the possible diurnal variations in the direction of flight as determined by celestial orientation mechanisms, one of the questions being whether these birds can fully account for the changes in the azimuth position in the sun (cf. e.g. HOFFMANN 1954, BRAEMER 1960, BRAEMER & SCHWASSMANN 1963, BIRUKOW, FISCHER & BÖTTCHER 1963). GEHRING's (1963) results from Switzerland demonstrate a diurnal change in the direction of migration suggesting that birds do not use the local sun azimuth curve, which would indeed be surprising considering that their internal clocks are probably in phase with conditions at their starting point and not at the point of observation. Because the rate of change of sun azimuth shows a diurnal variation the magnitude of which changes with latitude, birds moving fairly rapidly northwards or southwards will be exposed to changing conditions in this respect.

Another question is whether any kind of compensation of drift takes place manifest as a change in the innate heading, for instance after persistent winds from one direction. This would require some more elaborate navigation system than pure direction finding.

In order to make a more detailed analysis possible, work now in progress has been aimed at securing the best possible wind data at the actual time of the radar observations by specially arranged pilot balloon observations.

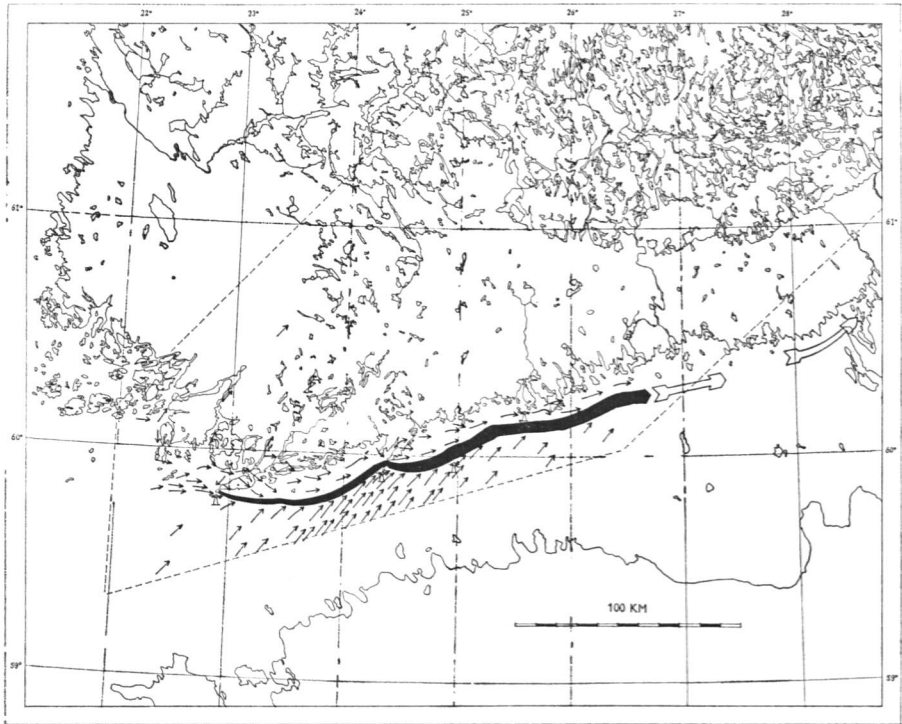


FIG. 14. General course of the migration in daylight with high or medium visibility. Note general absence of migrants over land, except a few flocks in the lake region (see p. 42 and 52).

3. The influence of topographical factors on the direction

The analysis described in the preceding paragraphs has deliberately been carried out with material from areas that show only little of the very clear effects exerted upon the direction of migration by local topographical factors. An effect of this kind is, however, even there manifest in the fact that the birds under certain conditions when approaching the Finnish coast from SW tend to take a more eastern course already at a relatively great distance from it (p. 28, Fig. 10). This deflection is gradually increased when the flocks come nearer to the coast and often leads to an extremely great accumulation of flocks flying approximately parallel to it just outside or at the level of the outer archipelago (Fig. 14). These reactions of the birds are very clearly illustrated by the radar films, but are difficult to describe and analyse in a quantitative way, due to the great number of factors involved. They will therefore be described here qualitatively only. At the end of this paragraph

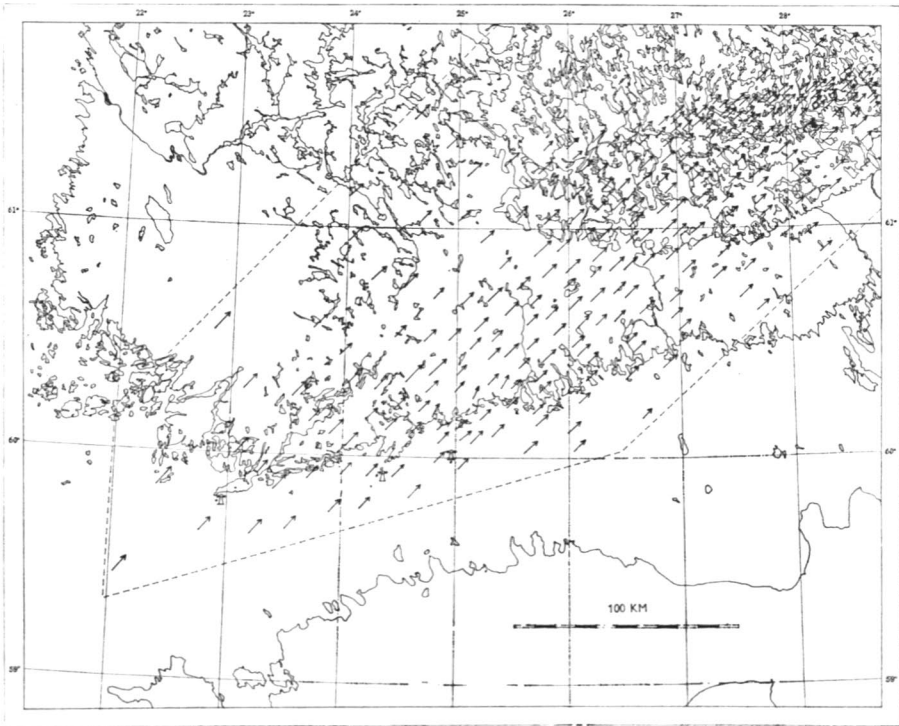


FIG. 15. General course of the migration during the night.

an attempt will then be made to summarize the kind of general behaviour and reactions of the birds that are predictable on the present material.

