# VISIBLE MIGRATION WITHIN FENNO-SCANDIA *.

By GUNNAR SVÄRDSON.
(*Bromma, Sweden.*)

## INTRODUCTION.

The flight of diurnal migrants may be directly studied in the field but the nocturnal travellers, except in some special cases, must be studied when they rest during the day.

In the average landscape even the movements of the diurnal travellers proceed rather unnoticed. The bird flocks are scattered in distance and time. They tend to fly over familiar habitat as long as possible and they are mainly concentrated at extreme transitions of habitat. The birds of the wood concentrate where the tree-covered ground narrows to points near meadows or plains, land-birds crowd at large points protruding into the sea and the shore birds preferably move along their year-round habitat. It follows that the number of flying birds is disproportionately great along the shores of big lakes and at the coasts.

The concentration to flyways along the coasts was pointed out by Palmén (1874), who gathered information about the occurrence of some arctic species which have attracted the attention of ornithologists. Later, the famous field ornithologist Kolthoff (1897) studied the concentration of arctic waders at the south point of Öland in the southern Baltic, which is passed by one of Palmén's " ways ". In modern times, regular field observations on migration have been made at the south coast of Finland (Helsinki), on the westernmost islet of the Åland archipelago (Signilskär), on the opposite side of the Åland Sea at the coast of Uppland (Rönnskärs udde), at the southern point of Öland (Ottenby), at the southwestern point of Skåne (Falsterbo), on the west coast of Norway near Stavanger (Reftangen) and finally on the small isolated island, Utsira, west of Haugesund. But a great quantity of information has also been obtained in many other localities, both at the coasts and inland, where more short-term observations on arrival and departure dates, heavy passages and the occurrence of irruption birds have been made for a long time by local ornithologists. As migration phenomena are so numerous within Fenno-Scandia, people interested in birds are always interested in migration as well and the literature is extensive. The great general interest in the subject is illustrated by the fact that the first act of the Swedish Ornithological Society, on its foundation in 1945, was to build Ottenby Bird Station at the south point of Öland. The station is devoted solely to the study of bird migration (Edelstam 1951).

* Serves as Ottenby Bird Station Report No. 14.

## MIGRATION AS AN ADAPTATION TO VARIABLE FOOD SUPPLY.

Field observations may shed some light on the different " causes " of migration. It is here looked upon as an adaptation, by means of natural selection, to a food supply which does not vary in accordance with the varying demands of the birds. The total population of Fenno-Scandian birds has a peak in June–July when most young birds are fledged. After this peak there is a gradual decrease, if the emigration is not considered for a moment, to the population minimum in April. The amount of food, available with identical effort for the individual bird, could be constant only if the total food supply had a corresponding curve. Deviations from this " ideal " food-abundance curve are suggested as the ultimate factor responsible for the migration patterns of all birds breeding within the region.

The climate of Fenno-Scandia is severe and almost all insect-feeding birds must leave the region in winter, when snow covers the ground and the insect-fauna is greatly reduced. In the northern mountains and woods the winter lasts 6–7 months and the snow-depth is most often one metre or more. The lakes have an ice covering equally thick. Furthermore, the days are only 3–4 hours long and during the nights the temperature may drop to −40° C. Birds sedentary in such habitats must have special adaptations to meet the adverse conditions (Snow 1952). In southwestern Sweden and Norway, on the other hand, snow covers the ground only for a few weeks and in some winters there is none. The sea is free from ice, the days are not so extremely short as in the north and the temperature is much higher. In fact, Falsterbo has an average temperature above 0° C. in all months.

The 101 breeding passerine species of Sweden may be divided into 58 migrants, 26 partial migrants, 6 irregular migrants (migration only in some years) and 11 sedentary species. No sharp limits exist, however, and if the term " sedentary " is taken to mean that no migratory activity whatsoever has been observed within the region, only *Galerida cristata* falls into this category. The whole passerine fauna could be said to be potentially more or less migratory. In other bird groups conditions are the same. It is significant that in the last decade a number of species have been found to be more migratory than was formerly thought.

In the partially migrant species the proportion of migrating individuals rises from probably zero in Skåne to 100 per cent in the far north, *e.g.* Crow *Corvus c. cornix*. As far as present knowledge goes, all partial migrants have corresponding clines in northerly or northeasterly directions. A gradual change is obtained to those species which breed in the far north and regularly winter in the southern parts of the region, *e.g.* Great Grey Shrike *Lanius excubitor* and Dipper *Cinclus cinclus*.

For some species the southwestern parts of Fenno-Scandia and its surrounding waters are the main wintering area for populations breeding far outside the region, notably to the east. Swans are regularly found on lakes, streams and on the coasts of western Sweden in winter and their spring movements and local concentrations are traditional, as proved by ancient names of villages and lakes. On 25 March 1951 a total of 9400 Swans were counted in western Sweden, the great majority of which were Whooper Swans *Cygnus cygnus* (Linnman 1952). This figure very much exceeds the known or estimated breeding population in northern Fenno-Scandia. The wintering population of Long-tailed Ducks *Clangula hyemalis* in the Southern Baltic is of Russian origin, as proved by ringed birds, and their eastward spring migration along the south coast of Finland was studied by Bergman (1941).

The Fenno-Scandian climate has changed in the last few decades, being now on the whole milder. Severe winters have become rarer and the spring and autumn have become warmer as well. The food situation in winter has improved for a number of species. Most partial migrants have reacted and the number of wintering Crows, Jackdaws, Greenfinches, Blackbirds, ducks, gulls, Moorhens and Coots has greatly increased. In the southernmost parts of the region Song-thrushes and Wood-pigeons can now be found in winter fairly regularly. Formerly this was not the case. Furthermore, the arrival in spring has been affected (Kalela 1952).

On the whole, therefore, it can be said that the Fenno-Scandian migration-patterns are perfectly adapted to local conditions and are capable of rapid changes, should the environmental conditions be altered, regionally or in time.

A number of species, e.g. *Carduelis carduelis*, *C. spinus*, *C. flammea*, *Pyrrhula pyrrhula*, *Parus major*, *P. caeruleus*, *Bombycilla garrulus* and *Buteo lagopus*, are on the move every year, though in some years the emigration is much more intense. The autumn emigration of Great and Blue Tits was quite remarkable in 1949 both in Sweden and Norway (Svärdson 1950, Haftorn 1950, and unpublished Swedish data). Population fluctuations or failure of food items is believed to be the fundamental factor. There is a gradual overlap to the phenomenon of " irruption birds " which are on the move only in some years. Lack (1951) summarized some of the evidence suggesting a correlation between irruption sand food shortage. Individuals showing this specialized form of migration also tend to " home " less in the following spring. *Loxia leucoptera* has repeatedly bred in Sweden after irruptions from the east. *Tetrao urogallus karelicus* arrived from the north-east in northern Sweden in the winter of 1943–44 and the northern breeding population of Capercaillie increased in the next spring. *Turdus pilaris* and *Fringilla montifringilla* both invaded southern Sweden in January 1951 and the arrival from east was evident from the gradual spread westwards as well as from direct field-observations at Ottenby (Edelstam, pers. comm.). In May 1951 an increase of breeding Fieldfares was reported and some evidence was obtained that Bramblings bred south of their normal range. This trend of irruptions may be looked upon as a further adaptation to a food supply which is normally not good in two consecutive years. The evolutionary significance of irruptions was discussed by Kalela (1949).

There are several other cases of specialized migrations, where food abundance as the ultimate factor is suggested. Young Starlings *Sturnus vulgaris* move when just fledged. The emigration from Fenno-Scandia culminates in late June. This ***Zwischenzug*** goes to the Danish Islands where they stay for months until the movement continues to the British Isles in September. The Fenno-Scandian cherries are not ripe when the young Starlings leave, but the Danish are. A retarded movement thus occurs when the birds meet with a good food-supply.

The arctic waders leave their breeding territories very early, in June or July, the young being left by themselves to move roughly a month later. In several species the female, which takes the lesser part in brooding and rearing young, starts before the male (Kolthoff 1897). This hurried departure suggests an adaptation to secure maximum availability of food for the young when the swamps are partly dried out in late summer. Moreover, field observations and ringing data tend to show that the rapid flight of the adult birds is retarded when they meet with the tidal zone of the North Sea, e.g. *Calidris alpina* (Svärdson 1950).

The Arctic Tern *Sterna paradisea* moves along shores where its food is most abundant and its arrival as well as departure periods seem to coincide with changes in food abundance (Kullenberg 1946). This tern has the farthest migration known for any bird.

Moult migration within the Baltic area is performed by *Tadorna tadorna*, *Somateria mollissima* and, most extensively, by *Melanitta nigra*. *M. fusca* and the *Anas*-species perform movements in summer, which probably also must be classed as moult-migration. The adult Sheld-ducks move in June–July, followed by the young birds in August–September. In July–August the proportion of young birds within the flocks steadily increases, as is easily seen at Ottenby. The Eider males start in early June (Svärdson 1943) and are followed by probably immature birds in July–August. The " ordinary " migration of females and young of the year takes place along the same route in October. The male Common Scoters pass middle Finland in the beginning of July (Pynnönen 1941), having been observed at the southwestern Finnish coast (Bergman 1952) and at the Uppland coast (personal observations), and are regularly in passage in July–August at Ottenby. They probably moult off the west coast of Jylland, where they are extremely numerous in late summer (Ferdinand, pers. comm.). Autumn migration of females and young takes place in October. The separation of sexes and age groups in moult-migration secures the best available food-supply for all categories of birds.

The manifold patterns of migration, outlined in this section and based on field observations, strongly suggest the importance of food abundance. More knowledge, however, about the abundance of the different kinds of food in different seasons is urgently needed. The young Golden Eagles *Aquila chrysaëtos*, from the mountain and forest region in the far north, crowd in winter to the plains of southern Sweden, where hares are abundant. The difficulties they have in finding food are illustrated by the finds, each year, of starved Eagles in the region through which they pass. As regards flycatchers and warblers, however, nothing is known about the availability of their food in July and August, when they leave. It is often stated, but prematurely, that they anticipate the shortage later on in the autumn.

