A RADAR STUDY OF THE AUTUMN MIGRATION OF WOOD PIGEONS *COLUMBA PALUMBUS* IN SOUTHERN SCANDINAVIA

THOMAS ALERSTAM & STAFFAN ULFSTRAND

Received 23 June 1973

INTRODUCTION

The relationship between bird migration and meteorological conditions has been widely discussed. Several meteorological variables have been invoked as stimuli responsible for the release of migratory activity (Lack 1960, Nisbet & Drury 1968). The process and pattern of migration have also been shown to be affected by various aspects of weather. Similarly, the significance of topographical features, above all coastlines, as leading or deflection lines has roused much interest (Geyr von Schweppenburg 1949, Rudebeck 1950). The whole field has recently been surveyed by Schüz (1971).

In early days, when direct visual observation was the only means of study available, most evidence was derived from birds flying at low altitude; a given bird or flock of birds, moreover, could be followed only for a short distance. Later results, acquired with the aid of radar, have clearly demonstrated that the so-called 'visible' migration is only part of the whole phenomenon. The picture obtained from earlier investigations was also influenced by another restriction, namely, the choice of observation sites. Ornithologists naturally selected islands or promontories where large numbers of birds concentrated, although clearly conditions at such places may differ markedly from those prevailing elsewhere, over most of the land and the sea (Ulfstrand 1960, Evans 1966a).

Whether birds compensate or not for wind displacement is a particularly intricate and important problem. Results suggesting complete compensation for nocturnal passerine migration over the land or coastal regions have been presented by Bellrose & Graber (1963), Drury & Nisbet (1964), Evans (1966b, 1968), Nisbet & Drury (1967), Bellrose (1967) and Steidinger (1972). Variations in mean track, significant but less than would be expected from wind deflection assuming no compensatory efforts, were interpreted as due to 'pseudodrift', that is, to the effect of populations with different inherent primary directions participating in different proportions in the migratory movements under different wind directions (Evans 1966b, Nisbet & Drury 1967). In other investigations, such as Lack (1963a, b), Steidinger (1968), Parslow (1969) and Alerstam & Ulfstrand (1972), involving both diurnal and nocturnal migration, varying mean tracks seemed to be explicable assuming no compensation for wind deflection. Later, however, Lack (1969) concluded that compensation was the rule, but displacement was assumed to occur when birds encountered strong crosswinds over the sea.

For non-passerines, few investigations are available. Rudebeck (1950) found that the geographical pattern of the migration of the Common Buzzard *Buteo buteo* and other birds of prey over Skåne was strongly influenced by prevailing wind directions, these soaring birds allowing themselves to be drifted with the wind but also having special mechanisms to check the amount of displacement. Ulfstrand (1958) examined in some detail the relationship between wind and the passage of Honey Buzzards *Pernis apivorus* over Skåne. Bergman & Donner (1964, 1971) concluded that no compensation occurred in the Common Scoter *Melanitta nigra* and the Long-tailed Duck *Clangula hyemalis* migrating across Finland during the night. Bergman (1964) and Alerstam & Bauer

(1973) showed the existence of compensation during the spring migration of the Crane *Grus grus* in Fenno-Scandia.

The Wood Pigeon *Columba palumbus* for several reasons is an almost perfect subject for radar studies (Gehring 1963, Alerstam & Ulfstrand 1972). The birds move in large compact flocks producing very distinct and specific echoes on the radar scope, they often fly at a considerable altitude, and they have a restricted peak migration period when, moreover, echoes deriving from Wood Pigeon flocks so strongly dominate the display that one may justifiably regard all echoes with certain defined exceptions as Wood Pigeon flocks. On the radar scope such echoes may often be followed for hundreds of kilometres.

The Scandinavian Wood Pigeon population is almost completely migratory and spends the winter mainly in southwestern France and the Iberian peninsula (Rendahl 1965). The autumn migration in southern Scandinavia usually takes place between the middle of September and the first week of November, with a peak in the first half of October (Ulfstrand *et al.* 1974). A certain transit passage of Wood Pigeons from Finland to Sweden in autumn occurs, but its quantitative importance is not known. Only very small numbers are recorded at Ottenby on the island of Öland, southeastern Sweden (Edelstam 1972).

The only previous study from Scandinavia bearing upon the migratory behaviour of the Wood Pigeon is Mathiasson (1967) in which, amongst other things, the diel periodicity of activity is briefly discussed. In this report we shall describe and discuss the pattern of Wood Pigeon migration in southern Scandinavia, based on radar monitoring supplemented by observations from aircraft and from the ground, during the autumns of 1971 and 1972.

Relevant geographical features of southern Scandinavia are shown in Figure 1 where also all place names used in the text may be identified.

METHODS

Romele radar (R in Fig. 1) in Skåne (23 cm, MTI-equipped; further details in Alerstam & Ulfstrand 1972) was filmed throughout the autumns. A high power 10 cm station at Gothenburg (G in Fig. 1) was also filmed from 17 September to 8 October 1972. Time-lapse filming technique (2·5 frames/min) was used. Both stations normally were operated at a wide range (270 and 200 km, respectively).

Flight paths of individual echoes were plotted on maps. The daily track direction over an area was assessed through fitting by eye a mean direction to about 50 such tracks (rarely fewer) selected to represent different echo cohorts in approximate proportion to their size; checks by repetition produced mean values differing by less than 2°. These data were also used for the calculation of ground speed over different areas. Mean daily values were based on accurate measurements of about 25 echo tracks. Values on direction and speed used in the text below thus refer to daily means over certain defined areas. The distinctiveness of the echoes permitted Wood Pigeon cohorts to be quantified by means of direct counting of echoes. We located echo-counting areas and lines so close to the radar stations that the effects of range and angle should be negligible.

In autumn 1972 we carried out observations from a light aeroplane. One of us was watching the radar scope, the other patrolling the southwestern part of Skåne in the aircraft at altitudes between 100 and 1200 m. By radio, the observer in the aircraft was told the position of interesting echoes, and frequently was able to detect their sources. About 40 echoes suspected by the radar watcher to represent Wood Pigeon flocks were spotted from the aircraft, and all were found to have been correctly identified.

A detailed comparison of numbers of echoes ascribed to Wood Pigeon movements with numbers of flocks and individuals recorded by field observers presented by Alerstam & Ulfstrand (1972, also unpubl.) fully supports the identification of echoes treated in this paper as virtually nothing but Wood Pigeon flocks. Mixed with the Wood Pigeons there