The effects to be described refer to the only condition where the effect of the topography is quite obvious, namely when the birds on their flight meet a coastline, either on the mainland or islands of the archipelago on the open sea. These reactions are well illustrated by the radar films from the Helsingfors—Porkkala area, as well as from the region around the Hangö peninsula. In both these regions the migrating flocks, flying over the Gulf of Finland in an approximately NE direction, in daylight gradually change their direction of flight when approaching the coast so that they finally fly on a course parallel with the coastline (Fig. 14). This change of direction is under conditions with good visibility already quite distinct around the lighthouse Helsinki, situated about 20 km off the coast to the south of the city (see Fig. 10 B, p. 29). Apparently the distance at which this deflection begins depends on the distance at which the coast is clearly seen by the birds. This applies for migration in daylight with medium or good visibility, but may occur to some extent on nights with a full moon and a good visibility. On the other hand,

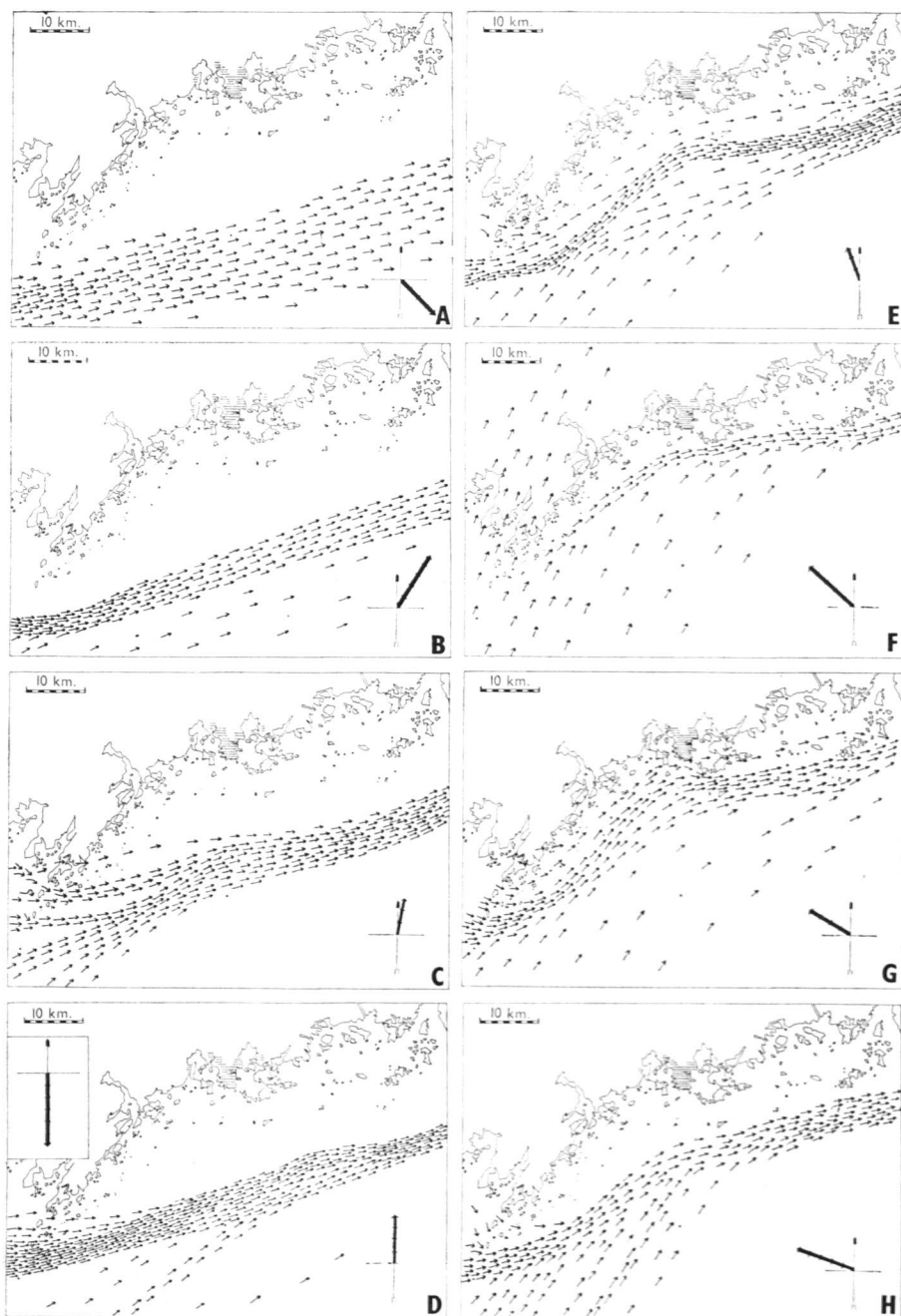


FIG. 16. A—H. Routes of daylight migration in the Porkala—Helsingfors area during different conditions of wind and visibility. Thick arrows in the lower right-hand corner of the maps indicate strength and direction of the wind at sea level. *A.* Wind: NW, 4 m/sec, visibility > 30 km. *B.* SW, 5 m/sec, 30 km. *C.* SSW, 3 m/sec, 25 km. *D.* S, 4 m/sec, 15 km (Hangö: N, 6 m/sec, 30 km). *E.* SSE, 3 m/sec, 15 km. *F.* SE, 5 m/sec, 6 km, in the western part of the area only 300 m. *G.* SE, 4 m/sec, 30 km. *H.* ESE, 5 m/sec, 25 km.

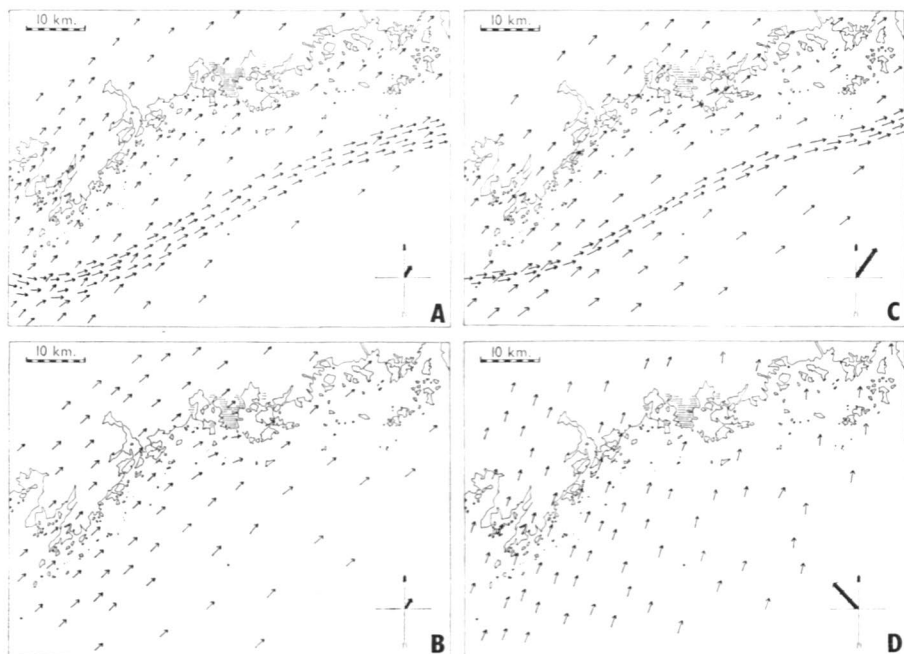


FIG. 17. A—D. Routes of night migration in the Porkala—Helsingfors area during different conditions of wind and visibility. Symbols used same as in Fig. 16. *A.* Wind: SW, 0—1 m/sec, visibility 30 km, moonlight. *B.* SW, 1 m/sec, 20 km. *C.* SW, 3 m/sec, > 30 km. *D.* SE, 3 m/sec, 15 km, upper wind E, 6 m/sec.