### TEMPERATURE AS A PROXIMATE FACTOR IN AUTUMN.

The fact that some migrants start when food is becoming short or stop the journey when it is abundant does not prove that food scarcity is the proximate factor releasing migratory flight. But it suggests that *Zugdisposition* is of metabolic origin. The same is true regarding the most important proximate factor, the temperature, which could be recognized by the bird by changes in heat-losses and food-intake, and thus add to the more general change, brought about by innate rhythm or by food abundance.

Temperature has been known for a long time to be a proximate factor for the late migrants, but it is often thought to be insignificant for the early ones. The purpose of this section is to demonstrate, from material gathered at Ottenby, the importance of a drop in temperature for all sorts of emigration. Owing to lack of space only some selected typical bird-avalanches will be dealt with here. (Avalanche of birds is a term, used at Ottenby, for a rush of birds, since their passage most often is not so regular as a " wave " but displays " lag " some days after a sudden peak.) The data are included in Tables 1–4 (at end).

*October*: (Table 1, at end). The avalanche began on 25 October but did not culminate until the 27th and then it gradually decreased during the next three days. All the species that normally migrate at this season were involved but the majority were geese and ducks. They arrived one day later than most passerines, suggesting a longer distance travelled. The partial migrants of invasion character, Redpolls, Fieldfares and Crossbillls may be especially mentioned. A most intense reaction was recorded in the Eider, the number of passing birds on 27 October being 70 per cent of the season's total (June–October).

On the 25th, in the morning, a depression covered northern Finland. Next morning the centre had moved east of the White Sea and on the 27th it had moved further east into Russia. From behind the depression polar air swept down from northwest, the cold air successively moving further east and southeast during the three days. The cold air had built an anti-cyclone, with its centre over Estonia, on the morning of the 27th. Northern Fenno-Scandia experienced a cold spell and the morning temperatures at Helsinki were $+9°$, $-5°$ and $-9°$ C. on the three days.

The visibility was rather bad, owing to the contrast between the cold air and the warm lakes and sea. Fog was found in many places in the early morning. The avalanche was also observed at Stockholm on the morning of the 27th, where, in spite of hazy air, several hundreds of Hooded Crows and some large flocks of Mallards flew southwest.

*September* : (Table 2). The peak day was the 17th and then the avalanche died down during the next three or four days. A number of passerine birds were affected and the reaction of Tree-pipits and Sand-martins is of special interest. Both are typical " instinct migrants " as opposed to the " weather migrants " of the October avalanche but, nevertheless, their reaction was intense, for again roughly 70 per cent of the season's total passed in one single day (*cf.* Svärdson 1951 a, for the season's passage). It is also significant that on the avalanche day some species had their first, others their last individuals for the season. The Goldfinches, Yellow Buntings and Blue Tits were in this case the first of their species, the Oystercatchers and Swifts (except one in October) the last. The Wigeon were four days late, a phenomenon which will be discussed below.

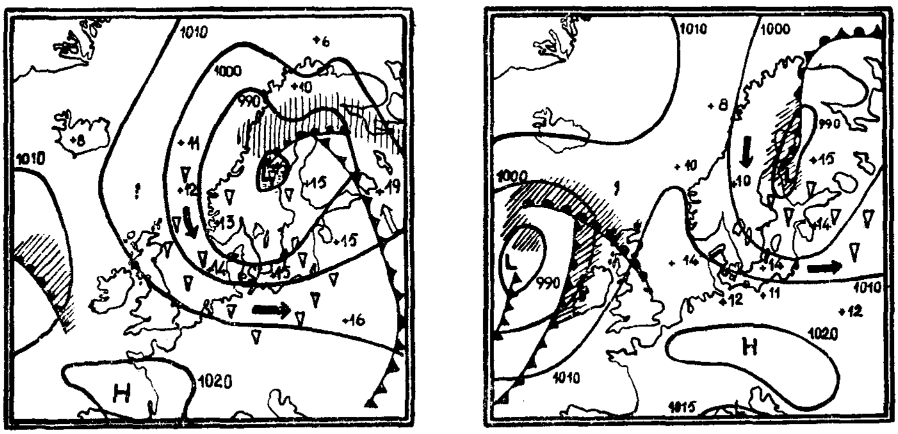
The weather maps show a depression over middle Sweden on the morning of 16th. Next morning its centre was over northern Finland and its cold sector, coming from the west, prevailed over the Baltic region. The temperature drop was 2–3° C. in southern Finland and middle Sweden, on an average 3–5° C. in southern Sweden. The westerly winds were light, because a new depression, causing southern winds over Germany and the southern Baltic, already had its centre over Scotland. At Ottenby the weather was fine, but on the mainland morning fogs were frequent.

*August* : (Table 3). This time the bulk of birds were waders and terns and the avalanche occurred when their passage is normally at its height. Though " instinct migrants ", the birds reacted just as intensely as in the avalanches mentioned above. Roughly half the season's Dunlins passed on the first day and a number of species had high relative figures for this single day (*cf.* Svärdson 1950 for the detailed figures). Some species, such as Starlings and Black-headed Gulls, were participants in the previous heavy passages as well and all species on the move in this season were in fact involved, *e.g.* Eiders and Scoters on moult-migration, which were late.

Fig. 1 summarizes the weather situation. A depression, officially stated to be exceptionally strong for the season, again passed over Fenno-Scandia. The first cold front swept over the area on the 4th but the temperature dropped still more the next day. According to the depth of the depression a westerly gale hampered the bird movements on the 4th and next morning, on the day of the avalanche, the wind was still 15–16 metres per second (about 30 m.p.h.), though it decreased during the day. Several short showers of rain occurred at Ottenby on the 5th, as is typical in cold-front weather. Visibility, however, was extremely good, except during rain.

*July*: (Table 4). The avalanche, selected as typical for the month, occurred on the 5th, was foreshadowed the day before and lasted some days. In spite of the differences suggested by the terms "*Zwischenzug*" applicable to the Starlings, "*Frühwegzug*" to the Lapwings, "ordinary migration" to most of the waders, "moult-migration" to the Sheld-ducks and Eiders and "dispersal" by the Black-headed Gulls, all in fact moved

FIGURE 1. Weather maps for 4 and 5 August (right) 1949, at 7 a.m.




at exactly the same time, no doubt as a response to the stimulus of the common proximate factor.

The weather maps (fig. 2) show that the situation was very much the same as before. A depression over central Finland on the 4th moved to northern Finland the next morning. Polar air swept down behind it, causing the usual drop in temperature. Winds were moderate at Ottenby and visibility was good.

*June*: No avalanche has so far been recorded for mid-June, except for Swifts and Starlings. The relatively high figures for 1 July in Table 4, however, are due to the lagging of an avalanche on 29–30 June. The extreme mobility of Swifts, recorded in the table, was released by this earlier avalanche when the weather again was the same.

The observations at Ottenby were started on 1 June the first years, but some ringing operations have been performed in spring in 1950–52.

However, the avalanche-phenomenon, which at Ottenby always refers to departure, as other movements are not concentrated there, continues to occur in the spring months too, but now as *Rückzug* or reversed migration.

*May*: On 29 May 1950 the ringers observed a heavy southwest flight of 3329 Swifts, 1922 House-martins, 640 Swallows and 46 Sand-martins.

FIGURE 2. Weather maps for 4 and 5 July (right) 1951, at 7 a.m.

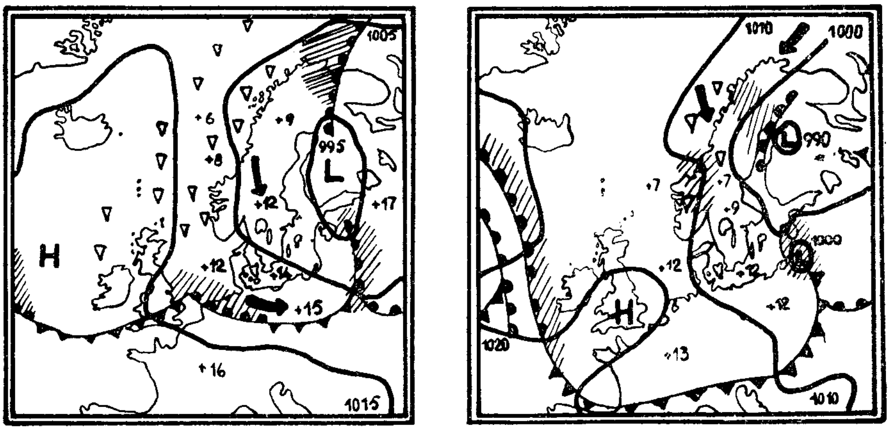
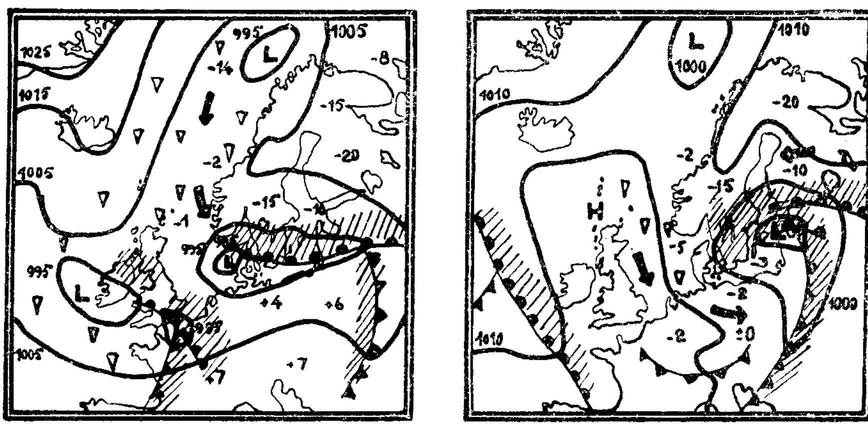



FIGURE 3. Weather maps for 19 and 20 March (right) 1951, at 7 a.m.




The figures might have been higher had the observations been continued the whole day. In the same period of observation, 8 Starlings, 2 Lapwings and 14 Oystercatchers were observed flying southwest, the first seen for the season taking that course. This proves that *Rückzug* and *Frühwegzug* were caused by the same weather situation.

On 28 May a depression moved over Scandinavia. On the morning of the 29th its centre was over northern Finland and cold air, coming from the west, prevailed over Sweden. The recorded drop in temperature was very slight, 1–2° C. on an average, though the night temperature had a greater change owing to loss of heat during the clear night.