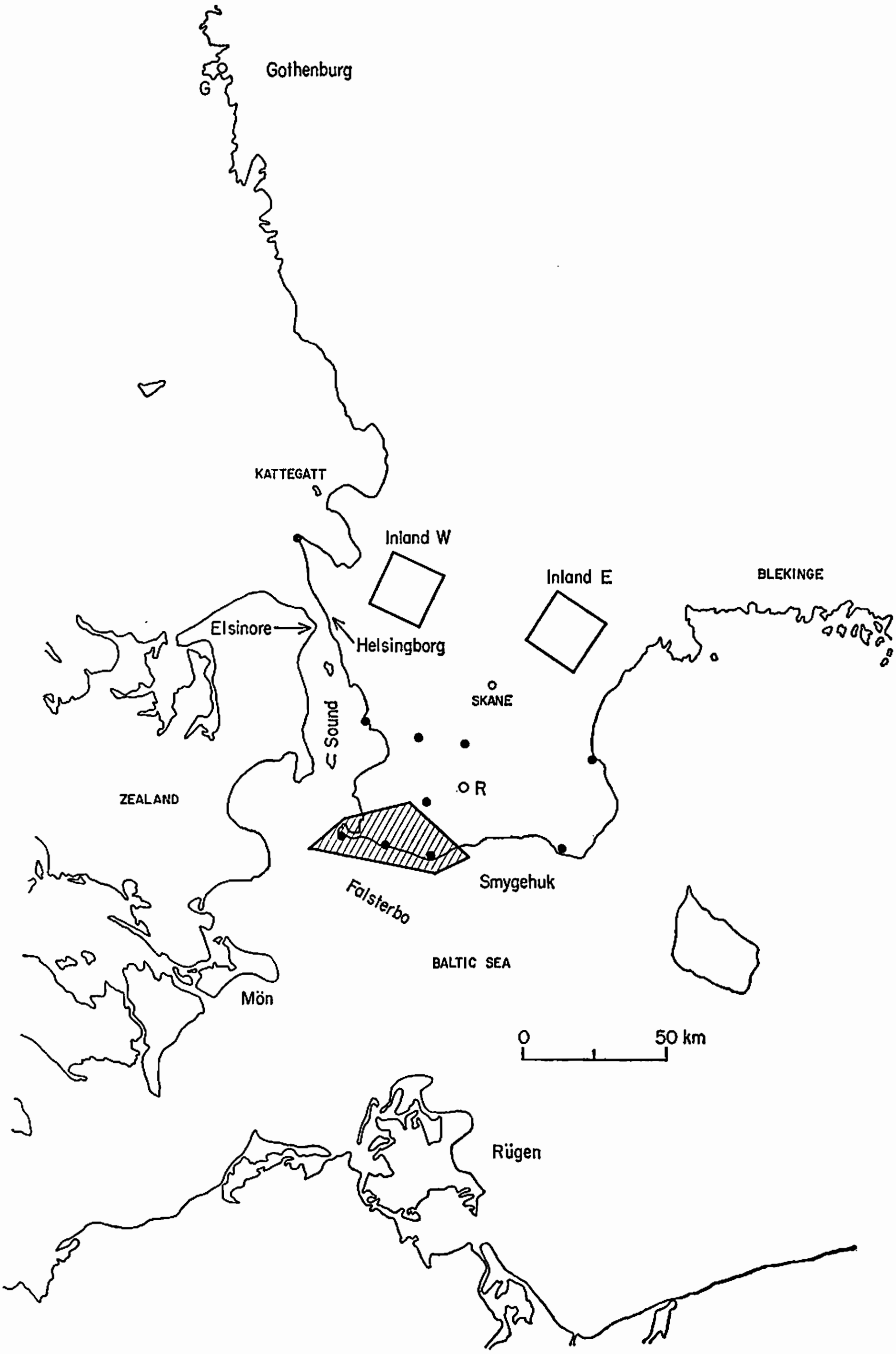

FIGURE 1. Study area. Radar stations (G and R, ○) and field observation sites (●) are indicated as well as area of aircraft observations (▨).

were usually a few Stock Doves *Columba oenas*, but this species practically never amounted to more than a few percent of all columbids.

Wind direction and speed were evaluated to the nearest 22·5° and 5 km/h, respectively, from synoptic maps at 07.00 and 13.00 hrs each day. Our wind data reflect conditions prevailing at 500–1000 m altitude, that is, where most of the pigeon flocks travelled according to our aircraft observations. Other meteorological data were obtained from the monthly reports of the Swedish Meteorological and Hydrological Institute.

QUANTITY AND SPEED OF MIGRATING WOOD PIGEONS IN RELATION TO COLD FRONT PASSAGES

Synoptic weather situations in Scandinavia may be conveniently described in terms of east-bound cyclonic passages associated with marked fronts alternating with interludes of anticyclonic weather zones. We shall examine the daily quantity of Wood Pigeon migration in relation to the cold front passages accompanying low pressure movements across our study area.

It appears that the number of radar echoes is a satisfactory approximation of the total migratory activity. There was a very close correlation between quantities of echoes on the radar scope and of flocks recorded by field observers. We have had no occasion of appreciable Wood Pigeon migration below the level of radar detection, which strengthens our conviction that the radars miss only a very small proportion of the total Wood Pigeon migration within our selected study area. Large and small Wood Pigeon flocks, however, create echoes that appear to us indistinguishable; we are preparing a study of daily and local variations of flock size, but at this stage we have no evidence invalidating the assumption that echo numbers reflect migratory activity.

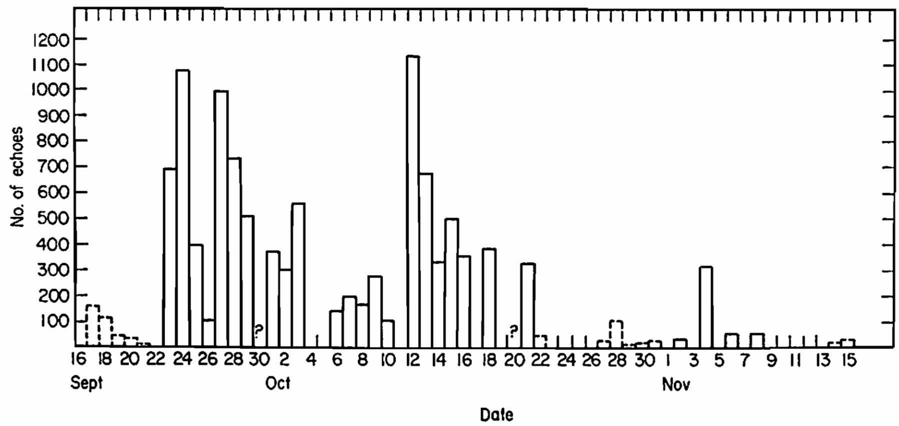

FIGURE 2. Total number of echoes from Wood Pigeon flocks departing from south Sweden in 1972 as recorded on the radar display in Skåne. No data were available from 30 September and 20 October. Broken lines are used in some cases of partially doubtful echo identifications.

Daily figures for migrating Wood Pigeons in 1971 were presented by Alerstam & Ulfstrand (1972, Table II). On four occasions in this autumn, cold fronts passed towards the south or southeast over the study area (24 and 30 September, 3 and 7 October). By far the heaviest Wood Pigeon migration took place on 4 and 5 October, that is, in the wake of a cold front passage which was the only one during that autumn that penetrated as far as central Europe and was followed by northerly winds.

In 1972, ten cold front passages were recorded between 16 September and 16 November, viz. 22 and 26 September, 11, 17 and 20 October, 1, 3, 5, 7 and 10 November. A close association between front passages and a subsequent increase in migratory activity is clearly seen in Figure 2. The synoptic situation during the front passages in September and October 1972 closely resembled that described for 3 October 1971, and was characterized by a high pressure area that covered the British Isles and/or the North Sea and a low pressure that moved east over central and/or northern Scandinavia with its accompanying cold front extending from about WSW to ENE and being followed by strong northerly winds. Weather changes after such front passages regularly included a temperature drop, improving visibility and increasing wind velocities as the wind shifted northwards. Most often northwesterly winds dominated on the first day after the front passage, later changing towards north or northeast.

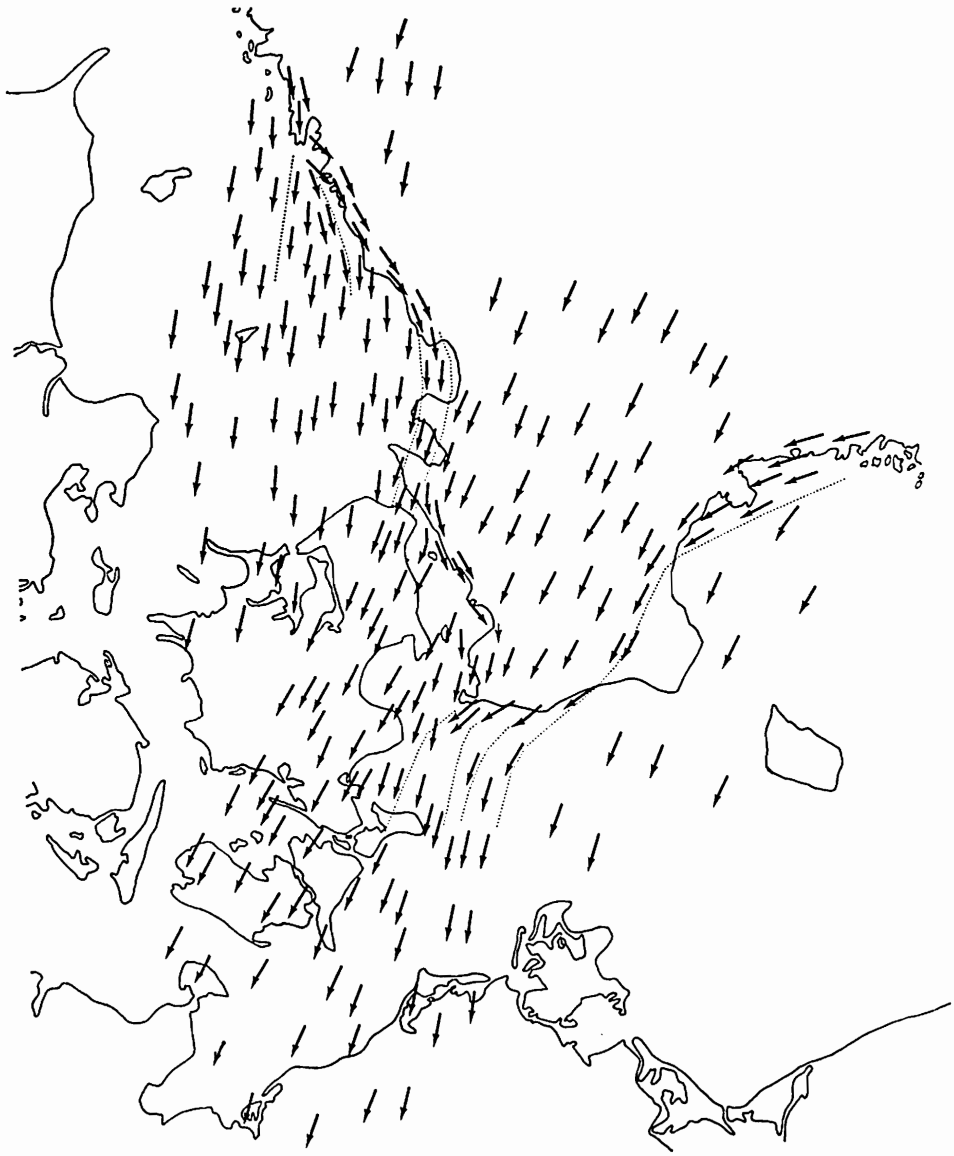

FIGURE 3. General geographical pattern of the Wood Pigeon migration over south Sweden. (····) zones of particularly dense migration.