the direction of migration during nights with a faint twilight only is not to any greater extent influenced by the coast, even in clear weather with good visibility, but usually continues over land without any change in direction (Fig. 15). This also occurs in daylight under conditions when there is a haze or a low fog over the coast. Then nearly all the flocks of Common Scoters and mostly also the Long-tailed Ducks continue their flight undisturbed over land. Typical examples of the routes taken by the migrants under various external conditions in the Helsingfors—Porkala area are given in Fig. 16 A—H (day migration) and Fig. 17 A—D (night migration).

A marked effect on the migration is exerted by particularly conspicuous coastal configurations as, for instance, narrow bays and capes protruding into the sea. These effects are most clearly manifest in daylight with medium visibility, but similar effects are observed to some extent also in the night, especially with moonlight. Such parts of the coast and archipelago that do not form a clear obstacle in the direction of flight but still protrude from the coast, produce a local deflection of the birds away from the point most clearly visible to them. Usually this results in a deflection towards the open sea. But with a peninsula that protrudes towards the SW from the coast a condition may arise where the birds obviously see the point of the peninsula east of their

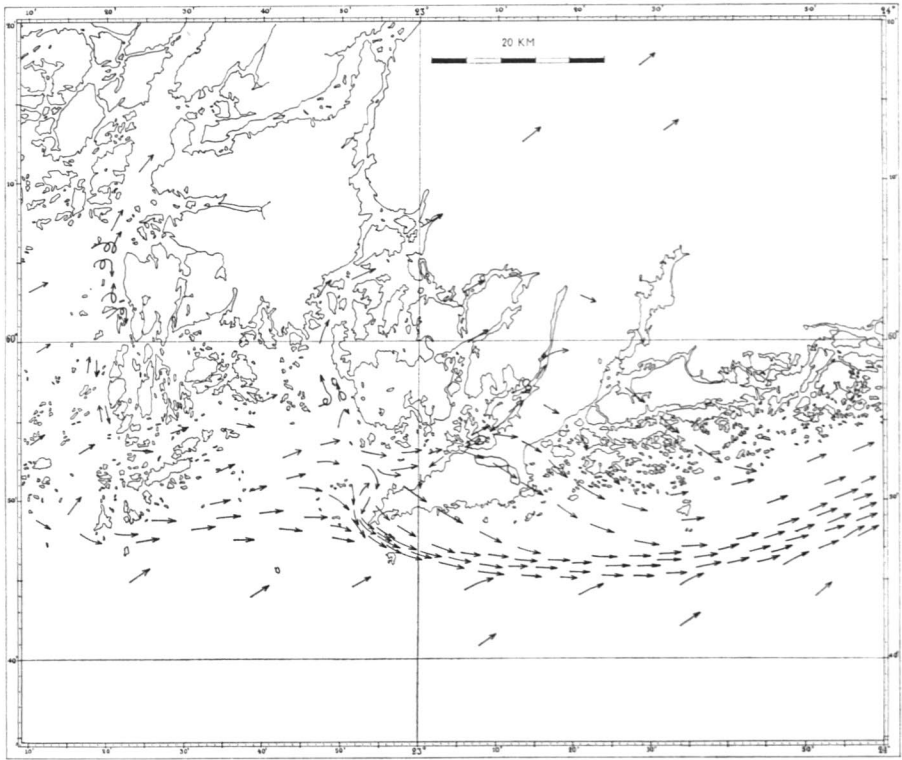


FIG. 18. General map of the area around Hangö peninsula illustrating details of the reactions on islands and the coastline during daylight migration.

direction of flight and consequently turn northwards and become trapped on the western side of it. There they finally reach a point where open water is nowhere to be seen in front of them, which results in a rather radical change of behaviour, as has been observed both west of the Porkala peninsula and west of the Hangö peninsula. The details of the courses followed are seen in Figs. 18 and 19. The following typical features may be mentioned: Flocks flying straight towards a land mass regularly increase their flying altitude and display, with an interval of a few minutes, a kind of panic that shows up as an interruption in the rise towards higher altitudes by a kind of sudden and irregular diving flight. The flight altitude, which initially may have been 50–200 m but due to the tendency to rise may be 500–1 200 m, quickly drops to about 20–150 m with a subsequent rise. This is especially characteristic of the Long-tailed Ducks in the area W of the Hangö peninsula at the western coast of it, facing the open waters between the peninsula and the Bromarf land. The increased altitude of flight after the diving flight, which is accompanied by frequent turning so that no progress in the direction of migration is made, is followed in