*April* : As no excessive reversed migration phenomena have been observed so far at Ottenby in this month, some other cases may be cited from Swanberg (1948 a) and Bergman (1949). The latter author, moreover, has summarized 7 cases of returning Chaffinches, 5 of which have been previously discussed and analysed in the Finnish literature. Both authors find that the reversed flight was released by snowfalls (the route being later modified by the coast in the Finnish cases) and they think that the temperature was not involved. The local temperature, however, does not prove anything when it is not known from where the birds have started their flight. Snowfalls tend to indicate air-masses of different temperatures and the presumed pyschological effect of the snow is not supported by the fact that the Chaffinch normally returns to northern Fenno-Scandia when the winter's snow-layer is still more or less unbroken, sometimes thick.

*March* : A striking case of reversed migration occurred at Ottenby on 19–20 March 1951 (Edberg, pers. comm.). About 10,000 Skylarks had crowded on the meadows (within an area $3 \times 0{\cdot}4$ kilometres), indicating a blocked migration. On the 19th some Snow-buntings, Mistle-thrushes, Curlews and Common Gulls were seen departing southwest, but more birds took the opposite route, arriving at Öland from southwest or south. Small numbers of Crows, Starlings, Sky-larks, Blackbirds, Ringed Plovers, Golden Plovers, Oystercatchers, Stock-doves and Herring Gulls were actually seen arriving. Light rain was falling in the morning, some light snowfalls later in the day. Wind light, northeast.

On 20 March, however, things were different. All larks were gone in the morning and a stream of large flocks of Lapwings flew southwest, amounting to at least a thousand individuals, which is an exceptional figure at Ottenby. They were accompanied by Crows, Rooks, Chaffinches, Snow-buntings, Wood-larks, Fieldfares, Mistle-thrushes, Song-thrushes, Dunlins, Ringed Plovers, Oystercatchers, Stock-doves and various gulls in considerable numbers. All flew eagerly southwest and there was no hesitation like the day before and no birds were coming in. The weather was overcast, no snowfalls and a strong northwest wind.

Fig. 3 gives the general weather situation. On 19 March cold and warm air met at a front just south of Öland. The differences in temperature were marked and as the depression moved eastwards next day, the cold air from northwest swept down causing a significant drop in temperature.

Dahl (1938) reported a similar occurrence on the Swedish west coast on 25–28 March 1937. The participating species were partly the same, but Brambling, Redwing, Peregrine Falcon, Mute Swan, Bean Goose, Sheld-duck, Mallard, Wood-pigeon and Whimbrel may be added to the list of reversed migrants. The weather was very similar; the cold front, however, came from north and it was outflown by some birds, which were seen flying southwest before the front arrived at the observer.

*Winter* : Crows and Mallards flying southwest are known from all winter months and birds moving north or northeast may occur in February. The movements of wintering birds are not so striking in Fenno-Scandia as further south, where Drost (1929) and Vleugel (1948) found movements according to the temperatures of different air-masses during the winter. The recorded " weather-movements " of waders from the British Isles ('Handbook of British Birds') and France suggest a protracted *Zugdisposition* in winter in birds which do not take up winter territories. It has a parallel in the movements of non-breeding birds in summer, *e.g.* in Swifts (Svärdson 1951 b), which probably are not so exceptional as thought only some years ago.

Siivonen and Palmgren (1936) demonstrated in experiments that cold spells released *Zugunruhe* in a caged Song-thrush. Based on field observations, Hennings (1937), Haartman and Bergman (1943) and Bergman (1951 b) found a drop in temperature released flight in a number of late-moving migrants. Schenk (1923) analysed three avalanches of Woodcocks on Heligoland and found that all had occurred when a deep depression was covering northern Scandinavia. Clarke (1912) found that nocturnal migrants arrived in the British Isles when anticyclonic weather prevailed in Scandinavia ; and Rudebeck (1950) found the diurnal migrants, especially birds of prey, passed Falsterbo in fine weather when the air pressure was high. Clarke thought temperature was important but Rudebeck found it probably played a minor role. Both deal with late migrants. For early migrants, *e.g.* waders, experience at Ottenby shows anticyclonic weather to be the worst " bird weather " when the number of passing and resting birds is at its minimum. Later in the season anticyclonic weather more often gives numerous birds.

These seemingly contradictory experiences in the field can, however, be made to form one single picture, covering all the known facts. First, it must be stressed that anticyclonic weather in summer is warm, due to long insolation by day, while the same weather in autumn tends to give cold nights, due to long periods of loss of heat. Moreover, depressions are deeper in autumn, cause stronger winds and very often cold air-masses sweep down behind them. These are heavy and build up anticyclones if there is no other depression coming along in the next few days.

Secondly, the distances travelled by the birds, when they are observed, must be taken into account. In order to demonstrate this " distance factor " two species were selected from the Ottenby diaries. The Sheld-duck does not breed further northeast than Öland and Gotland (except the Estonian islands in the Baltic, which birds might not pass Ottenby), but the Bar-tailed Godwit is not known to breed nearer Ottenby than about 1300 kilometres (to the northeast). Every marked influx of cold air recorded in the weather maps during July in the five years 1947–1951 was noted separately for the southern Baltic and the region Ladoga-Kola. It is clear from Table 5 that the Sheld-duck reacts at once to every drop in temperature in the southern area, but the Godwits do not pass Ottenby until 2–4 days after a cold spell in the northern region, which very approximately may indicate their starting point. In some cases the Godwits, well on their way, may meet and react to situations in the southern area, but on the whole the different origin of the two species is evident from their passage figures. This explains the " lag " typical of avalanches at Ottenby, where the releasing weather situation is usually passing northeast, contrary to the birds. If the weather and the birds move in opposite directions, delay in the passage of some species must inevitably occur. The 3–4 days delay of Wigeons and moult-migrating Eiders and Scoters, reported in Tables 2 and 3, in fact agrees with their relatively early passage, according to season. Table 1 also suggests the delay of birds known to be of northeastern origin.

In Sweden the Stock-dove is a more southern bird than the Wood-pigeon. It follows that, on the average, the Stock-dove must reach Falsterbo earlier in an avalanche. This was also observed by Rudebeck (1950).

As was suggested by Tables 1–4, all sorts of birds seem to react to the proximate factor in the same way and Rudebeck found Crossbills and Nutcrackers, not to mention Magpies, on the wing on avalanche days. But the proximate factor may sometimes be associated with retarding weather elements, *i.e.* strong winds. In the August avalanche the lateness (one day) of Tree-pipits, Yellow Wagtails and Kestrels was more probably caused by the strong wind on the 5th than by a long distance flown. Birds of prey and other soaring birds, *e.g.* Cranes, also tend to be late. *Buteo buteo*, being more of a soaring bird than *Pernis apivorus*, tends to arrive later and more " sluggishly " at Falsterbo (Rudebeck 1950).

Rapid flyers or short-distance arrivers, therefore, tend to pass the observer when a depression dominates the weather situation, but slower travellers, or birds coming from distant areas, tend to pass later, when, especially in late autumn, anticyclonic and " fine " weather is predominant.

This complicated picture makes it difficult to find another meteorological element, associated with a drop in temperature, which could possibly be either a secondary or the real releasing factor. Falling temperature is normally followed by good visibility in summer but not so regularly in autumn, when the relatively warm waters tend to give rise to fog and haze. Bad visibility, like strong winds or heavy rain, retards the actual movement but it need not follow that the opposite extremes stimulate it.

A study of the co-variation between daily temperature fluctuations and the number of birds counted at a bird station would be most welcome. But the origin of the birds is never known except in general terms. Therefore, several meteorological stations must be selected, covering the most probable area of departure. The weather maps, though, will often show a cold front, situated between the selected stations, thus levelling the day's average to a less significant value. The recorded birds may start from the cold part of the area but the temperature drop is lessened when the larger area is averaged. Weather maps are better, though space-consuming.

### TEMPERATURE AS A PROXIMATE FACTOR IN SPRING.

The start of a spring flight is very seldom observed within Fenno-Scandia. The writer, in a few cases, saw Great Grey Shrike *Lanius excubitor*, Dipper *Cinclus cinclus* and Rough-legged Buzzard *Buteo lagopus* leave their winter territories during a warm spell.

No ornithologist could spend a spring in Fenno-Scandia without being struck by the close correlation between rising temperature and arrival of migrants. Diurnal as well as nocturnal, early as well as late migrants, all are affected. Bergman (1941) found resting Long-tailed Ducks and Common Scoters starting when the warm sector of a cyclone approached. Rudebeck and Svärdson (1946) found diurnal and nocturnal migrants arriving exceptionally early in 1944, regionally and in time coinciding with the warm sectors of two successive depressions. Svärdson (1947), collaborating with a hundred observers looking for exact arrival dates of Wood-warblers, found the birds arriving on warm nights. Bergman (1951 b) noted increase of migrants on the isle of Signilskär after warm nights. Ulfstrand (1952) found a close correlation between rising temperature and the arrival of several late migrants. Palmgren (1937) was able to verify the effect experimentally and a great many unpublished records are known to the writer. The reaction is nowadays regarded as fully proven and Svärdson and Durango (1951) stressed its importance for population fluctuations.

A cold spell in spring blocks further migration or releases a reversed one. The reversed migration of early migrants has been dealt with in another section. Most later ones, however, are nocturnal and their movements are difficult to interpret. A ringed Pied Flycatcher *Muscicapa hypoleuca* performed a reversed migration of at least 120 kilometres (Schüz 1935). In a cold spell in May 1952, all seven *Lanius collurio* in a well-studied area, two of which were colour-ringed in 1951, disappeared. After the spell, seven birds appeared again but in new territories, and none was ringed (Durango, pers. comm.). This phenomenon might well be much more common than hitherto recognized.

Temperature thus seems to have the power, not only of releasing migratory flight at the proper season, but also of directing the flight. In autumn, warm air is not known to give rise to northward flight, only to delay departure. This suggests an important difference between emigration movements and the true spring flight, the *Zugdisposition* of which is more restricted in time and may have another physiological origin. As the early-arriving birds must often switch over to emigration movements, any theory about orientation must take this ambivalence into account.

MIGRATION RHYTHMS.