Within the general pattern schematically represented in Figure 3 two sub-systems of Wood Pigeon migration are distinguishable. One consists of cohorts travelling over the Kattegatt and the Swedish west coast, and the other of cohorts travelling over central/ eastern Skåne and the Baltic (Plate 12). The ratios between the number of flocks over these two areas, respectively, calculated from echo counts on the Romele radar, are related to wind directions in Figure 4. There was a distinct tendency of movements along the west coast and the Kattegatt to be relatively more frequent under northwesterly than under northeasterly to easterly winds.

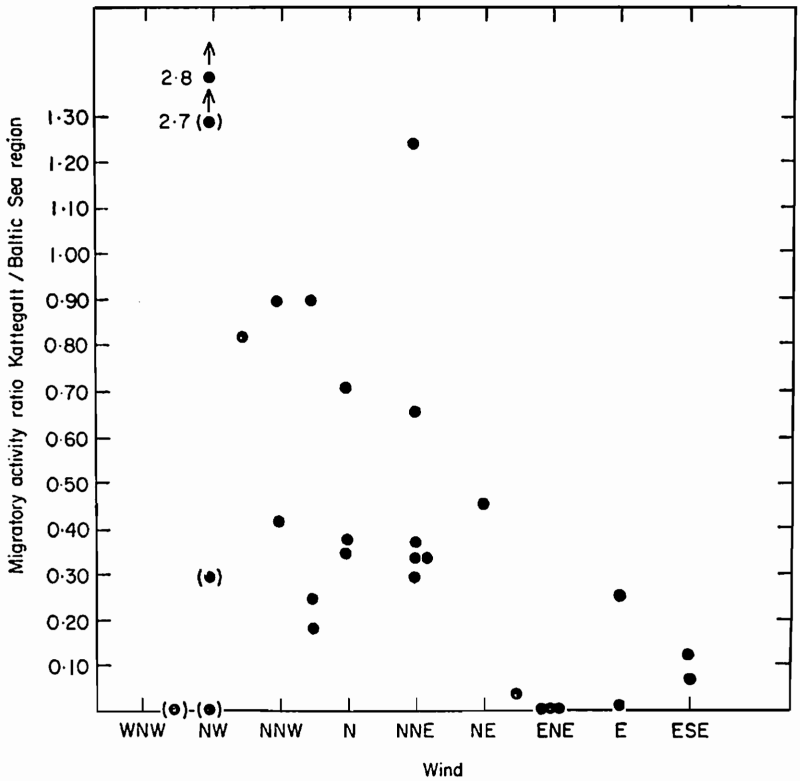

FIGURE 4. Ratio of numbers of echoes from Wood Pigeon flocks in the Kattegatt region to numbers in the Baltic Sea region in relation to wind direction. If wind directions over the two areas were different, the mean direction was used. Ratios calculated from <100 echoes are bracketed. The correlation is significant ($r = 0{\cdot}60$, $P < 0{\cdot}005$).

Because enhanced migratory activity was associated with near northerly winds, Wood Pigeon flocks generally moved with high ground speeds. The mean true air speed of migrating flocks was calculated to be 60 $\pm$ s.d. 8 km/h ($n = 59$, each value representing >20 echoes). There was no correlation between air and ground speed. This suggests that the main source of variation in the calculated air speed was uncertainty about wind conditions at the altitude where the pigeons were flying, rather than behavioural changes on the part of the birds. This justifies the contention that, as shown in Table 1, only 10% of all Wood Pigeon flocks were retarded by a headwind component. Most flocks flew faster than 80 km/h ground speed, evidently aided by considerable tailwind forces. It is interesting to note that migration across the Kattegatt was very largely limited to periods when strong tailwinds permitted high ground speeds (Table 1).

TABLE 1

Ground speeds of Wood Pigeon flocks migrating over different sea areas

Ground speed (km/h)	Percentage of all echoes Kattegatt	Baltic Sea	Total
40–60	3	13	10
60–80	13	35	29
80–120	84	52	61

TOPOGRAPHICAL INFLUENCE

No topographical features other than coastlines were found to affect the geographical pattern of echo movements over southern Scandinavia (Fig. 3). This is not to deny that, for example, forested areas may attract migrating pigeon flocks and cause local concentrations of migrating and resting birds, sometimes of impressive size (Malmberg 1955).

Blekinge. Echoes arriving over the province of Blekinge (see Fig. 1) flew WSW, clearly influenced by the coastline. Many flocks travelled over the sea within 10–15 km from the shore, obviously retaining a certain contact with the land. Off the coast northeast of Skåne the direction usually shifted more towards the south. After reaching the land, these flocks flew on courses similar to those of flocks arriving from the north over the interior. Only a small proportion of all echoes departed from the Blekinge coast and started a long crossing of the open sea.

The south coast of Skåne. Most Wood Pigeons left Sweden over the coast between Smygehuk and the Falsterbo peninsula (Figs 1 and 3). Flocks approached the coast over land on track directions around SSW, but after passing the shore they frequently changed towards WSW. Often birds flew along the coast for 10–15 km, only slowly and gradually deviating from it, until they were at a distance of 5–10 km off it. Then, more or less suddenly, they readjusted their course to about the same as that over land, i.e., SSW. The effect of the coastline was sometimes still stronger: flocks would fly over or just off the coast the whole distance from east of Smygehuk to Falsterbo (see below).

The west coast of southern Sweden. Overland movements along the west coast were recorded from north of Gothenburg to Falsterbo. Narrow bays did not affect the straight flight lines of the flocks. The pigeons usually crossed the Sound just north of Helsingborg, to continue over Zealand. During the passage over northwestern Skåne and the Sound their direction gradually changed from SSE to SSW. A small portion of the flocks did not cross the Sound at this place but proceeded along the west coast of Skåne. Some of these left the coast fairly soon, and only a few continued so far as to become involved in the cohorts recorded over the Falsterbo peninsula. Variable proportions of the echoes were noted over the land and over the sea, respectively, in both cases moving parallel to the coast.

The Kattegatt. Flocks often continued flying along the coast for distances up to 50 km after having crossed the coast, but a certain portion immediately broke contact with the land.

Maximum topographical influence. On certain days the Wood Pigeon flocks appeared particularly reluctant to leave the land. According to the field observers' records they circled over the shore and made repeated abortive departures. Echoes were seen on these same days to make for conspicuous landmarks (such as the islands of Mön and Rügen) on straight courses; from the Falsterbo peninsula flocks made directly for Stevns Klint, its tall white cliffs visible from afar (Fig. 5, Plate 13). The same inclination could be recognized in some flocks leaving Blekinge and flying southwest over the sea, later to veer towards the southeastern corner of Skåne. On the radar display we could sometimes follow echoes turning back to the land after having been 20 km offshore.