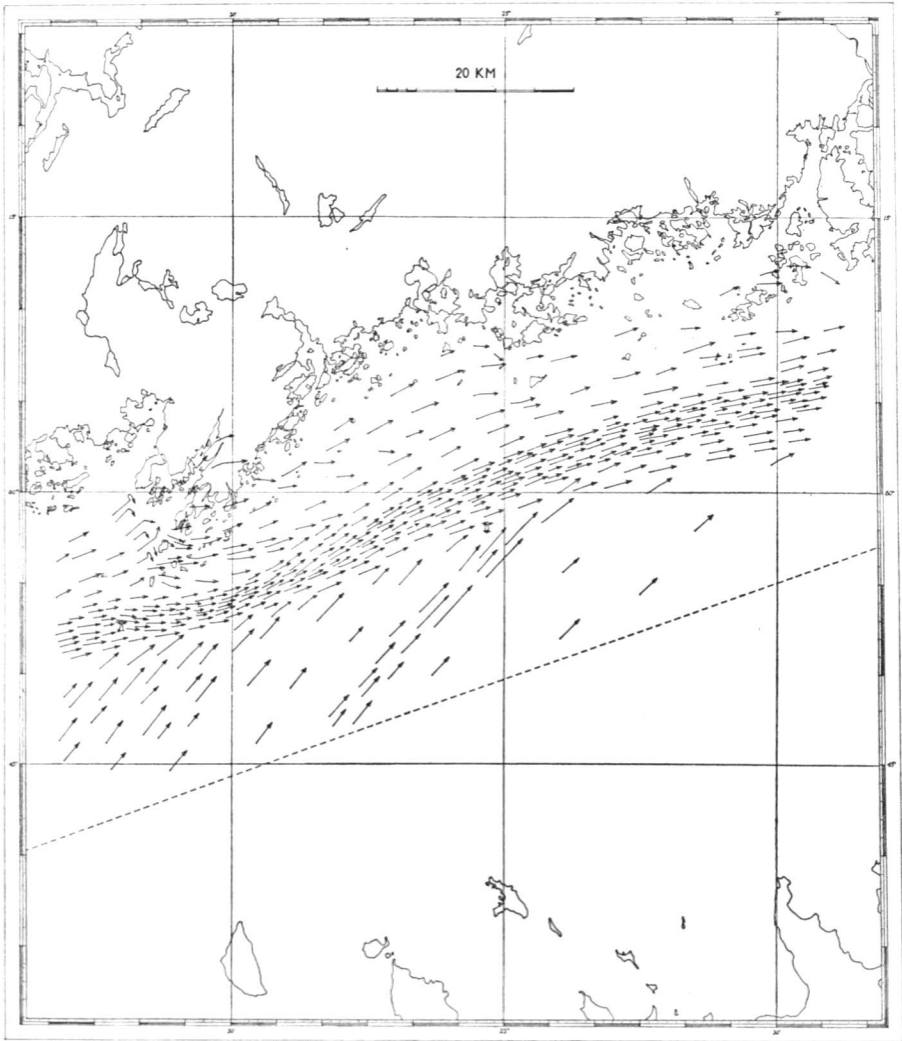


FIG. 19. General map of the area around Porkkala peninsula and Helsingfors illustrating details of the reactions on islands and the coastline during daylight migration.

a few minutes by continued flight either over the land in front where it is narrowest, or back to the point of the peninsula and from there onwards along the coast. Obviously the higher altitude creates a situation where the waters visible on the eastern side of the peninsula reduces the inhibitory effect of the land. The lower the visibility the easier this trapping effect leads to continued flight in over the mainland. This is apparently always the case if the birds cannot see the waters on the other side of the peninsula or the point. The term visibility here includes both effects due to the prevailing atmospheric

conditions and effects due to changes in illumination, i.e. between day and night.

Locally, the 10–20 km long and frequently more than a kilometer wide fiordlike bays north of the Hangö peninsula deflect the migrants even 30° from their normal direction of flight (Fig. 18). This effect is strong in daylight but can be traced also at night when flight altitude is still fairly low after the short flight over the archipelago, considerably lower than inland (p. 15). Single flocks have been found to change their direction to SE from the inner parts of the bays of Gennarby and Pojo and to return to the sea. In the Porkala area, the absence of large lakes and bays in the region north and northeast of Porkala apparently explains why flocks crossing the coast here continue their flights in rectilinear paths in their normal NE direction of migration. North of the Hangö peninsula this situation is reached only after the birds have passed all the bays of the coast that stretch deeply inland.

On an average the flight altitude in the region studied in SE Finland is higher than in the vicinity of the coast (cf. p. 15). This is presumably the reason why the influence of lakes and rivers appears to be negligible. During the half hour before sunrise changes in direction can be observed that seem to correlate with the position and occurrence of large lakes. This is presumably connected with the fact that a part of the flocks at this time tends to find resting places on these lakes, and in doing so can be expected to reduce their altitude of flight. Some effect of the topography is also seen around the large lake Päijänne, where daylight migration passes along the lake in a more northern direction than normally, at any rate this lake is found to cause a deflection of the normal direction of migration.

The situation and width of the zone within which the migration becomes concentrated outside the coast at Porkala and Helsingfors under conditions when the birds are deflected when approaching the coast, appears to be determined by visibility, amount of drift and flight altitude (Figs. 16–17). The lower the visibility and the higher the altitude, the nearer to the coast the migrants pass. This is in full agreement with earlier observations on the flight altitude over different parts of the archipelago (BERGMAN 1941). Field observations show that the more uniform the flight altitude is, the narrower is the zone within which the migrants pass along the coast; flocks at the same altitude are at the same distance from the coast deflected by an equal amount. On the other hand, if the altitude varies the flocks flying lower as a rule take a course further out at sea. This results in a widening of the zone where migrating flocks are observed. Strong drift caused by wind, deflecting the birds so that the resulting movement is more clearly directed towards the coast, results in a narrower zone of migration than with no or little effect of the wind. It is clear that northern and northwestern winds will act in an opposite manner.

If they are sufficiently strong the drift produced alters the direction of the actual movement of the birds with reference to the ground to that extent that the flocks never reach the Finnish coast but move parallel to it or even under extreme conditions away from it (Fig. 16 A). If the migration for a particular day consists of either of the species alone, the zone of migration is narrower than if both species are represented: the Common Scoters appear to react a little less strongly to the coast than the Long-tailed Ducks. Local fog, conspicuous cloud formations and rain showers, as well as the movements of ships on the sea finally also affect the details of the migration to some extent. Strong local showers and thunderstorms are generally avoided by the birds, which change their course and are observed flying round such local disturbances. Flocks that reach a larger area with rain, moving northeastwards, interrupt their migration. Ships and especially naval manouevres cause resting flocks to enlight and start their migration even at times of the day when migration is otherwise weak.

A striking feature always observed when migrants have been deflected by some protruding island or point on the actual coast is that the original direction of flight is not resumed immediately after the obstacle has been passed but after they have definitely left the deflecting configuration behind (Figs. 18—19). The deflecting effect of the land thus still lasts when the distance to it from the birds is greater than the smallest distance to it when the deflection started. The birds' inertia in resuming their normal direction of flight is manifest in the fact that after having turned away towards the sea from an island or peninsula, the flocks fly along a curved path which may have a radius of 10—15 km and only gradually resume their normal direction of flight. This is particularly evident when the migrants pass the island of Nargö, which causes a northward deflection of the flocks so that when they leave the island they may even fly towards the NNW. Although there are no islands between the Finnish coast and Nargö, the flocks resume their normal NE direction approximately halfway between Estonia and the Finnish coast.