A rise or drop in the temperature is so frequent an occurrence within the temperate region that variations in the year's migration cycle are small. The Bar-tailed Godwit had a peak 28–29 July in four out of five years (Table 5). In 1949, which was the abnormal year, the species did not have the season's peak until 14–15 August, though a smaller one was included in the avalanche of 5 August. In 1949 other northern or arctic waders were also late. Five adult Dunlins, marked on passage 1948, were again trapped in 1949. One bird was a day earlier, the other four 10–18 days late. As the huge majority of Dunlins rest for less than a day at Ottenby, these ringing data confirm the field observations. The summer of 1949 was cold and rainy in northernmost Fenno-Scandia and probably in northern Russia as well. The breeding very likely was late and may have been disturbed by frequent re-layings.

A closer knowledge of average migration is needed for the study of abnormal cases. Similarly, meteorological records are necessary for many years to obtain the averages, which are the basis for fruitful studies of daily or yearly variations. From the very start at Ottenby it was realized that the best method, however tiring and time-consuming it might be, was to count all passing birds during the whole day, defined as the time the sun was over the horizon. Rudebeck (1943) had already started much the same work at Falsterbo in 1942.

Preliminary migration diagrams can now be drawn up for all diurnal travellers at Ottenby. As the ringing is performed in the same way and within a very small area the numbers of ringed birds can be used to construct corresponding diagrams for the nocturnal migrants (Hylbom 1951) though there are additional sources of variation in this case (water-level fluctuations for the waders and haziness in the night for the passerine nocturnal travellers).

Figs. 4 and 5 illustrate the passage of Starlings and Cranes. The Starling is, however, known to move in November as well, after the close of the station, and its emigration period extending over roughly half the year is exceptional. The first peak consists of young birds (*Zwischenzug*) while the adults dominate the second one. The Cranes move in combined flocks of young and adult birds. Not noted in the diagram is the very small movement of Cranes in June–July, in which probably non-breeding birds, summer-visitors to Öland, take part. Passage curves for 14 wader species have been constructed (Svärdson 1952).

All departing birds at Ottenby are recorded the minute they fly out over the sea. The material, illustrating the diurnal rhythm, comprises nearly two million birds.

All writers, dealing with the diurnal rhythm of migrants, stress the marked flight in the morning hours. The stream of birds gradually diminishes later in the day, often before noon (Haartman and Bergman 1943, for literature, Rudebeck 1950). It is also known that exceptional passage may change the rhythm and Sick (1935) found nocturnal birds flying in the day. Specific differences in rhythms occur : birds of prey move in the late morning or at noon and the Yellow Bunting starts earlier in the morning than most other passerine diurnal migrants (Bergman 1951 a).

FIGURE 4. Migration of Starlings at Ottenby.

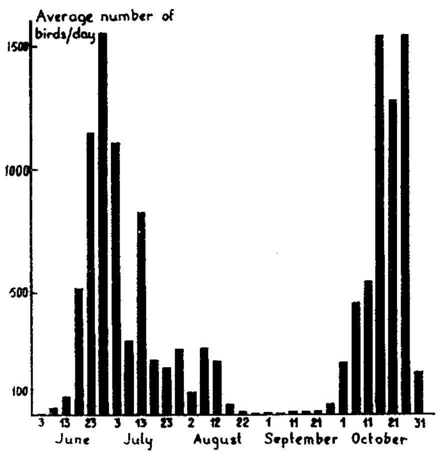
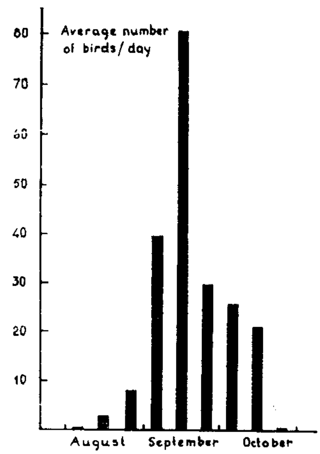



FIGURE 5. Migration of Cranes at Ottenby.



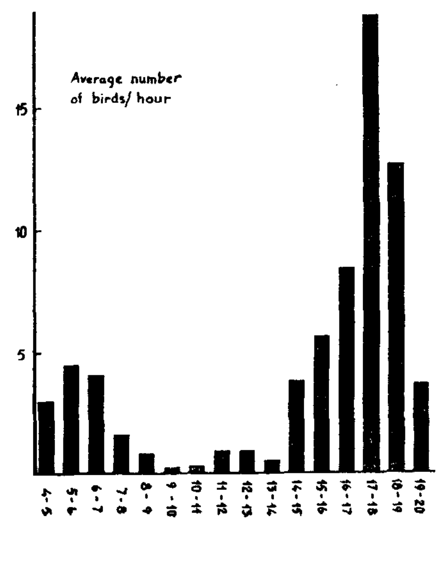

Palmgren (1944, 1949) found in caged birds two peaks of activity : one in the morning and another in the evening. The latter one, however, gradually decreased in a Robin as its migration period approached. Instead, a nocturnal activity arose. Bergman (1948 a) found White Wagtails with two peaks of flying at Ottenby in September, but stressed (1950) that the increased evening activity of caged birds most often may be due to unsuitable places for roosting.

When preliminary studies began at Ottenby (Bergström and Svärdson 1938, 1939) it was found that, apart from the morning activity, some species also were on the wing in the afternoon. When the work was carried on after the war, this two-peak migration of many species was confirmed. The trend Palmgren found in caged Robins in fact characterizes migration as a whole, *e.g.* a two-peak rhythm in summer changes to a single-peaked one in autumn. The morning peak is the dominating one in all visible

Starling migration, but in July and August it also has an afternoon maximum, which gradually declines with the advance of the season. In October it is indicated mainly by roaming about, when the birds seek a roost and occasionally some may move out over the sea. The White Wagtail has a marked evening peak in August, which gradually decreases during September. There is strong evidence that both species are exclusively diurnal migrants in the early parts of the emigration but partly nocturnal later on. The transformation of the second diurnal peak to a nocturnal one is suggested, just as Palmgren found in the Robin. At Ottenby adult Bar-tailed Godwits, Dunlins and Grey Plovers greatly outnumber the young birds, which move comparatively late, mostly in the first week of September (Svärdson 1952). This curious circumstance is stressed by the fact that in the early moving *Tringa*-species the young birds are most numerous, which seems more natural. Young Dunlins, etc., therefore, probably are more nocturnal, according to the season, and do not concentrate at Ottenby (see above).

As space is restricted and the autumn-rhythm best known, only the two-peak rhythm is dealt with here. A ten-day period (29 July–7 August) has been selected throughout the five years 1947–1951 and all birds passing per hour have been averaged for these 50 days of 16 hours' observation (Table 6). Average sunrise is 4 a.m. and sunset 8 p.m. Biased figures due to different observers probably do not occur and most of the birds have been recorded in the field by the writer. Fig. 6 illustrates the daily rhythm of the Redshank *Tringa totanus* at that time of the year.

FIGURE 6. Diurnal rhythm of Redshanks departing at Ottenby.



The most striking fact recorded in the table is the adherence to the two-peak rhythm by almost all species, whether dominantly diurnal or nocturnal travellers. *Capella gallinago*, *Calidris temminckii*, *Tringa hypoleucos*, *T. ochropus* and *T. erythropus* no doubt are nocturnal but nevertheless their tendency to the general rhythm is pronounced. The Stock-dove is known to be a morning flyer in late autumn, like the Starling. Ducks, terns and gulls also adhere to the general rhythm.

There are some exceptions however. The Kestrel has the rhythm known also late in the season for birds of prey. The maximum of Swift passage coincides with the period of strongest winds (which are probably the main cause) and the passage falls within the period of maximum activity outlined by Haartman (1949). House-martins breed in a large colony not far from Ottenby bird station and the figures are uncertain, as these birds tend to roam about a great deal by the shore. The midday peak, however, as well as the evening absence certainly are real. The last trend is contrary to that of the Sand-martin, which when observed at Ottenby is always on the move, since it does not breed anywhere near.

Though recording the flight in the field has not the pitfalls of the method used by Palmgren, where different kinds of activity could not be separated, the field method suffers from other pitfalls. As Öland is much broader north of Ottenby, a concentration of birds at the point occurs. If a number of birds all start at the same time, say sunrise, the stream at Ottenby will increase for the first hours after sunrise, the more the birds from the broader land-area to the north arrive at the point. The observed peak after sunrise therefore may give a fallacious idea of the genuine rhythm. Gotland provides another possibility for error. Many birds, notably waders, certainly pass over Gotland and rapid flyers could arrive at Ottenby in 3–6 hours, depending on where they started on Gotland. The apparent peak of Bar-tailed Godwits at 9–10 a.m. is probably such a false one. No statistical treatments have been applied so far to test the reality of the averaged rhythm of rapid flyers, such as Curlews and Godwits.

In the summer of 1952 the writer found that the two-peak rhythm of early migrants was also evident at Rönnskärs udde, on the Uppland coast. The same species were involved but their numbers were smaller and could not assist in the interpretation of the Ottenby data. The observations on passage migrants at Falsterbo have not yet been worked out but they will probably have some bearing on the problem of separating genuine from observed rhythms.

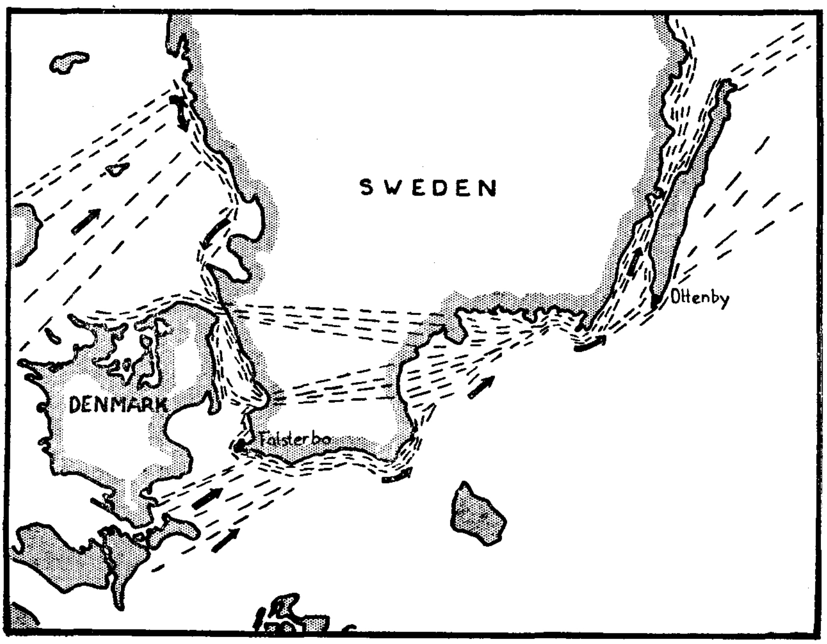
Some subjective impressions of nocturnal movements may be added. In summer most birds seem to move after sunset or before sunrise, but the passerine migrants are most frequently observed at the lighthouse before midnight, though variation is large.