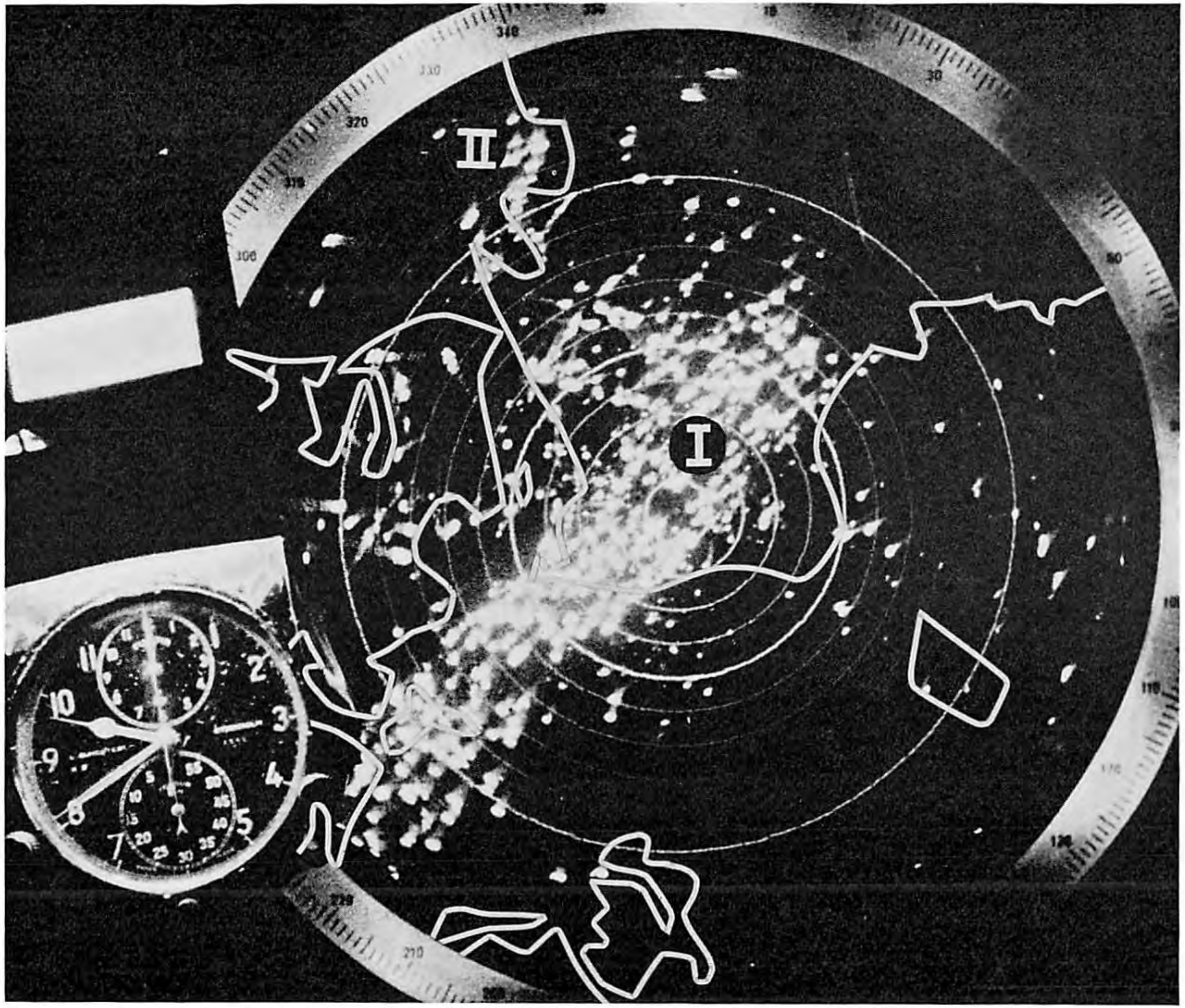

PLATE 12 5 October 1971, 09.41 hrs. Massive Wood Pigeon migration across the whole width of Skåne (I), with a cohort following the west coast (II).

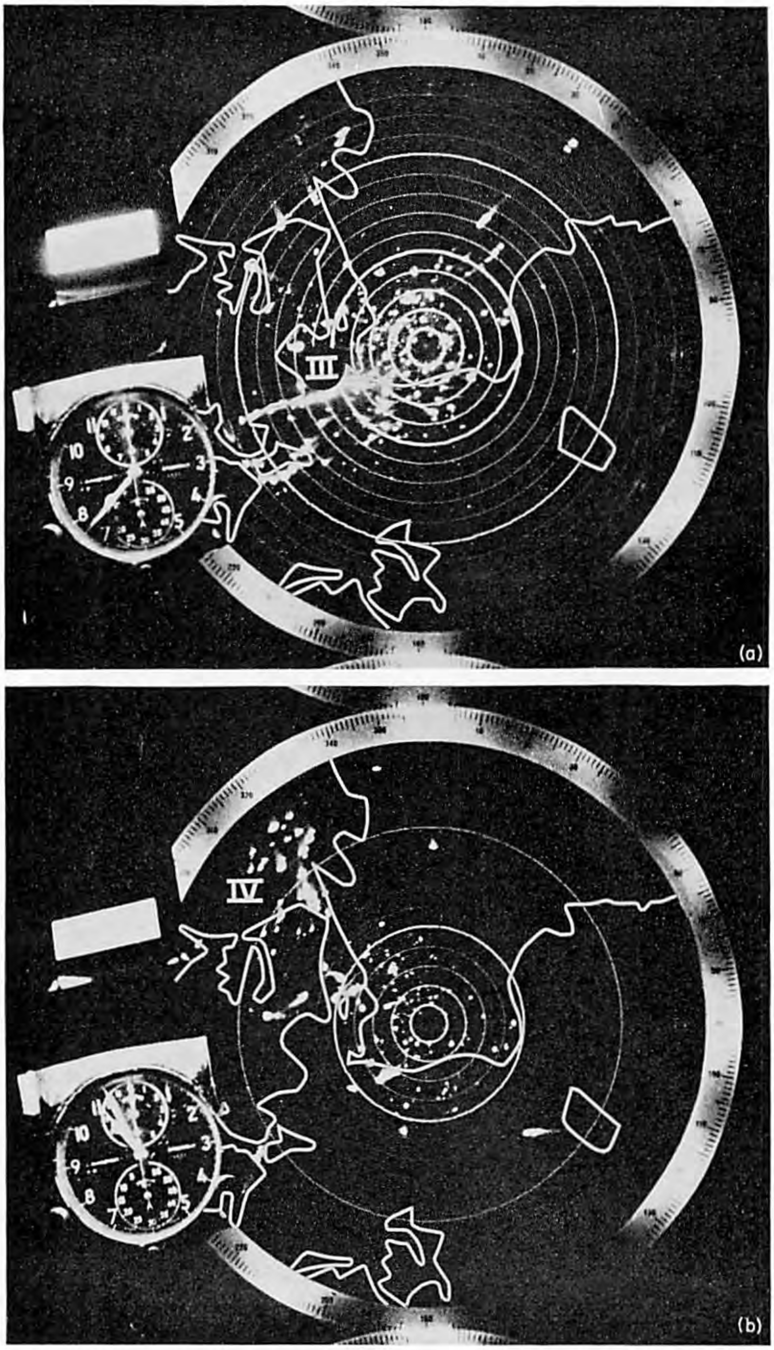

PLATE 13(a) 29 September 1971, 07.38 hrs. 'Corridor' migration of Wood Pigeons (III). Some echoes are visible outside the corridor. (b) 3 October 1971, 10.57 hrs. Large Wood Pigeon cohort (IV) travelling SSE over the Kattegatt from Norway. Note the late time of day.

When the influence of topography was at its greatest, some or all flocks departing over the south coast of Skåne were moving within a narrow corridor (Fig. 5, cf. Fig. 3). In Figure 6 the 'corridor cases' are related to wind direction and speed. It is apparent that this pattern occurred only with winds from the sector SW—ESE or with slow wind speeds, and thus was associated with slow ground speeds. In fact, mean values over the Baltic ranged between 44 and 76 km/h, and on no less than six out of eleven days the pigeons' ground speed was slower than their air speed. On days with the more usual pattern (Fig. 3) ground speeds ranged between 53 and 102 km/h, and on only two out of 22 days were they lower than the pigeons' air speed. On these two occasions strong northwesterly winds prevailed, so that any birds flying towards Stevns Klint would have faced a strong headwind component.