The changes in direction observed as a response to islands and coastlines in front of the birds, when flying over the sea, can be looked upon as being governed by a compromise between two conflicting tendencies: 1. to maintain the rectilinear normal direction of flight, and 2. to fly in a direction that leads to continued migration over the open sea. These conflicting effects vary in relative strength depending on the distance to the coast and the visibility, so that with low visibility in daylight and nearly always at night, no deflections can any longer be observed. The other extreme is represented by the cases where the birds in full daylight fly directly towards a point on the coast or an island. In that case there is no change in direction until the birds are very close to the land, apparently because the tendency to maintain the normal

direction of flight is strong enough to suppress a tendency to turn, which may be weak so long as the land is right in front of the birds. The situation is then symmetrical with reference to stimuli that may give rise to a change in direction and gives no clue regarding which way to turn. At a certain moment the birds are so close to the land that the kind of »panic» behaviour described above follows, with a sudden and radical change in the direction of flight.

When approaching a coast at a small angle the necessary correction in the direction of flight is small in magnitude, theoretically equal to the angle between the normal direction of flight and the general direction of the coast if it results in a movement parallel to it. Under such conditions the prevailing wind may enter as a factor that increases the movement towards the coast, and finally brings the migrating flocks so close to it that they compensate for this with a greater change in direction. The result is that migration becomes dependent on topographical factors only and is thus in effect also compensated for drift by wind. The border between the area on the open sea, where the direction of flight is influenced by the coast but not compensated for drift, and the coastal area with direct orientation according to the topography as described above, is diffuse and varies depending on the visibility and the prevailing wind as well as on the kind of coastline encountered. It appears that in the present case the flight is strictly guided by the topography at protruding points on the coast and at islands fairly far off the coast (Hangö, the Jusarö islands, Porkala, Helsingfors—Sveaborg—Mjölö, the Söderskär islands and Pellinge). Between these points the strict guidance of the coast may be absent if the migrants are not drifted by strong sidewinds to such an extent against the coast that they even here come to follow the topography completely.

V. The effect of meteorological factors on the intensity of migration

The previous analysis has shown that the Common Scoter and the Long-tailed Duck fly during their spring migration approximately in the direction 40° but are in addition subject to drift by wind, whereby the direction of the finally resulting movement varies between fairly wide limits. The wind also enters as an important factor for the ground speed. In addition, celestial orientation is necessarily dependent on a more or less clear sky. During the migratory period weather conditions may change continuously. Some conditions are clearly favourable for migration, for instance, a SW wind directly increases ground speed, while on the other hand SE and NW winds result in lateral displacement with reference to the normal direction of migration.

It is obvious that the drawbacks of unfavourable weather conditions can be avoided and the advantages of favourable conditions utilized if the release of migration is governed by these in an appropriate way. The existence of such effects should be manifest in correlations between certain meteorological variables and the intensity of migration. After what has been said, the most obvious factors to test for such an influence are wind and cloudiness.

1. Strength and direction of the wind

A general picture of the effect of both the strength and direction of the wind is obtained in Fig. 20, which gives the intensity of migration in relation to the direction of the prevailing wind.

Here data are given for each evening (open circles) and night (filled circles) for which radar observations are available from the central parts of the Gulf of Finland. There is a clear predominance of cases with winds between S and SW. In a qualitative way Fig. 20 demonstrates that there is indeed a connection between wind direction and the intensity of migration, so that winds from the NE appear to reduce or abolish migration completely, whereas the really high intensities of migration are to be found with winds between S and W. In other words the migration of these ducks takes place mainly with tailwinds.

This dependence, in Fig. 20 presented only in relation to the direction of the wind, appears to be a gradual one where naturally wind strength should enter as one of the variables. To include this, the material is presented in Fig. 21 in relation to the speed decrease or increase caused by the prevailing wind to a bird flying in a northeastern direction. The symbols used in this figure for each case denote the degree of overcast reported, filled circles indicating full overcast and open circles a completely clear sky. This because, as will be

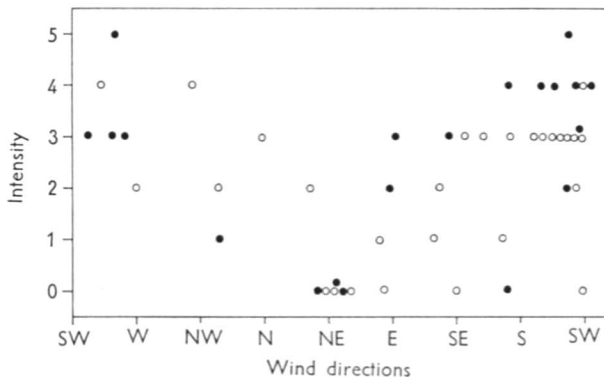


FIG. 20. The intensity of migration in relation to the direction of the prevailing wind. Open circles = day migration, filled circles = night migration.

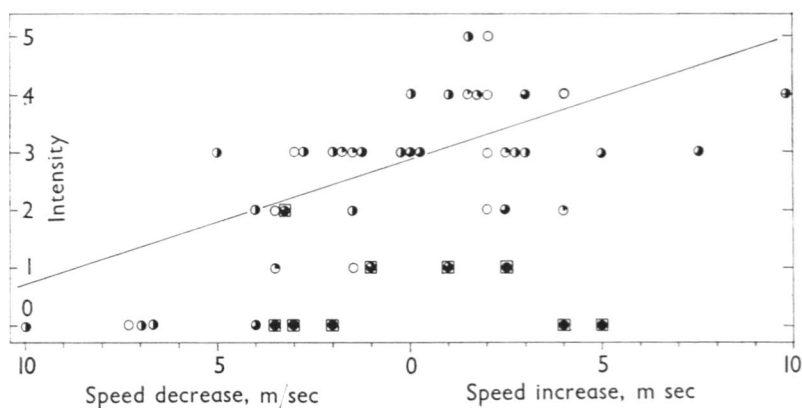


FIG. 21. The intensity of migration in relation to the speed increase or decrease produced by the wind. The degree of overcast indicated in each case by the degree of filling of the circles. Circles with squares denote cases with full or nearly full overcast ($\leq 75\%$) which have not been included in the statistical treatment. Regression line $y = 0.244x + 2.81$.

shown below, there is very good reason to believe that migration is inhibited by a high degree of overcast ($>60-70\%$). These cases have been specially indicated in Fig. 21 by small squares, and they have not been included in the statistical treatment. The calculated correlation coefficient is found to be 0.66 corresponding to a P-value of >0.001 and the line of regression is that drawn in the figure.

These data then suggest that the effect of the wind is such as to abolish migration completely when there is a headwind of about 13.5 m/sec, which is the value obtained corresponding to the intensity 0 when inserted in the equation for the regression line. However, it is clear from Fig. 20 that with an NE wind migration has stopped completely although the strength of the wind has not exceeded 6 m/sec and with less than 50% overcast. Because of this it seems possible that the effect of the wind is twofold: 1) a decrease or increase in the intensity of migration related to the speed decrease or increase produced by it, and 2) a further reduction of the intensity if there is a more or less straight headwind; i.e. an effect of wind direction as such.