Another subjective impression is that the diurnal rhythm is more pronounced on sunny days than when the sky is overcast. The material does not permit of tabulation on this point so far. The general trend of the rhythm and its gradual change with the advance of the season suggests dependence on the sun and, moreover, some physiological rhythm, which permits two peaks on long days, but later in the season only one diurnal and one nocturnal. As orientation is also sun-dependent (Kramer 1952 and references there) a connection may exist. It is very fortunate that Kramer has used the Starling, as the long emigration period of this bird and its gradual change of day-rhythm prove it to be important for future studies. Kramer found that the Starling has an " astronomical analyser ", allowing the bird to compensate for the movements of the sun. The two-peak rhythm, where 6 a.m. and 6 p.m. seem to be " important hours ", may be taken as suggesting a connection with the polarized belt of the sky, which has its maximum (north–south) at these hours. The reactions of Starlings to an artificial sun (Kramer, *op. cit.*) may have been a special case.

## INFLUENCE OF TOPOGRAPHY.

Diurnal migrants tend to modify their route according to the local topography. Chaffinches, Meadow-pipits and thrushes in northern Sweden are observed moving along the valleys of the large rivers. These valleys

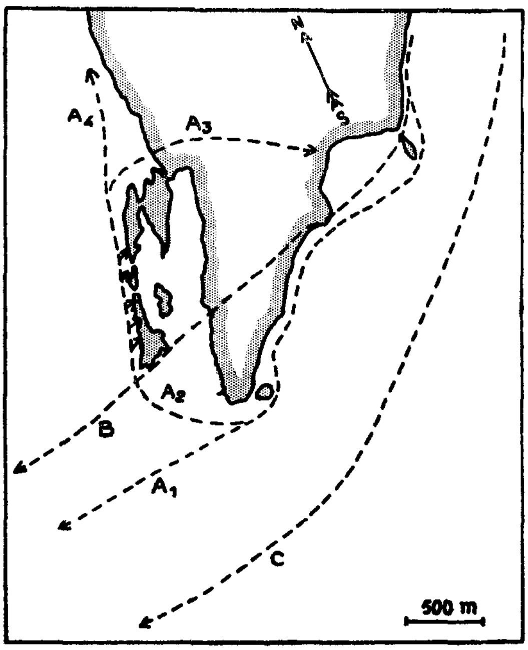
FIGURE 7. Spring migration route of the Eider entering the Baltic from the winter areas. The figure is based on published records by Rudebeck (1939, 1949) and Ulfstrand (1950), and unpublished observations by Rudebeck, Reuterwall, Ulfstrand, Ramberg and Svärdson, as well as ringing data.



run northwest–southeast and thus the birds deviate about 90° from their more general southwestern route (Fabricius and Svärdson, unpublished). Local small concentrations are often found at many places along lakes and rivers, valleys, edges of woods, etc., preferably if the lines run at not too marked an angle to the general southwest–northeast trend. As a striking case may serve the spring migration of the Eider (fig. 7), where the birds along some coasts take a direction almost opposite to their main one. The effect of the coast is very strong in both sea-birds and land-birds. The latter follow the coast, if possible, rather than fly out and cross the open sea. Even if the birds can see the other side and the distance is not very great (as at Falsterbo and Ottenby), their hesitation is often very marked. Land-birds generally move at a moderate height over land but rise over the sea. The Eider when crossing Skåne in day-time, flies at a great height (observed at 800–1000 metres), but when over the sea it moves just over the water.

Fig. 8 gives the local topography at Ottenby. Route A is used by a number of birds, notably waders and terns. If the motivation is strong

FIGURE 8. Different routes of migrants at Ottenby.




(as in an " avalanche ") most birds follow A 1. If motivation is less strong (due to " wrong " wind, strong wind, fog, haze, rain, " wrong " time of the day or earliness of season) a number deviate at the point and take A 2. This may lead to a rest at the western reef, or " circling " back over the meadows to the east coast and a new trial (A 3) ; or, finally, the birds may disappear northwards (A 4). In several hundred cases flocks of Dunlins have been seen to split at the point, the eastern half departing, the western half being more influenced by the shore and taking A 2. If the birds, however, have already attained height over the meadows (route B), the influence of topography is less and most depart. Route C applies to Common Scoters, which move farthest from land, other ducks flying closer to the shore. Passerine birds have corresponding routes, though over land, preferably crossing the small gardens at the point itself. Their reluctance to fly over the sea very often increases rapidly and, after 100–200 metres of flight, the " resistance " overcomes the motivation to go and the birds suddenly return.

Displacement activities at the point of return may occur and adult waders often have outbursts of song. Gulls may indulge in flight gyrations (Svärdson 1949) and flocks of Sheld-ducks alight on the water, stretching head and body upwards with flapping wings.

For seven years in succession, 1945–1951, the writer observed the behaviour of two or three *young* Green Woodpeckers *Picus viridis* during July–August at Ottenby. The birds appeared almost daily at the very point and made numerous attempts to depart over the sea. Their daily rhythm of flying, reaction to the weather as well as to the shore, suggest fundamental similarities between dispersal of independent young birds and growing migratory behaviour.

Thanks to the scarcity of birds of prey at Ottenby, certain individuals have been observed coming in, " returning ", after having been out over the sea, southwards, for an hour or two. Koskimies (1944) found that White Wagtails flying out in the archipelago at the south coast of Finland in the early morning, returned later in the morning after a rest at the outermost islets (*cf.* Bergman 1948 a). This was typical for the early season, illustrates the two different drives in the birds, and should not be confused with real *Rückzug*.

Apart from the different reactions to topographical lines due to motivation, there is also a difference between species. Rudebeck (1950) found Buzzards and Kites more reluctant to fly over the sea than Ospreys and the *Circus* species. The Wood-sandpiper and the Redshank both perform various evolutions in the air before departing at Ottenby. Both rise to a considerable height (300–800 metres) and both certainly see the mainland coast to the west, but the Wood-sandpiper flies southwest–south and the Redshank southwest–west. Some weeks later, a number of ringed Wood-sandpipers are found mainly in northern Italy, but the Redshanks are recovered at the west coast of France. The different routes when they depart therefore suggest weaker adherence to the coast in *Tringa glareola*. The conflict between inherent sense of direction and the topographical lines is evident in many cases and the term "guiding-lines" must not be understood to mean that orientation is always favoured along the lines. Sometimes they certainly have an opposite effect.

The flight of nocturnal migrants cannot be studied directly, but indirectly it can be demonstrated that they do not adhere to topographical lines, or, at any rate, they do this very much less. The evidence may be summarized in the following paragraphs :

(1) Diurnal migrants are known to concentrate in autumn at several localities, notably at Falsterbo and Ottenby. In spring, no topographical lines lead them to these localities and no concentration is observed. Passerine nocturnal migrants never concentrate at any of the localities in numbers as do the diurnal species, whether in spring or autumn.

(2) Some wader species can certainly be judged as dominantly nocturnal migrants, based on the frequency of birds observed resting and departing at Ottenby. The concentration at Ottenby of passing birds is closely correlated with their dominant tendency to move by day, and is independent of the actual population size of the species. Redshank and Turnstone both breed to the extent of 300–350 pairs on the southern coast of Finland (Bergman 1948 b) and would be thought to pass in roughly equal numbers at Ottenby. The count, however, reveals that a total of 3000–5000 Redshanks pass in daytime as opposed to 100–200 Turnstones. Their passage period is the same and there is no evidence that Turnstones would pass Ottenby in the night by thousands. Most probably therefore, the Turnstones move on a broader front and are not concentrated. This, in turn, means that the recoveries of ringed Turnstones at the coast of western Europe and the observations there may be strongly biased, suggesting a closer adherence to the coast than is really the case. Oystercatchers are not so abundant within the Baltic area as Redshanks and Turnstones and yet they pass Ottenby in larger numbers, 4000–7000 being counted in a season. It is suggestive, that Redshanks and Oystercatchers, being the most diurnal of the waders, both move along the coast of the English Channel, but only on the continental side. Both have subspecies in the British Isles, the evolution of which must have been favoured by the fact that the coast-adhering birds from Fenno-Scandia preferably do not cross the Channel.

(3) The Common Scoter is an abundant migrant over land in southern Sweden, in both spring and autumn, but only at night. In the day they may be seen resting inland, but on the wing they are found only along the coasts and in large numbers. In the night, therefore, the coasting is overcome in favour of the inherent direction. Much the same occurs with many arctic waders. As these are observed inland mainly when resting in the day, some authors have thought that they moved along fixed routes, roughly coinciding with localities where they can find food and rest. When new localities, suitable for rest, arise, the birds, however, are found there immediately, suggesting a movement on a broad front.

(4) Heligoland, Fair Isle and—to some extent—Utsira (west of Haugesund) are famous for their resting nocturnal migrants. Diurnal travellers, however, are less significant or rare. Small isolated islands seem to have achieved their fame mainly because they are harbours of refuge for birds, some of which would otherwise fly to their death over the sea. It is strange that the islands mentioned are famous for their eastern birds, not known from other localities or at least found much more seldom elsewhere. These eastern species sometimes have evolved more westerly routes than populations breeding in northwestern Europe (Rudebeck 1950 and unpublished) and it is logical that they should constitute a relatively high proportion of the birds flying to their death each year over the northern Atlantic. Certainly more intensive studies have been carried out at Ottenby than at Utsira, nevertheless the eastern element of Utsira's autumn avifauna, includes species and numbers never seen at Ottenby (Schaanning 1937). The more the island has the character of a refuge, the more dominant are the eastern birds. The passage migrants of Utsira are few and the proportion of "rarities" is absurd. It is very interesting to find in the last few years that Ottenby has relatively more resting nocturnal migrants in spring than in autumn (numbers about the same, in spite of the reduced spring population), indicating an "insular effect". Though eastern birds are extremely rare at Ottenby in autumn, southeastern birds have been found in much higher proportions in spring, including two species, new to the Swedish list, in 1952. A critical evaluation of the frequency of "rare" birds, according to season and locality in Europe, could be of much interest.