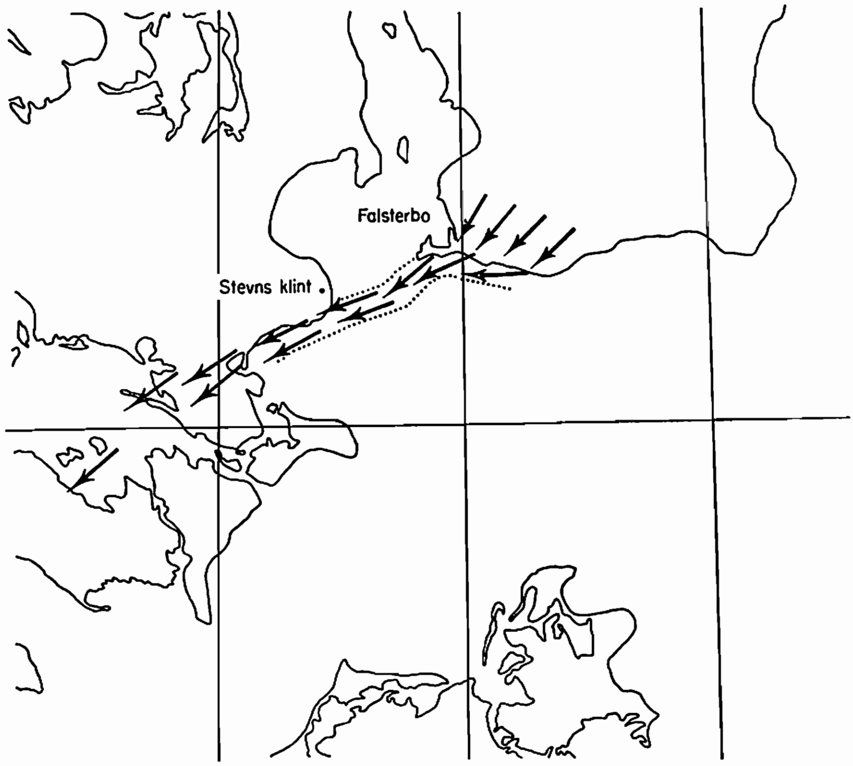

FIGURE 5. Pattern of Wood Pigeon departures from the south coast of Skåne under heavy topographical influence ('the corridor cases').

ANALYSIS OF DIRECTIONS

Track directions of migrating Wood Pigeon flocks were measured, and means were calculated, within three restricted areas, viz. inland over northern Skåne, over the Baltic Sea off the south coast of Skåne, and over the southern Kattegatt. These three areas were selected to avoid major topographical influence on the flight directions, and departures from, for example, the south coast under obvious influence of the nearest land opposite ('the corridor cases') were ignored.

Track directions at 08.00, 10.00, 12.00, 14.00 and 16.00 hrs were compared, but no consistent change of direction in relation to the time of the day were found, either over land or over sea (cf. Gehring 1963).

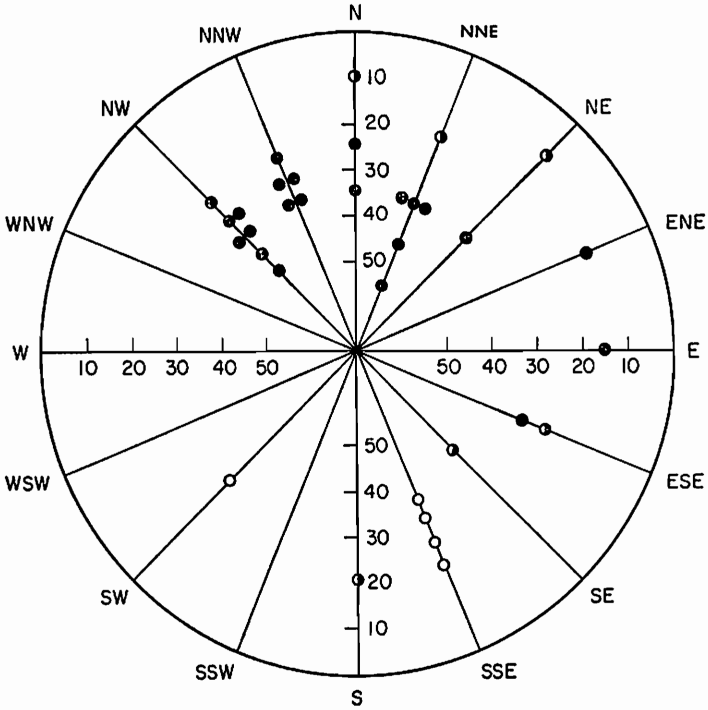

FIGURE 6. 'Corridor cases' (Fig. 5) in relation to wind direction and speed (km/h, radial axes). (○) denote that exclusively corridor movements occurred, (◑) both such movements and, simultaneously, departures towards SSW took place, (●) refer to days when SSW-departures but no corridor movements were recorded.

Mean track directions were inland 208 ± s.d. 5° ($n = 21$), over the Baltic 207 ± 11° ($n = 24$), and over the Kattegatt 189 ± 5° ($n = 14$). In these cases each value represents an average for a whole day. The direction over the Kattegatt differs significantly from the other two which are not demonstrably different. Since the same pigeons were involved inland and over the Baltic, this is according to expectation. Extremely few pigeon flocks deriving from the Kattegatt coast travelled sufficiently far south to become involved in

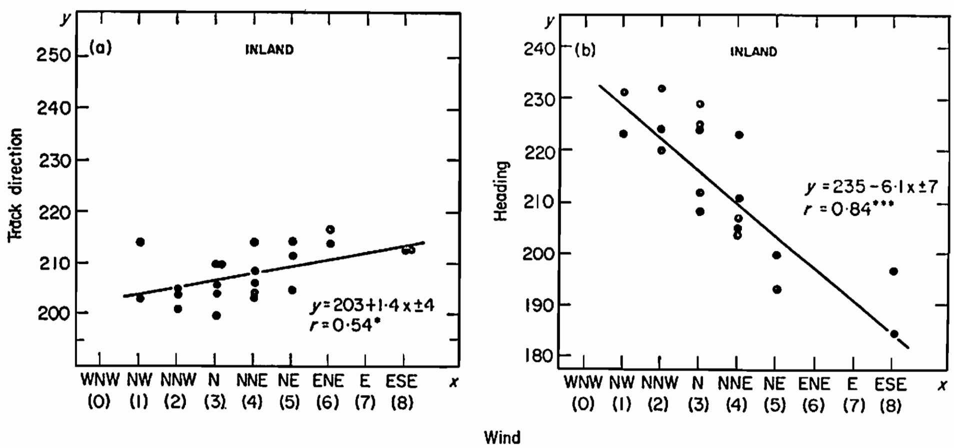

FIGURE 7. Daily mean track directions (a) and calculated headings (b) over Skåne in relation to wind. The correlations are significant: (a) $P < 0{\cdot}025$, (b) $P < 0{\cdot}001$.

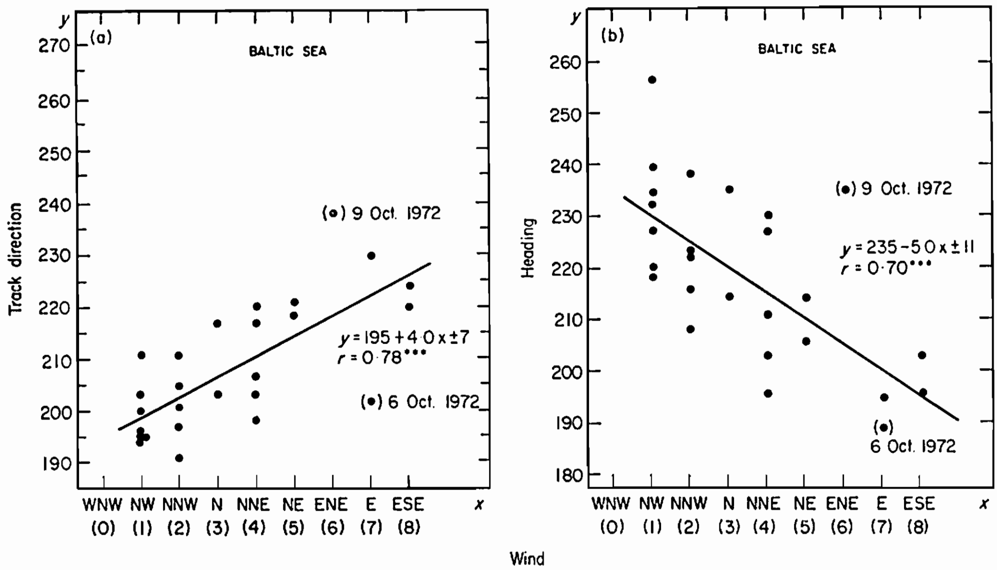

FIGURE 8(a) and (b). Same as Fig. 7 for migration over the Baltic Sea. Directions of 6 and 9 October, when fog prevailed, are omitted from the regression analyses. Correlations are significant ($P < 0{\cdot}001$).

the cohorts over the Baltic. The larger scatter of track directions over the Baltic hence cannot be ascribed to the influence of flocks from the Kattegatt, nor to those few flocks that, with unknown primary direction, entered Skåne from the east, obviously under the influence of the Blekinge coast.