Naturally the choice of intensity units largely affects the kind of correlation obtained, and it can be questioned whether the relationship is linear at all. The present intensity scale is roughly a logarithmic one, with an average increase of the number of flocks per unit area of about 2-3 times for an intensity increase of one unit (p. 9). From Fig. 21 it can be worked out what percentage of the flocks for all observation periods migrated during head- or tailwinds: it is found that about 70% of the flocks migrated with tailwinds and about 10% in weather giving neither a speed increase or decrease by the wind. Fig. 21 also shows that this is not due to a dominance of days with tailwinds in

the material. Biologically, the occurrence of a relationship of this kind is easy to understand because it is bound to make migration more economical, reducing the energy expenditure of the birds per unit distance considerably.

The results thus confirm PUTKONEN's (1942) statement about the lack of migration of the present birds with NE winds. On the other hand, the interpretation put forward by BERGMAN (1941) is not generally valid. He found that winds between E and S were especially favourable for migration, as long as their strength did not exceed 8 m/sec. The inconsistency is, however, explained if the general effect of the wind on the direction of migration is considered together with the reactions of the birds when they approach the southern coast of Finland (p. 36). With S and E winds it is clear that the birds tend to drift more to the north and this will accumulate them along the coast, which they will avoid to cross in daylight. Under such conditions an observer in the archipelago (BERGMAN's observations were carried out at Kopplorna 12 km WSW of Helsingfors) will record the highest intensities of migration, although the effect is only a local one not directly depending on the general intensity of migration.

A similar tendency to migrate in following winds is evident from HARPER's (1957) first report and is demonstrated by LACK (1962 b, 1963 a, b) in his analysis of the migration across the southern North Sea. His data for the spring migration (LACK 1963 b) show a change in the intensity of migration of 1.2–1.6 units when there is a change in the wind from E to W during eastward emigration. These units refer to a scale of 0–4, on our scale of 0–5 the change is approximately 2 units. When only wind-direction is considered inspection of Fig. 20 shows that in the present material a change from NE to SW wind results in an increase in intensity of about 3–4 units.

2. Cloudiness

The significance of celestial orientation for the migration of both day and night migrants naturally requires that the birds have at least a restricted view of the clear sky. With a completely overcast sky celestial orientation is eliminated and two possibilities remain if the possible existence of unknown orientation mechanisms is disregarded: orientation according to the topography based on previous experience from earlier seasons, or no migration at all under such conditions. In the present case, it has been shown above (p. 30) that when the degree of overcast exceeds 60–70 % the direction of flight strongly suggests orientation based on landmarks only.

Fig. 22 gives the intensities of migration recorded here in relation to the degree of overcast. It appears that as long as the cloud-cover is below $\frac{2}{3}$ both high and low intensities of migration have been recorded. The five cases with

are not always reliable. During the night mentioned, Helsingfors reported 100 % overcast, although there were within a radius of 15 km from the town numerous openings in the clouds even over the town itself. Only with the continuous cloud-cover of the passage of a weather front associated with a depression do the data from the coast stations appear fully reliable. These inaccuracies observed can, however, hardly have any influence on the conclusion reached here.

3. Visibility

Under conditions of low horizontal visibility the orientation of such birds that orientate according to land-marks, for instance coastlines etc., may be impaired. Such conditions may thus also be thought to have an adverse effect upon the tendency to migrate. The present data (Fig. 23) suggest that this factor is of little or no significance. A slight tendency towards higher intensities of migration with good visibility can perhaps be traced, the correlation coefficient being 0.217 corresponding to a probability of $0.2 > P > 0.1$. The line of regression is drawn in the figure, indicating only a rise of the intensity of migration with about one unit when visibility increases from 0 to 30 km. It should be observed that although the highest intensities of migration have been recorded with good or very good visibility (polar air masses from NW and NE) fairly strong migration (intensities 3 and 4) have also been observed on both occasions when there was a dense fog at ground level. The fact that there probably is a correlation between SW-NW winds and high visibility,

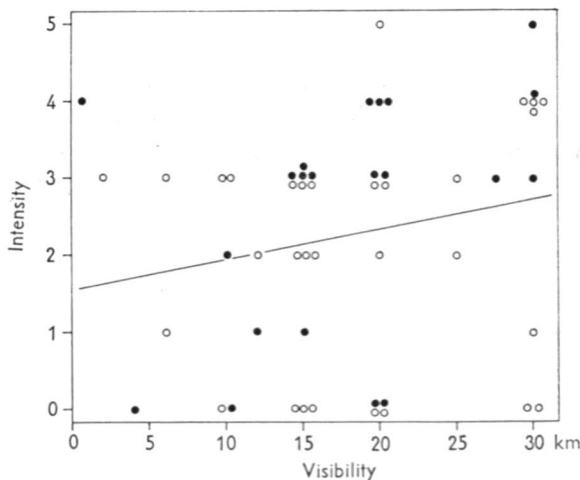


FIG. 23. Relation between intensity of migration and visibility. Open circles = day migration, filled circles = night migration. Regression line $y = 0.404x - 5.01$.

and on the other hand SE-E winds and low visibility may indicate that the weak correlation observed in Fig. 23 is an effect not due to changes in visibility at all but related to the direction of the wind.

4. Temperature

Because the migration studied is concentrated to only two weeks and because the temperature of the sea water, showing hardly any variation from day to day, is a factor that largely determines the air temperatures encountered by birds resting on the water, as is the case with the Common Scoter and the Long-tailed Duck, an analysis of a possible short-term effect of temperature on the intensity of migration would appear to be unfruitful. It must further be observed that the temperature data given by the coast stations do not refer to the altitudes at which migration is carried out.

Good indication of a more general effect of temperature on the migration of the present birds was, however, observed in BERGMAN'S earlier studies (1941, 1951). If the spring is early and warm, the onset of migration is thus on average earlier than when the spring is late and cold. In the present material no clear effect is evident because of the relative similarity of the general weather conditions, except perhaps that the migration during the coolest spring (1962) appears slightly more prolonged than during the two others.

VI. The geographical distribution of the migration

The radar films clearly demonstrate that the stream of migrants mostly, but not always, is very unevenly distributed over the area around the Gulf of Finland. In some regions large concentrations of flocks are observed, whereas in others the density may be quite low. The innate heading of these birds in combination with their reactions when approaching a coastline will clearly favour certain routes, although in a variable way depending on the external conditions (direction and strength of the wind, visibility, cloudiness). Already the fact that the birds during normal celestial orientation are unable to allow for drift results in, for instance, that persistent winds from one direction during several days cause a considerable lateral displacement of all the migrating flocks. On the other hand, they will finally all reach the southern coast of Finland and then — if the weather is not misty — in daylight, sometimes even at night, react on the sight of the coast so that they fly parallel to it in the general direction ENE. This leads to a marked concentration of the migration in a fairly narrow zone outside the coast. This occurs with good or medium visibility, especially when the direction and strength of the wind

is such that there is no lateral drift or drift towards the coast. Further, the general situation should be such that no or very few flocks cross the coast anywhere to the west of the area under consideration. The width and position of the zone, where the migrants are concentrated during various conditions, is described on p. 36—38.