## INFLUENCE OF THE WIND.

A nocturnal migrant flying over open sea, having a moderate lateral wind in relation to its direction, is bound to drift to one side. The Ring-ouzel *Turdus torquatus* normally moves west of southern Sweden and Swanberg (1948 b) found they occurred in numbers at Skara (southwestern Sweden) in April 1947, after two periods of strong southwest–west winds. After westerly gales, Ring-ouzel and Greenland Wheatear *Oenanthe oe. leucorrhoa* have appeared at Ottenby in autumn, indicating what probably happens to tens of thousands of migrants every year.

Rudebeck found the large birds of prey drifting with different winds within the boundaries given by the land masses of Skåne and Sjaelland. Their drifting was restricted by coasts, functioning as "guiding lines". It seems very probable that in diurnal migrants the drift is restricted or minimized by the adherence to various topographical lines and it may be suggested that this tendency in diurnal migrants has evolved partly as an adaptation to counter the disastrous effect of the wind. The drift may often cause pitfalls to the student of bird migration. Rudebeck found the Honey-buzzards drifting northwest to northern Sjaelland with southeasterly winds, instead of concentrating at Falsterbo. In northern Sjaelland the birds were thought to be " stimulated " by this wind, as they were apparently on the move only on those days. Moreover, as their course was more southerly, compensating for the drift, their origin could be easily mistaken. Eagle Clarke (1912) found that a northwest wind brought migration from Scandinavia across the North Sea to a standstill, while southeasterly winds brought migration to its climax. Southeasterly winds are likely to occur in this region when there is high pressure over Scandinavia and Clarke concluded that migration was most intense in that weather. The avalanches at Ottenby, however, often occur with northwest winds, which bring cold air down over Scandinavia ; but the birds, were they over Denmark, should not drift over to the British Isles, which is probably the main reason why Clarke found such weather giving low intensity of migration. Both in spring and autumn British observers are likely to overestimate the influence of anticyclonic weather, owing to drift phenomena. Williamson (1952) fully realizes the scale of drift visitors to the British Isles, but still adheres to the opinion that anticyclonic weather releases the start of migration. The avalanche, giving exceptional numbers of arrivals in England on 1 October 1951, was noted at Ottenby from 27 September. In fact, the birds started *before* the establishment of anticyclonic weather.

The wind, however, may interfere with the bird's flight in the opposite way, causing deviation against the wind. Though birds may be seen on their way in all light winds, there is an increasing tendency to move against the wind the stronger it is. A northwest wind gives a more westerly directed departure at Ottenby the stronger it is. Only ducks are known to fly regularly even in a strong tailwind, while most species head such a wind if they move at all.

The strong tendency to head the wind may be due to the turbulence of winds in lower air-layers, which in accordance with aerodynamical principles (*cf.* Bergman 1952) favours flying against the wind. Moderate " steering up " against the wind should result in the " calculated " course as opposed to the " duffer's course " (Smith 1945) and so the drift to one side should be minimized. There are further indications that the widespread tendency to head stronger winds is an adaptation. A field observation at Ottenby in the summer of 1951 may be cited.

A southwesterly wind gradually increased to storm force during the day. At the force of 20 metres per second (about 40 m.p.h.) only Swifts continued to depart, all the other species having stopped their movement. The last Swifts were seen departing when the air current had a velocity of 23 metres per second. Three hours later, at 27 metres, a small party of 15 Swifts came whirling back *with* the wind. Their speed was tremendous when they flew forwards with the wind, but during the few seconds they were visible they made two or three weak attempts to face it. If there had been some trees instead of open meadows they might have been able to find lee and stop. This observation suggests a survival value in the reaction. If a bird experiences a growing wind over the sea and continues to head it, "the motivation" probably will decrease when the bird is tired and after making a "return" it has a fair chance, with the velocity of the wind added to its own, of reaching the starting point again. The exceptional cases of transatlantic drift probably are due to this reaction, and the observed behaviour of departing birds at the shore can be harmonized with the known facts of long-distance drift in general, which postulate flight *with* the wind.

There are often conflicts between the supposed inherent sense of direction and modifying influences of topographical lines and wind. Bergman (1949) and Svärdson (1949) reported very aberrant flight directions of Chaffinches in spring and gulls in late summer, owing to such combined effects. In August 1952 the writer witnessed such conflicts in Swifts, which were "drawn" by a strong eastern wind to the Uppland coast from inland. When reaching the coast, they rose very high over the sea, hesitating as they often do when the influence of the coast interferes. Eventually they followed the shore southwards, again and again making "trials" far out over the sea. Some days before, when winds were westerly, Swifts arrived in a stream from Åland or Finland, rather low over the waves. This time, too, the shore was followed in a southern direction, when they were on the leeward Swedish side.

No Fenno-Scandian birds are more often seen heading the wind than the Swift and the hirundine species. Except for some stray specimens which probably were returning, no other birds have been seen to be induced by the wind to move contrary to the normal route, simulating *Rückzug*. In 1947 the strange situation arose that more House-martins were observed at Ottenby flying north than south during the season, owing to a long peripo of northern winds. The extreme reaction of these birds may correspond either to their gliding flight or to their aerial life, which makes an adaptation against drift all the more necessary.

## SUMMARY.

1. The adaptation of migration patterns to the climate of Fenno-Scandia is outlined. It is suggested that food supply is the ultimate factor for all the manifold types of migration.

2. Falling temperature is the proximate factor, releasing emigration in autumn or summer, and it causes *Rückzug* (reversed migration) in spring. A rise in temperature releases the spring movement or stimulates further flight, if the birds have reached temperate regions.

3. The annual and diurnal migration rhythms of some migrants are described. Most early migrants have a two-peak rhythm, which gradually changes to a single diurnal one in autumn. The second day-time peak in summer is probably transformed to a nocturnal one in autumn in some species.

4. Topography has a strong modifying influence on the routes of diurnal migrants but much less—or none at all—on the flight of nocturnal travellers.

5. Wind is the disastrous factor in migration. Its detrimental effect is minimized by the tendency to follow topographical lines and head the wind, at least when it is strong.

TABLE 1. *Number of departing birds at Ottenby, 23–30 October* 1951.

| Species* | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 |
|---|---|---|---|---|---|---|---|---|
| *Corvus c. cornix* | 3 | 22 | 9 | 4 | 86 | 88 | 70 | 74 |
| *C. monedula* | — | — | — | — | — | — | 79 | 139 |
| *Sturnus vulgaris* | 7510 | 964 | 5150 | 3160 | 345 | 4650 | 237 | 122 |
| *Chloris chloris* | 70 | 19 | 518 | 71 | 89 | 114 | 234 | 25 |
| *Carduelis flammea* | 92 | — | 95 | 200 | 110 | — | — | — |
| *C. flavirostris* | 25 | — | — | 60 | — | — | 12 | — |
| *C. cannabina* | 333 | 12 | 200 | 60 | — | — | — | 24 |
| *Fringilla coelebs* | — | — | 212 | 55 | — | — | 63 | 14 |
| *F. montifringilla* | 43 | — | 194 | 70 | — | 2 | 15 | — |
| *Emberiza citrinella* | 26 | 6 | 90 | — | 15 | 291 | 209 | 16 |
| *Passer montanus* | 22 | — | — | — | — | 2 | 7 | — |
| *Alauda arvensis* | 6 | 14 | — | 9 | 30 | 98 | 41 | — |
| *Turdus pilaris* | — | — | — | 250 | 23 | 47 | — | — |
| *Cygnus cygnus* | — | — | — | — | 129 | 142 | — | — |
| *C. columbianus bewickii* | — | — | — | — | 73 | 17 | — | — |
| *Anser fabalis* | — | — | — | — | 149 | 280 | — | — |
| *Branta leucopsis* | — | — | — | — | 11 | 108 | 88 | 54 |
| *B. bernicla* | — | — | — | 10 | 662 | 154 | 360 | 29 |
| *Anas platyrhynchos* | — | — | — | 45 | 1113 | 72 | 5 | 2 |
| *A. crecca* | — | — | — | 1 | 41 | 2 | 4 | — |
| *A. penelope* | — | — | — | 103 | 1285 | 458 | 956 | 16 |
| *A. acuta* | — | 66 | — | 27 | 301 | 20 | 102 | — |
| *Bucephala clangula* | — | — | — | 143 | 319 | 20 | — | — |
| *Clangula hyemalis* | — | — | — | 38 | 57 | 11 | — | — |
| *Somateria mollissima* | — | — | — | 80 | 5335 | 389 | 57 | — |
| *Melanitta nigra* | — | — | — | 168 | 744 | 33 | 22 | — |
| *M. fusca* | — | — | — | 110 | 68 | 51 | 17 | — |
| *Mergus merganser* | — | — | — | — | 26 | 4 | — | — |
| *M. serrator* | — | — | — | 6 | 105 | 20 | — | — |
| *Columba palumbus* | — | 2 | — | — | 15 | 85 | 27 | — |
| *C. oenas* | — | 19 | — | — | 17 | 42 | 6 | — |
| *Calidris alpina* | 7 | — | — | — | — | 40 | — | — |
| *Larus ridibundus* | 60 | — | 3 | 1 | 460 | 230 | 3 | 1 |
| *L. canus* | 4 | — | 32 | 3 | 52 | 13 | 6 | 5 |
| *L. argentatus* | — | — | — | 76 | 47 | 10 | 10 | 17 |

* In addition, the following species were participants in the avalanche, though not reaching 20 specimens on any single day: *Corvus frugilegus*, *Loxia* sp., *Motacilla alba*, *Falco columbarius*, *Buteo lagopus*. *B. buteo*, *Accipiter nisus*, *Ardea cinerea*, *Anser anser*, *Colymbus arcticus*, *C. stellatus*.