Track directions varied with the wind direction (see Appendix). Northwesterly winds were associated with tracks more to the south, whereas track directions more towards the southwest were recorded with easterly winds. However, the changes in track direction with different winds are not nearly as great as would be predicted if birds were being drifted from a constant heading. For a change in wind direction of 22·5° this effect amounted to 1·4° over the land, but to 3–4° over the Kattegatt and the Baltic Sea (Figs 7(a) to 9(a)).

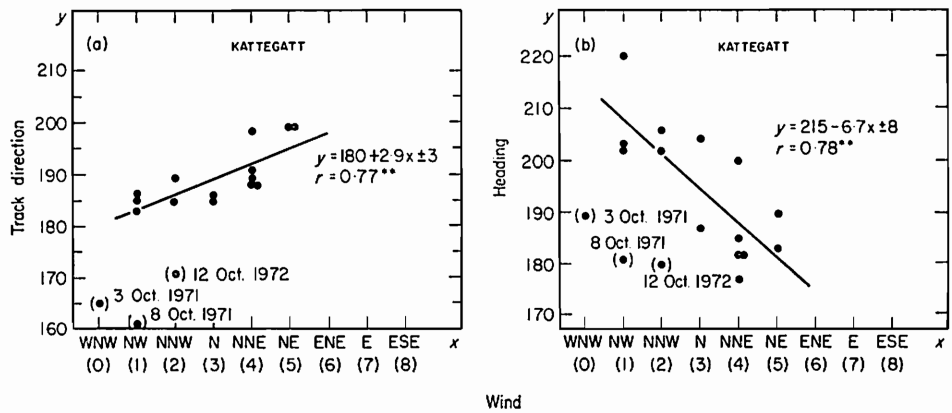

FIGURE 9(a) and (b). Same as Fig. 7 for migration over the Kattegatt. Directions for echoes arriving from Norway on 3 and 8 October 1971 and 12 October 1972 are omitted from the regression analyses. Correlations are significant ($P < 0{\cdot}005$).

Figures 7(b) to 9(b) demonstrate that birds change their headings in relation to the wind direction, i.e. with northwesterly winds the birds head more to the west and with easterly winds more to the south. A difference of 22·5° in wind direction made the birds shift their heading by 5–7° against the wind.

On three occasions (Plate 13b) tracks over the southern Kattegatt were directed east of south (161–173°). These echoes entered the display at about 10.00 hrs and obviously consisted of Wood Pigeon flocks that had departed from southern Norway in the early morning. These echo cohorts were sharply distinct from those representing departures from the west coast of Sweden. Movements towards SSE/S were never recorded over southern Zealand nor over southern Skåne but on 3 October 1971 some echoes keeping this course over the Kattegatt could be followed for a long time and were seen departing over the Baltic, significantly, however, after having changed their bearing to SSW.

DIRECTIONS OVER THE LAND

Inspection of the radar display showed clearly that track directions over Skåne were more southerly in the northwestern part of the province and more southwesterly in the northeastern part. This difference indicates that the larger the proportion of the total daily migration taking place in the west, the more southerly would the total daily mean track become, and vice versa. This prompted a closer study of mean track directions over two areas in northwestern and northeastern Skåne, respectively, designated Inland W and Inland E (see Figs 1, 10 and 11).

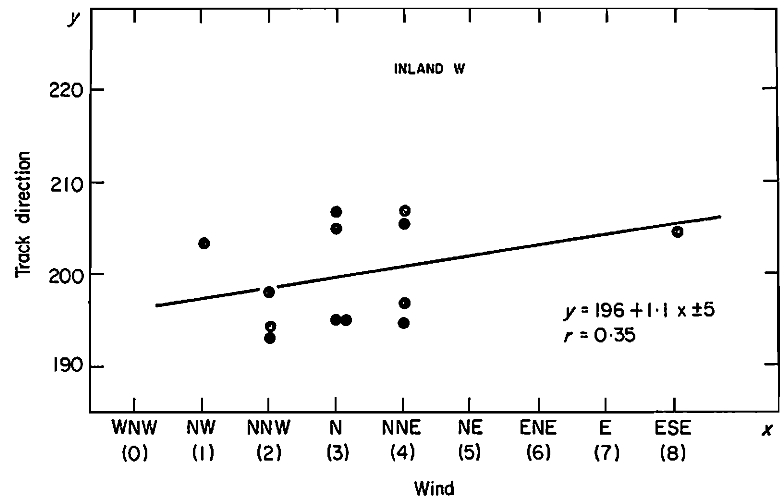

Figure 10. Daily mean track directions over Inland W (Fig. 1) in relation to wind directions. The correlation is not significant ($P > 0{\cdot}10$).

The mean track over Inland W was found to be 200 ± 5° ($n = 13$) and over Inland E 211 ± 5° ($n = 18$); n here represents the number of daily average values. The difference is highly significant. Eleven days yielded data from both Inland W and E. Restricting the comparison to these eleven days yields a mean difference of direction of 10°, that is, practically the same value as for the whole sample.

We wish to stress that, because only echoes arriving from the north and proceeding on straight courses were included, no direct influence of topographical features will have affected the result. There was probably a continuous gradient of mean track directions from the east to the west across northern Skåne. Whether track directions further west, at Gothenburg, for example, were still more southerly could not be definitely established, but we have two cases suggesting this is so; in the first, the mean track direction of Wood Pigeon flocks in the Gothenburg area was 201°, and in Inland W at the same time 206°; in the second, a value at Gothenburg of 202° was measured simultaneously with 207° in Inland W and 212° in Inland E.

As borne out by Figures 10 and 11, track directions over Inland W and E were not demonstrably influenced by prevailing winds. In other words, wind compensation appears to have been complete.

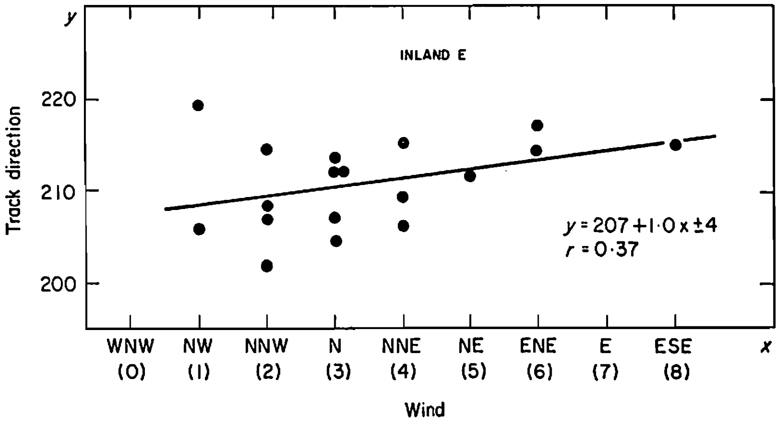

FIGURE 11. Daily mean track directions over Inland E (Fig. 1) in relation to wind directions. The correlation is not significant ($P = 0{\cdot}10$).

DIRECTIONS OVER THE SEA

Figures 7–9 have shown that the variation of daily mean track directions over the sea under the influence of winds was two or three times larger than over the land. Examples of the migratory patterns over the Baltic under different wind conditions are illustrated in Figure 12. The majority of Wood Pigeon flocks arriving over northern Skåne later departed over the south coast and the Baltic Sea. Cohorts inland and over the Baltic thus were identical, and so the greater effect of wind on flight directions over the sea can scarcely be attributed to anything but real wind deflection (drift) and hence to incomplete compensation. This is further supported by subtracting the daily mean track value over the land from that over the Baltic Sea, and relating the resulting difference to wind direction (Fig. 13). Usually only small changes of track direction took place in the course of the day. Occasionally, however, such changes were of larger extent. The most marked case was on 12 October 1972. On this day, while no changes were recorded over land, the track direction over the Baltic shifted 20° southwards. One likely explanation is that cohorts with different primary directions succeeded each other. The pigeons moving late in the day arrived from the north according to the usual pattern, but the massive morning movement consisted of birds starting from resting places in the southwestern corner of Skåne, for which no measure of track direction over land could be made. Thus, on this day, the reaction to the wind was compared in two possibly different (in terms of primary direction) cohorts, whilst on all other days the reactions of the same pigeons over the land and the sea were compared.

We therefore conclude that the total deflective effect of 3–4° over the sea for a wind shift of 22·5° is partly caused by changes in track direction having occurred already over the land and partly by true wind deflection (drift) and thus incomplete compensation. Drift was found to amount to approximately 2° for each 22·5° of change of wind direction, that is to say, the birds tended to underestimate the deflective effect of the wind force.