Thus the reactions of the birds and the properties of their orientation mechanism make it obvious that the observed geographical distribution of the migration in different parts of the Gulf of Finland, Finland and Estonia must be strongly influenced by the weather and by physiographic factors.

One important factor for the distribution of the migrants in the Gulf of Finland is the question whether birds that start from the region around the Bay of Riga take a course directly towards the NE across the Estonian mainland or follow the coast of Estonia to the straits between the islands of Ösel and Dagö and from there continue in their normal direction.

The radar films give indirect evidence in favour of the interpretation that migration over Estonia, from the Bay of Riga towards the NE, takes place even in daylight when visibility, according to the reports of the meteorological stations, is low. Such an altitude of flight that the flocks are clearly seen on the radar screen when flying over the southern parts of the Gulf of Finland, indicates according to the experience gained from SE Finland that the birds have for a considerable length of time flown continuously over land. The absence of greater lakes in the inner parts of Estonia excludes the possibility of birds resting there, consequently these birds must fly straight from the Bay of Riga to the Gulf of Finland. The direction of flight of the flocks that can be demonstrated under these conditions flying over the southern parts of the Gulf of Finland, shows that they cannot possibly have passed west of the islands of Ösel and Dagö or through the straits between these islands and the Estonian mainland. These flocks arrive at the Gulf of Finland so early in the evening that it is necessary to assume that they have crossed the coast at the Bay of Riga in full daylight. In the night the flocks apparently pass over land from the Bay of Riga as regularly as they do so at the southern coast of Finland, but these flocks reach the southern parts of the Gulf of Finland 1—2 hours later than those that have started in daylight.

On the other hand, when visibility is good over the whole area, and in nights with additional moonlight, a large part of the population of Common Scoters and Long-tailed Ducks will be led, due to their tendency to avoid crossing the coast, along the western coast of Estonia and into the Gulf of Finland where they follow the Finnish coast eastwards.

An additional factor is the drift caused by wind, which can be considerable. The combination of western or northwestern winds and low visibility at the western coast of Estonia, although rarely occurring, will especially promote

the number of flocks crossing the Estonian mainland, while winds between E and S and good visibility mainly constitute conditions that make the birds follow the coast round Estonia and partly also round the islands Ösel and Dagö. During this latter condition it may be assumed that the migration along the western coast of Finland is more intense than usually. Thus Mr. GÖRAN NORDSTRÖM, M.A. (pers. comm., and 1951) reports that about 25 000 Long-tailed Ducks have been observed in Kristinestad on a single evening. As a rule much smaller numbers of migrants are observed there. The map published by GRENQUIST (1954) also confirms that the Long-tailed Duck may be fairly numerous in the southern parts of the Gulf of Bothnia. Our observations from the Gulf of Finland suggest that the majority of the Long-tailed Ducks following the eastern coast of the Gulf of Bothnia should as a rule cross the coast and turn towards the NE already before Kvarken (the narrow middle part of the Gulf). Further north the very light nights in May, as well as the nearly NE direction of the coast, may be assumed to create a situation where the migrants almost exclusively cross the coast in the northernmost parts of the Gulf.

The intensity of migration over the mainland in southern Finland is naturally in turn influenced by the extent to which the birds cross the coast. A persistent wind from the NW will cause the flocks to drift further out from the coast, or at least prevents a pronounced accumulation of them. The result is that the birds cross the coast in the easternmost parts of the Gulf of Finland. During such conditions the number of flocks crossing the coast at Viborg or even at the Isthmus of Karelia may be assumed to be considerable, whereas with predominating southern and eastern winds and low visibility this number is reduced. The weak migration that even with W and N winds is observed in the inner parts of southern Finland is, as far as can be judged from the radar films, constituted by flocks that have crossed the coast between Hangö and Åbo, as well as by flocks that have been resting on some of the numerous lakes. The effect of the wind on the geographical distribution of the migration is stressed by KUMARI (1963) for the bird species studied here, but only radar observations can give a full view of the considerable importance of this effect and of how it is combined with effects of light or darkness, and visibility, as well as with the changes in direction caused by the landscape.

The radar films show that the stream of migrating flocks, passing the straits between the coast of Estonia and Dagö (where counts have been made at Puhtu, JÖGI 1958, 1961, VEROMAN & JÖGI 1961, KUMARI 1963), in fairly calm weather and with good visibility reach the southern coast of Finland within the area in which the present radar observations have been carried out. This migration constitutes a fairly even stream of flocks, which joins the stream of migrants that under the same conditions are observed moving along the Finnish coast in the approximate direction ENE. The point where these streams join depends

on the strength and direction of the wind. At Porkala peninsula for instance, the intensity of migration in the afternoon and evening is approximately 4 times stronger than at Hangö, due to the fact that the greater part of the flocks coming from Estonia have already joined the migration passing parallel to the coast. This happens slightly west of or just at the Porkala peninsula. A further addition to the migration along the coast is obtained more eastwards by flocks that have crossed the Estonian mainland.

Such flocks which arrive at the northern coastal waters of Estonia later than about 01.00 generally interrupt their migration for resting. This is evident from the daily rhythm of the migration at sea seen from the radar films. When these birds continue their migration, islands and capes of the Estonian coast in daylight give rise to narrow SW-NE zones with a higher intensity of migration than in the surrounding area. Especially marked is this effect at the island of Nargö. In calm weather it has been observed numerous times that from this island in daytime a stream of flocks with a high density moves towards the Finnish coast and joins the migrants flying along the coast in the region around Söderskär lighthouse. These flocks, having flown on a nearly straight-line course from the northern cape of Nargö, have obviously been deflected to the north and flown along the western coast of Nargö until they have reached the northern end of it and have then gradually turned into their normal direction of migration. It has been seen that the flocks at the northern point of Nargö are dispersed in a zone about 1 km wide and since the distance from Nargö to Söderskär is about 80 km, the fact that this zone is about 4 km wide at Söderskär gives some information about the accuracy of orientation in reaction to identical environmental clues. The widening of the zone from 1 to about 4 km in 80 km corresponds to an angle of about 3° . As a rule the flocks fly at distances from each other that do not allow optical or acoustical contact between the flocks; these data demonstrate that the accuracy of the mechanism of orientation is $\pm 1.5^\circ$. This figure is in good agreement with the results obtained in connection with the analysis of the direction of flight (p. 24).