TABLE 2. *Number of departing birds at Ottenby,* 13–21 *September* 1950.

| Species * | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |
|---|---|---|---|---|---|---|---|---|---|
| *Sturnus vulgaris* | — | — | 3 | — | 8 | 97 | 17 | — | 6 |
| *Carduelis cannabina* | — | — | — | — | 493 | 536 | 128 | 40 | 96 |
| *Fringilla coelebs* | — | 3 | — | — | 74 | 19 | — | 4 | — |
| *F. montifringilla* | — | — | — | — | 25 | — | — | — | — |
| *Emberiza citrinella* | — | — | — | — | 3 | 20 | — | — | — |
| *Alauda arvensis* | — | 3 | 10 | — | 334 | 17 | — | 9 | — |
| *Anthus trivialis* | 39 | 26 | 86 | — | 5020 | 32 | 5 | 1 | — |
| *A. pratensis* | 16 | 1 | 7 | — | 34 | 31 | 3 | 24 | — |
| *A. spinoletta* | 1 | — | 5 | — | 36 | 8 | 4 | — | — |
| *Motacilla alba* | 1930 | 1383 | 1375 | 239 | 1898 | 1083 | 485 | 587 | 471 |
| *Hirundo rustica* | 129 | 152 | — | 113 | 3900 | 1634 | 711 | 120 | 93 |
| *Delichon urbica* | — | 25 | 25 | 341 | 81 | 3048 | 3702 | — | — |
| *Riparia riparia* | 36 | 23 | 23 | 177 | 10964 | 1623 | 110 | 9 | — |
| *Accipiter nisus* | 2 | 26 | 16 | — | 35 | 53 | 13 | 33 | 5 |
| *Tadorna tadorna* | — | — | — | — | — | — | — | 48 | — |
| *Anas penelope* | 35 | 163 | 93 | 87 | 18 | 45 | 188 | 16 | 4177 |
| *A. acuta* | — | — | 167 | — | — | 75 | 35 | — | 41 |
| *Columba oenas* | 49 | 104 | 9 | — | 156 | 291 | — | 17 | 185 |
| *Calidris alpina* | — | 681 | 51 | — | 39 | — | — | 21 | 246 |
| *Pluvialis squatarola* | — | 1 | — | — | 5 | 3 | — | 5 | 23 |
| *Grus grus* | — | 6 | — | — | 249 | — | — | — | — |
| *Larus ridibundus* | — | — | 90 | — | 22 | — | — | — | 9 |

* In addition, the following species were participants in the avalanche, though not reaching 20 specimens on any single day: *Carduelis carduelis, Anthus cervinus, Parus caeruleus, Apus apus, Falco peregrinus, F. subbuteo, F. tinnunculus, Buteo lagopus, Circus aeruginosus, C. pygargus, Pernis apivorus, Pandion haliaetus, Anser anser, Anas clypeata, Philomachus pugnax, Haematopus ostralegus, Larus argentatus.*

TABLE 3. *Number of departing birds at Ottenby,* 1–9 *August* 1949.

| Species * | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| *Sturnus vulgaris* | — | — | — | — | 2500 | 1945 | 855 | 50 | 115 |
| *Riparia riparia* | 26 | 6 | 132 | — | 286 | 76 | 53 | — | 30 |
| *Apus apus* | 1340 | 829 | 890 | 60 | 178 | — | 3140 | 700 | 1037 |
| *Tadorna tadorna* | 44 | 8 | — | — | 248 | 37 | 54 | 7 | 46 |
| *Anas platyrhynchos* | — | — | — | — | 74 | 17 | 30 | — | — |
| *A. crecca* | 10 | 11 | 31 | — | 25 | — | 33 | — | — |
| *A. acuta* | 6 | — | — | — | 50 | — | — | — | — |
| *A. clypeata* | 23 | — | — | — | 17 | — | 41 | — | — |
| *Somateria mollissima* | 26 | 4 | 19 | — | 8 | 20 | 110 | 3 | — |
| *Melanitta nigra* | — | — | 43 | — | 15 | — | 310 | 120 | — |
| *M. fusca* | — | — | — | — | 1 | 6 | 20 | 7 | 1 |
| *Columba oenas* | — | — | — | — | 8 | 71 | 15 | 14 | — |
| *Limosa lapponica* | 20 | 110 | 23 | 12 | 151 | 10 | — | 5 | 12 |
| *Numenius arquata* | 6 | 4 | 7 | — | 63 | 59 | 3 | 13 | 9 |
| *N. phaeopus* | 1 | 5 | 3 | 5 | 51 | 7 | 6 | 9 | 4 |
| *Arenaria interpres* | — | 1 | 1 | — | 31 | — | 2 | — | — |
| *Calidris canutus* | 62 | 77 | 58 | — | 420 | 28 | 13 | 5 | 53 |
| *C. alpina* | 400 | 250 | 613 | — | 7200 | 570 | 390 | 400 | 162 |
| *C. testacea* | 10 | — | 5 | — | 62 | 3 | — | — | 7 |
| *C. alba* | — | — | — | — | 29 | 1 | — | 2 | — |

TABLE 3 (*cont.*).

| Species * | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| *Philomachus pugnax* | 26 | 2 | 9 | — | 9 | 11 | 5 | — | 3 |
| *Tringa glareola* | 16 | — | 15 | — | 22 | 4 | 5 | 3 | 1 |
| *T. totanus* | 4 | — | — | — | 603 | 89 | 15 | 69 | 3 |
| *T. nebularia* | — | — | — | — | 56 | 21 | 12 | — | 10 |
| *Charadrius hiaticula* | — | — | — | — | 176 | 28 | 2 | 3 | 12 |
| *Calidris/Charadrius* † | — | 120 | — | — | 5015 | 345 | 220 | 85 | — |
| *Pluvialis squatarola* | 7 | 14 | 2 | 15 | 46 | 25 | 2 | 16 | 3 |
| *Haematopus ostralegus* | 49 | — | 29 | — | 786 | 271 | 238 | 130 | — |
| *Chlidonias niger* | 24 | 2 | 8 | 5 | 66 | 12 | 4 | — | 4 |
| *Sterna sandvicensis* | 9 | 3 | 18 | — | 31 | 8 | 3 | 5 | — |
| *S. albifrons* | 48 | 11 | 14 | — | 117 | 44 | 77 | 7 | 17 |
| *S. hirundo/paradisaea* ‡ | 555 | 37 | 63 | 5 | 1843 | 278 | 802 | 73 | 202 |
| *Larus ridibundus* | — | — | 11 | — | 936 | 400 | 99 | 145 | 42 |
| *L. canus* | 1 | 2 | 6 | — | 341 | 31 | 32 | 23 | 16 |
| *L. argentatus* | — | — | 4 | — | 49 | 21 | 17 | 1 | 2 |
| *L. fuscus* | 4 | 13 | 20 | — | 38 | 19 | 43 | 76 | 93 |

* In addition, the following species were participants in the avalanche, though not reaching 20 specimens on any single day: *Anthus trivialis, Motacilla flava, Falco peregrinus, F. subbuteo, F. tinnunculus, Circus pygargus, Accipiter nisus, Ardea cinerea, Mergus serrator, Colymbus arcticus, Limosa limosa, Tringa hypoleucos, T. ochropus, T. erythropus, Charadrius dubius, Pluvialis apricaria, Vanellus vanellus, Recurvirostra avosetta, Hydroprogne tschegrava, Larus marinus, Stercorarius parasiticus.*

† Not certainly identified owing to long distance, probably more than 90 per cent of them were *Calidris alpina.*

‡ Species combined, as most of them could not be identified with certainty.

TABLE 4. *Number of departing birds at Ottenby,* 1–9 *July* 1951.

| Species * | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| *Sturnus vulgaris* | 2275 | 276 | 666 | 665 | 1287 | 1090 | 200 | 88 | 320 |
| *Apus apus* † | — | 14390 | 8043 | 8363 | 3222 | 9690 | — | 9220 | — |
| *Tadorna tadorna* | 21 | — | — | 3 | 236 | 8 | 13 | 24 | 87 |
| *Somateria mollissima* | — | 7 | — | 30 | 14 | 30 | — | 13 | — |
| *Melanitta fusca* | 21 | 9 | — | 10 | 24 | 49 | 8 | 25 | — |
| *Limosa lapponica* | — | — | — | — | 4 | 19 | — | — | — |
| *Numenius arquata* | 37 | — | 8 | 3 | 89 | 2 | 7 | — | — |
| *Calidris alpina* | 62 | — | — | 40 | — | 13 | 8 | 7 | — |
| *Philomachus pugnax* | 10 | — | — | 16 | 25 | — | 7 | 4 | — |
| *Tringa glareola* | — | — | — | — | 26 | 6 | 5 | — | — |
| *T. totanus* | 21 | — | — | 3 | 548 | 44 | 81 | 110 | 174 |
| *T. nebularia* | 3 | — | — | 4 | 11 | 3 | — | — | 2 |
| *Charadrius hiaticula* | 9 | — | — | 10 | 7 | 18 | 19 | — | 3 |
| *Vanellus vanellus* | — | — | — | 29 | 37 | 28 | 6 | — | — |
| *Haematopus ostralegus* | 17 | — | — | — | 250 | — | 1 | — | — |
| *Larus ridibundus* | 2 | — | — | — | 31 | — | 3 | — | — |
| *L. canus* | 5 | — | — | — | 3 | — | 14 | — | — |

* In addition, the following species were participants in the avalanche, though not reaching 10 specimens on any single day: *Ardea cinerea, Anser anser, Anas platyrhynchos, A. acuta, Columba oenas, Limosa limosa, Numenius phaeopus, Tringa ochropus, T. erythropus, Pluvialis squatarola, Recurvirostra avosetta, Larus argentatus, L. fuscus.*

† The Swifts were flying northwest on the 5th, arriving from south.