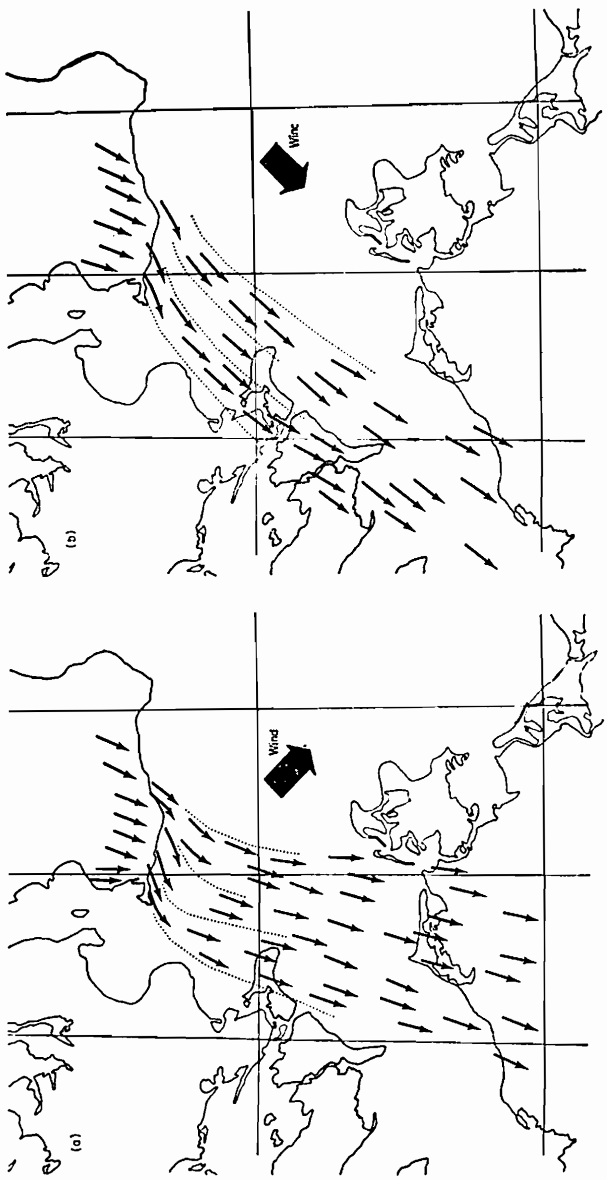

FIGURE 12(a) and (b). Principal patterns of Wood Pigeon migration over the Baltic Sea under northwesterly (a) and northeasterly (b) winds.

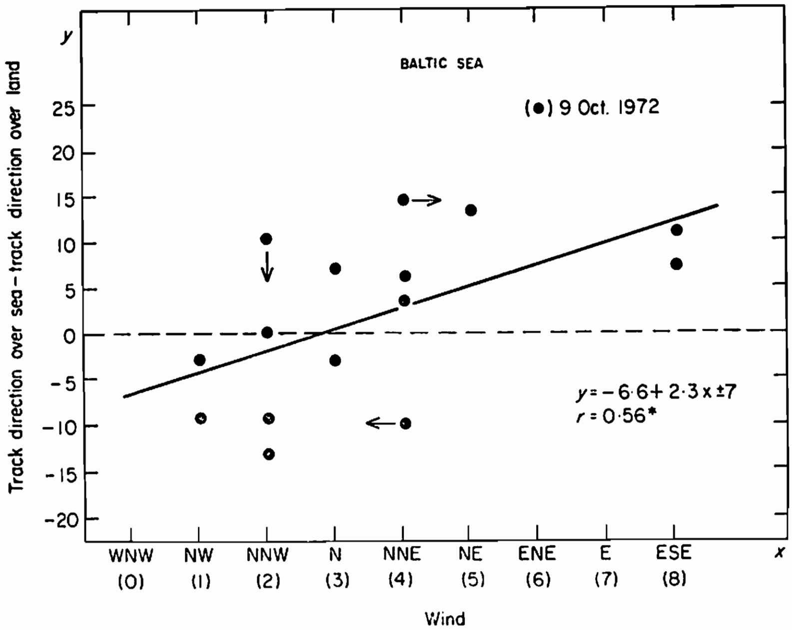

FIGURE 13. Differences between track directions over the Baltic and over Skåne in relation to wind direction. Values from 9 October 1972, with fog over the Baltic, are omitted from the regression analyses. The correlation is significant ($P < 0{\cdot}025$). Horizontal arrows indicate two cases when during the day the wind changed in the direction of the arrows. The vertical arrow indicates a case when the mean track direction over the sea changed according to the arrow's direction. See text, p. 533.

EFFECTS OF FOG

Conspicuous aberrations of typical migration patterns (as outlined above) were recorded on three occasions, all of which were associated with fog reducing visibility to less than 1 km over large areas. The first occasion was on 6 October 1972. Echoes arrived over middle Blekinge around 07.00 hrs, later to cross Skåne and the Baltic as illustrated in Figure 14(a). Only few echoes arrived from the interior further north than Blekinge. All echoes gradually changed their courses over Skåne, and no reactions at all to topographical features were discernible.

The second instance was on 8 October 1972, when fog covered the inland of northern Skåne, while visibility in southern Skåne was a good deal better (about 15 km). No divergences from the usual pattern were seen in the south, but inland migratory activity was low and restricted to the eastern part of the province. Track directions were variable with a mean of 232°, most echoes arriving from Blekinge, and moving on a much more westerly bearing than expected.

The final case of widespread fog was on 9 October 1972. The migration pattern of this day is illustrated in Figure 14(b). Large numbers of flocks departed over the Baltic Sea from Skåne during a short interval very early in the morning, suggesting that these birds took off from areas near the coast in southwestern Skåne. The birds paid little if any attention to topographical features and moved on courses more towards the west (mean track 238°) than on any other occasion, excepting cohorts under direct influence of deflection lines.

Regardless whether the Wood Pigeons were flying within or above the fog belt (cf. Gehring 1963), they were certainly unable to use landmarks for their orientation. The aberrations of their behaviour must be seen in this light.