In the inner parts of SW Finland migration is relatively sparse, which can be explained by the fact that the flocks in this region must have crossed the coast somewhere to the west and north of Hangö, where relatively few flocks appear to pass inland, although they are seen to do so regularly, especially the Common Scoters.

The radar observations from the St. Michel area show that the migration over land more frequently than over the sea, is directly continued in the morning without rest. A part of the flocks, reaching the inner parts of SE Finland at midnight, must have performed an uninterrupted flight from the western parts of Estonia in the course of a single evening and night. In the autumn there

are a series of radar observations for the days 2–5.XI.1961 from SE Finland and the Helsingfors region (the radar installation at the airport) which show that an intense migration of anatids (swans, geese, numerous Common Scoters) that reached the eastern border of Finland at about 10–12.00 arrived at the southern coast of Finland at 15–17.00 from the northeast. Everything points to the fact that a great many of these flocks every autumn fly the whole distance between the White Sea and the Gulf of Finland without resting. It is therefore likely that in the spring similar direct flights in the opposite direction frequently occur.

During the observations in Esbo BERGMAN (1941) found that the evening migration with a short interruption of about an hour, continued as intense night migration. The radar observations, however, show that any such »Einschlafpause» does not exist. The very clearly observed break in the migration is only a local effect. Flight in over land west of the Porkkala peninsula in the twilight of the late evening absorbs the greatest part of the birds flying at high altitude visible from the archipelago. These flocks would in full daylight still avoid the coast between Porkkala and Helsingfors. Before the migration after 22.45 reaches its full intensity, the intensity observed over the Esbo archipelago is at a minimum for some time, the flocks flying at low altitude still being too far out to be heard and the flocks at high altitude having already passed the coast.

Finally it should be stressed that the autumn migration of the Long-tailed Duck appears to be governed by the same principles that operate in the spring in daylight. The only difference is that the southwestern direction of flight in the autumn causes a concentration of the migrants at the northern coast of Estonia and not at the southern coast of Finland. This fact is illustrated by field observations in Estonia (see KUMARI 1963) and by some occasional radar observations in the course of the present work. Winds between S and E, however, increase the number of flocks of Long-tailed Ducks along the Finnish coast in the autumn too, a fact well-known from the autumn shooting of these birds in the archipelago. The Long-tailed Ducks seen in the spring and autumn are presumably of the same population, and there is no reason to believe that in recent years the route of migration has changed as stated by KUMARI (1963).

Summary

1. The concentrated spring migration of the Common Scoter, *Melanitta nigra* (L.), and the Long-tailed Duck, *Clangula hyemalis* (L.), occurring during the period May 10th–28th approximately, has been studied in southern Finland and over the Gulf of Finland with the aid of radar.

2. During the period mentioned the vast majority of NE migrants belong

to these two species. This is a great advantage when working with radar where species identification is often difficult or impossible.

3. This migration has been followed during three consecutive years (1960—62) by recording the PPI display of the radar equipment on 16 mm film with the exposure of one frame on the film for a full revolution of the radar antenna.

4. The speed of flight (air speed) is 84 km/hr for the Common Scoter and 74 km/hr for the Long-tailed Duck at low flight-altitudes (200—300 m), which occur during migration over the sea. Over land the birds fly at altitudes between 500 and 2 000 m (average 1 050 m). In that case the speed of flight is about 10 % higher. This is probably due to the reduced density of the air. (Figs. 2—4.)

5. Analysis of the direction of flight shows that the birds do not compensate for drift caused by the wind, the actual heading of the birds after correction for drift being on an average the same irrespective of the direction of the wind. (Figs. 7, 8.)

6. The birds, which migrate in large flocks with on an average 150 birds, show an accuracy of orientation during identical external conditions of $\pm 3^\circ$, perhaps even $\pm 1-2^\circ$. The accuracy is slightly greater than would be expected from what is known about the accuracy of the internal clock of birds. It is suggested that migration in flocks may improve the accuracy of orientation, because the direction of the flock will be an average of the headings of the individual members of the flock.

7. Directions of migration between 30° and 50° (wind-corrected values) are found in all the areas studied, suggesting a common orientation principle, whereas locally along the southern coast of Finland, directions of flight between 50° and 70° also frequently occur. If at the southern coast the cloud-cover exceeds 60—70 % directions between 30° and 50° are excluded. This direction component is then based on celestial orientation. On the other hand, directions of flight between 50° and 70° are observed along the coast even with a full overcast, which together with the fact that they occur only locally, suggests that they are determined by the topographical orientation of the birds. (Figs. 10—13.)

8. Day (evening) migration has the average direction 43.8° and night migration 46.1° (Fig. 12, p. 31). These directions do not differ in a statistically significant way. The standard deviation for the material referring to night migration is, however, 16.1° as compared to 8.8° for daylight migration. The implications of this as to what kind of celestial orientation mechanism is used (sun and star orientation or only sun orientation) are discussed.

9. The yearly averages for those directions of flight that can be considered as due to celestial orientation are: 1960, 39.4° 1961, 41.5° and 1962, 42.7° . These differences are, however, not statistically significant.

10. The material suggests the presence of a slight change in the heading of the birds when they move eastward, predictable on the argument that the displacement results in a change in local time not compensated for by a similar phase shift in the internal clock of the birds.

11. The influence of topographical factors is described. It is found that the birds in daylight by changing their direction avoid flying over land, which leads to especially high densities of migrating flocks along the southern coast of Finland. In the night and with low visibility the birds readily cross the coastline and continue their migration in their original direction. (Figs. 14—19.)

12. The intensity of migration is correlated with the direction and strength of the wind. Generally, headwinds (NE) tend to reduce or abolish migration. The highest intensities of migration have been recorded with fairly light (3—5 m/sec) tailwinds. A statistically significant correlation has been obtained between the intensity of migration and the speed increase or decrease produced by the prevailing wind. On an average it can be said that 80 % of the flocks migrate in tailwinds or in more or less calm weather or with winds giving no increase or decrease of the speed of flight. This is true although there are about the same number of observations from days with tailwinds as with headwinds. (Figs. 20, 21.)

13. As long as the degree of overcast is below 60—70 % there appears to be no effect of clouds on the intensity of migration. With a full overcast practically no migration can be observed. (Fig. 22.)

14. Changes in horizontal visibility appear to affect the intensity of migration very little or not at all. (Fig. 23.)

15. The actual routes taken by the migrating flocks as well as the geographical distribution of the migrants are strongly affected by local topographical conditions and by the prevailing weather (wind, cloudiness, visibility). Different combinations of these factors give rise to various specific routes of migration. Further, night migration differs from day migration so that in the night the reaction to coastlines is absent or less marked.

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