TABLE 5. *Number of Sheld-ducks and Bar-tailed Godwits observed departing at Ottenby in July* 1947–1951. *An influx of polar air in the southern Baltic is marked with italics for the Sheld-duck, a corresponding influx in the region Kola–Ladoga is indicated with italics for the Godwit. Note the delay of* 2–4 *days in the Godwit, in contrast to the immediate response by the Sheld-duck.*

| | Sheld-duck | | | | | Godwit | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1947 | 1948 | 1949 | 1950 | 1951 | 1947 | 1948 | 1949 | 1950 | 1951 |
| July 1 | 34 | — | 63 | — | 21 | — | — | — | 4 | — |
| 2 | — | — | — | 57 | — | — | — | — | — | — |
| 3 | — | — | 72 | 98 | — | — | — | — | — | — |
| 4 | — | *78* | 5 | *423* | 3 | — | — | — | 1 | — |
| 5 | 9 | 150 | 94 | 52 | *236* | — | — | — | — | 4 |
| 6 | — | — | — | 17 | 8 | — | — | — | — | 19 |
| 7 | — | 35 | 37 | *413* | 13 | — | — | — | — | — |
| 8 | — | 10 | *400* | — | 24 | — | — | — | — | — |
| 9 | 47 | 34 | 85 | — | 87 | — | — | — | — | — |
| 10 | — | — | 63 | 21 | 91 | — | 2 | 1 | — | — |
| 11 | — | 12 | — | — | 104 | — | 1 | — | 1 | — |
| 12 | — | — | 8 | *847* | 68 | — | — | — | — | — |
| 13 | *285* | — | — | 134 | *245* | 4 | — | — | — | — |
| 14 | 517 | — | 22 | 435 | 107 | 1 | — | — | — | — |
| 15 | 32 | — | *47* | 29 | *594* | 29 | 24 | — | — | 7 |
| 16 | 115 | *173* | *87* | 39 | 369 | *36* | 4 | — | *4* | 15 |
| 17 | 102 | 70 | 19 | — | 17 | — | 3 | — | — | 7 |
| 18 | 23 | — | 65 | — | 7 | — | 8 | 8 | 5 | 11 |
| 19 | — | — | — | — | *248* | 30 | 1 | 4 | 57 | 36 |
| 20 | 54 | — | — | — | 7 | 68 | 6 | 8 | — | 6 |
| 21 | — | 15 | — | 39 | 250 | *1* | 4 | — | *16* | 17 |
| 22 | 32 | — | *42* | — | 29 | 1 | 3 | 1 | 10 | 29 |
| 23 | 15 | *42* | 15 | 186 | 49 | 1 | 7 | — | 3 | *14* |
| 24 | — | *44* | — | — | 62 | *77* | 20 | *8* | 107 | 1 |
| 25 | 29 | 97 | — | *95* | 113 | *10* | 7 | *10* | 28 | 75 |
| 26 | 4 | 8 | — | 78 | 10 | 14 | *48* | — | 64 | *15* |
| 27 | 24 | 26 | 45 | 45 | — | 16 | 12 | 28 | 36 | *22* |
| 28 | 17 | 39 | — | *203* | — | 64 | 145 | 47 | 140 | 52 |
| 29 | — | 88 | — | 80 | *4* | 310 | 187 | — | 22 | 419 |
| 30 | *162* | 80 | 51 | *145* | *100* | 63 | 27 | 11 | 27 | 87 |
| 31 | — | 170 | 11 | 60 | 251 | 15 | 25 | 7 | 16 | 70 |

TABLE 6. *Average passage during the day at Ottenby, period 29 July–7 August.*

| Species* | 4–5 | 5–6 | 6–7 | 7–8 | 8–9 | 9–10 | 10–11 | 11–12 | 12–13 | 13–14 | 14–15 | 15–16 | 16–17 | 17–18 | 18–19 | 19–20 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Hour | | | | | | | | | | | | | | | |
| *Sturnus vulgaris* | 29·2 | 80·0 | 25·2 | 13·2 | 1·2 | 2·1 | — | 1·0 | — | — | — | 0·6 | 10·2 | 37·8 | 21·2 | 12·0 |
| *Delichon urbica* | 0·1 | 2·6 | 10·0 | 7·4 | 3·7 | 10·6 | 4·8 | 8·5 | 10·3 | 4·0 | 4·3 | 1·6 | 1·4 | — | — | — |
| *Riparia riparia* | 0·5 | 1·7 | 1·8 | 1·6 | 0·8 | 1·1 | 1·8 | 2·2 | 2·9 | 1·4 | 0·8 | 0·2 | 2·8 | 1·3 | 1·8 | 3·8 |
| *Apus apus* | 16·6 | 15·2 | 41·5 | 52·0 | 41·0 | 41·9 | 40·0 | 81·4 | 71·4 | 98·8 | 102·0 | 42·6 | 38·8 | 21·5 | 28·6 | 18·4 |
| *Falco tinnunculus* | — | 0·1 | 0·2 | 0·2 | 0·1 | 0·2 | 0·3 | 0·2 | — | 0·1 | — | — | — | — | — | — |
| *Tadorna tadorna* | 2·4 | 4·3 | 1·4 | 0·5 | 2·2 | 0·6 | 1·5 | 2·7 | 0·9 | 2·2 | 3·2.. | 6·2 | 6·0 | 12·1 | 7·3 | 8·3 |
| *Anas platyrhynchos* | 1·2 | 0·5 | 2·4 | 0·2 | 0·6 | 0·1 | — | 0·6 | — | 0·3 | 0·1 | — | 0·4 | 0·3 | 4·8 | 4·7 |
| *A. clypeata* | 0·1 | 1·6 | 0·8 | — | — | — | — | 0·5 | — | — | — | — | 0·4 | 0·4 | 2·0 | 1·2 |
| *Somateria mollissima* | 1·0 | 2·2 | 1·2 | 1·0 | 1·4 | 0·3 | 2·1 | 0·4 | 0·6 | 0·5 | 0·8 | 1·7 | 0·8 | 3·5 | 3·2 | 4·7 |
| *Melanitta nigra* | 2·1 | 9·9 | 8·7 | 14·2 | 5·7 | 5·7 | 1·8 | 1·8 | — | 0·7 | 1·9 | 0·4 | 5·4 | 0·5 | 6·4 | 13·7 |
| *Limosa lapponica* | 2·0 | 4·5 | 3·3 | 2·9 | 1·9 | 4·6 | 3·2 | 4·1 | 3·9 | 2·9 | 2·8 | 2·5 | 3·9 | 2·4 | 3·5 | 2·6 |
| *Numenius arquata* | 2·9 | 3·9 | 3·8 | 3·6 | 1·5 | 1·3 | 1·4 | 0·8 | 1·6 | 1·4 | 1·5 | 2·6 | 1·5 | 2·1 | 1·5 | 1·7 |
| *Calidris canutus* | 2·9 | 8·6 | 2·7 | 3·2 | 0·9 | 2·4 | 1·0 | 1·9 | 0·3 | 2·2 | 2·6 | 2·2 | 3·0 | 3·2 | 4·3 | 3·2 |
| *C. alpina* | 50·0 | 57·1 | 65·5 | 38·6 | 35·2 | 25·3 | 8·8 | 16·5 | 25·0 | 24·4 | 23·7 | 61·2 | 39·8 | 58·5 | 81·2 | 49·2 |
| *Philomachus pugnax* | 0·7 | 1·5 | 2·3 | 1·0 | 0·1 | 0·2 | 0·7 | 0·1 | — | 0·2 | — | 0·2 | 0·4 | 0·1 | 1·0 | 0·5 |
| *Tringa glareola* | 1·4 | 6·3 | 4·8 | 1·6 | 1·0 | 1·0 | 1·1 | 2·7 | 0·7 | — | 0·3 | 0·4 | 1·0 | 1·7 | 4·7 | 4·5 |
| *T. totanus* | 3·0 | 4·5 | 4·1 | 1·6 | 0·8 | 0·2 | 0·3 | 0·9 | 0·9 | 0·5 | 3·8 | 5·7 | 8·5 | 18·8 | 12·7 | 3·7 |
| *Charadrius hiaticula* | 1·1 | 4·5 | 2·8 | 1·5 | 0·2 | 1·1 | 0·6 | 0·8 | 0·7 | 1·1 | 0·2 | 1·1 | 2·1 | 3·8 | 2·5 | 3·0 |
| *Haematopus ostralegus* | 7·5 | 9·3 | 5·3 | 5·0 | 8·1 | 5·3 | 6·9 | 5·5 | 8·5 | 6·7 | 14·8 | 10·3 | 13·3 | 13·6 | 16·5 | 17·0 |
| *Sterna hirundo/paradisaea* | 5·6 | 6·2 | 7·5 | 7·5 | 7·9 | 6·4 | 4·7 | 7·5 | 9·8 | 8·7 | 14·7 | 11·0 | 7·3 | 9·7 | 11·6 | 16·0 |
| *S. albifrons* | 1·9 | 2·5 | 2·0 | 0·9 | 0·3 | 1·1 | 0·6 | 0·9 | 1·1 | 1·2 | 1·5 | 1·7 | 2·3 | 3·5 | 4·3 | 4·3 |
| *Larus ridibundus* | 16·8 | 14·8 | 16·2 | 9·0 | 3·1 | 3·4 | 2·4 | 3·5 | 1·9 | 3·6 | 4·0 | 5·6 | 3·8 | 7·0 | 8·0 | 20·0 |
| *L. canus* | 1·4 | 2·1 | 2·4 | 1·3 | 1·2 | 0·9 | 1·2 | 1·2 | 1·1 | 1·2 | 1·2 | 0·6 | 0·9 | 1·9 | 2·1 | 3·1 |
| *L. fuscus* | 0·9 | 0·7 | 1·4 | 1·3 | 0·8 | 1·0 | 0·9 | 0·6 | 0·5 | 0·9 | 0·7 | 0·9 | 1·5 | 1·3 | 0·8 | 2·5 |

* In addition the following species were observed during the period, passing mainly in the morning and the evening hours, though not reaching an average of 2·0 individuals for any one hour: *Anas crecca, A. acuta, Melanitta fusca, Columba oenas, Numenius phaeopus, Capella gallinago, Arenaria interpres, Calidris testacea, C. temmincki, Tringa hypoleucos, T. ochropus, T. erythropus, T. nebularia, Pluvialis squatarola, Vanellus vanellus, Recurvirostra avosetta, Chlidonias niger, Hydroprogne tschegrava, Sterna sandvicensis, Larus minutus, L. argentatus, L. marinus.*

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