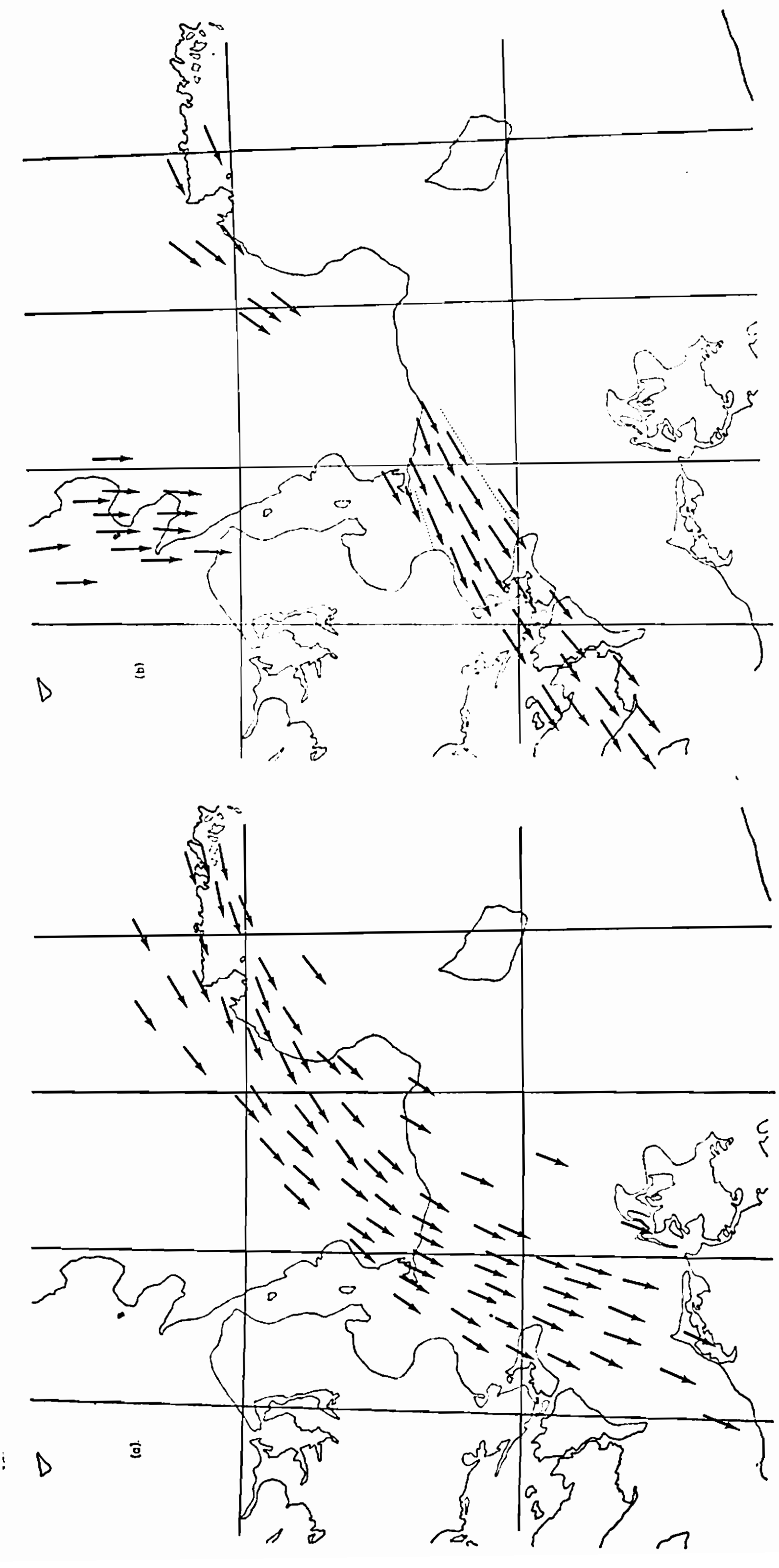

FIGURE 14(a) and (b). Geographical patterns of Wood Pigeon migration on days with extensive fog. (a) 6 October 1972. (b) 9 October 1972.

DISCUSSION

REACTIONS TO COASTLINES

Very large numbers of migrating Wood Pigeons annually are recorded by the observers at Falsterbo bird station (Ulfstrand *et al.* 1974), and Rudebeck (1964) listed the species among those which probably are most strongly influenced by topographical features. The radar display offers a better opportunity than field observations to study the reactions of the pigeons to the coastline, since their flight can be followed over much longer distances. We have been able to examine this phenomenon in three different situations (Figs 1 and 3).

The coast of Blekinge and the south coast of Skåne both run almost due east–west, but the birds obviously reacted in different ways. Wood Pigeon flocks were strongly affected by the Blekinge coast and most followed it, either over the land or off shore parallel to the coastline. The south coast of Skåne, on the other hand, usually had only a transient effect on the flight paths of pigeon flocks which on no more than a few occasions followed it for more than 15 km. On present evidence we can only speculate on the reasons for this discrepancy. A difference in primary direction between the birds involved would modify the leading line effect, which is partly dependent on the angle between birds' tracks and the coastline (Geyr 1949, Rudebeck 1950). On the other hand, from altitudes of 500–1200 m, the flight height of flocks observed from our aircraft, the pigeons must have an extremely wide range of vision, particularly since peak migration usually takes place under clear skies and good visibility. From the Blekinge coast, they may at an early stage see the landmass of Skåne, and be aware that they are not immediately facing an unavoidable sea-crossing, whereas over much of Skåne they will see water all around the horizon. It does not seem unreasonable to suppose that the prospect of even a short sea-crossing may affect the birds strongly; their behaviour when approaching a coastline at more or less a right angle is sometimes extremely hesitant even when they obviously can see land on the opposite side of a narrow sound.

The reaction of migrating pigeons to the Swedish west coast could be examined over a large area, owing to the cooperation between radar stations at Gothenburg and in Skåne. A good many flocks followed the coast, over the land or off shore, for distances up to 200 km. Flying south from Gothenburg, the birds will have the Kattegatt on their right—an expanse of sea too wide to allow them to see across to Denmark. Further south, only the Sound separates Sweden from Denmark, and where this is at its narrowest, most Wood Pigeon flocks break off from Sweden and cross to Zealand. Quite a number, however, do not leave the land even at this site, but veer towards the southeast and continue along the coast of Skåne. A few flocks reach as far south as the Falsterbo peninsula before departing over the sea, but most cross further north, mainly where they 'get trapped' over promontories or where islands in the Sound apparently serve as stepping-stones.

The reaction of the Wood Pigeon flocks to the coastline differed from day to day, at least partly in relation to meteorological factors (Rudebeck 1950). The deflective effect of the south coast of Skåne was found to be greatest when the birds were approaching it against a relatively strong headwind component, or under calm conditions. In both cases, clearly, the pigeons' ground speed was comparatively low. In many birds it has been demonstrated that under headwinds migration tends to take place at low altitude and that the leading line effect attains a maximum (Gruys-Casimir 1965). Whether this is a reaction to the headwind and ground speed as such, or to the low flight altitude, is an open question. Speculatively one might mention the possibility that a stimulus suitable for integrating the important variables of speed and altitude would be the bird's apparent speed of movement in relation to the ground.

Schnell (quoted in Bellrose 1967) found that hirundinids changed their true air speed in relation to wind direction and velocity, and Bellrose (1967) and Bruderer (1971) provided additional evidence for the same thing in other migrating passerines. Clearly birds are capable of reacting to wind conditions when aloft. However, in the Wood Pigeons we found no correlation between true air speed and ground speed.

REACTIONS TO FOG

Days with fog provided evidence that Wood Pigeons sometimes start or continue their migratory flight without being able to see the terrain overflown (cf. Gehring 1963). Track directions differed from those expected under prevailing wind conditions in good visibility. This strongly suggests that landmarks other than coastlines play a role in the determination of flight paths. On the other hand, the behaviour of migrating flocks also showed that the birds were capable of keeping an approximately correct direction in the absence of direct visual contact with the ground (cf. Bellrose, 1967, for nocturnal migrants and Keeton, 1969, and Schmidt–Koenig, 1973, for domestic pigeons).

TRACK DIRECTIONS AND MIGRATORY GOALS

Rendahl (1965) summarized the ringing recoveries of Fenno-Scandian Wood Pigeons, showing that the winter quarters of birds from Norway, Sweden and Finland are the same and include southwestern France, Spain and Portugal. Very large numbers of Wood Pigeons pass through and rest in the French provinces of Girondes, Les Landes and Basses-Pyrénées, but most birds proceed to winter in the Iberian peninsula, chiefly its central and western parts. A straight line from Falsterbo to the centre of these winter quarters has a bearing of about 218°, and will run across Europe near the cities of Hamburg, Bonn, Luxembourg, Limoges and Biarritz. The ringing recoveries are concentrated within a surprisingly narrow zone along this transect, and are almost wanting from the coasts of the North Sea and the English Channel as well as from more easterly areas, for example, Switzerland.

The mean track over Skåne was 208°. If the pigeons were to proceed on their migratory flight across Europe on this bearing, they would end up in southeasternmost France and northeastern Spain (about Barcelona). We therefore conclude that the Scandinavian Wood Pigeons change their primary direction during the journey between their breeding areas and their winter quarters. Perdeck (1970) found a similar pattern in Scandinavian Chaffinches *Fringilla coelebs*.

If Norwegian and central to north Swedish Wood Pigeons were to travel to their winter quaters on a straight line ('Idealzugrichtung' in Schüz's, 1971, terminology), they would have to undertake extensive sea-crossings. It has generally been considered that this is hazardous for land birds (cf. Lack 1959), even though evidence is accumulating that birds cover enormous distances in one step during their migration (e.g., Moreau 1972, Nisbet & Medway 1972). However, we showed above that the Wood Pigeons lost the capacity of compensating accurately for wind drift when flying over the sea; this would seem to be a good reason for staying within sight of land as long as possible.

PRIMARY DIRECTION AND WIND EFFECTS

Analysis of the daily mean track directions over Inland E and W in northern Skåne revealed no correlation with wind direction (Figs 10 and 11). The daily mean track direction over the whole land area, however, showed a significant correlation with wind direction (Fig. 7). Drift is ruled out by the complete wind compensation demonstrated over Inland E and W. The alternative explanation is that different proportions of birds with different primary directions were participating in the movements observed.

The mean track directions at Inland E and W differed significantly, and it appears that the ratio of birds between the western and eastern zones changed in relation to the prevailing wind (Fig. 15). Clearly northwesterly winds were associated with a high migratory activity over Inland W and easterly winds with proportionally high activity over Inland E. A comparable relationship was also illustrated for wider areas in Figure 4, where migratory cohorts travelling over the Kattegatt and the Baltic, respectively, were used for the comparison.

Thus, the different flight directions of birds over Inland W and E, together with the different proportion of the total migration passing over one area or the other from day to day (in response to varying wind directions) may account for the correlation established in Figure 7(a). Figure 15 provides supporting evidence that this is at least part of the truth, i.e., a case of 'pseudodrift' (see Introduction).

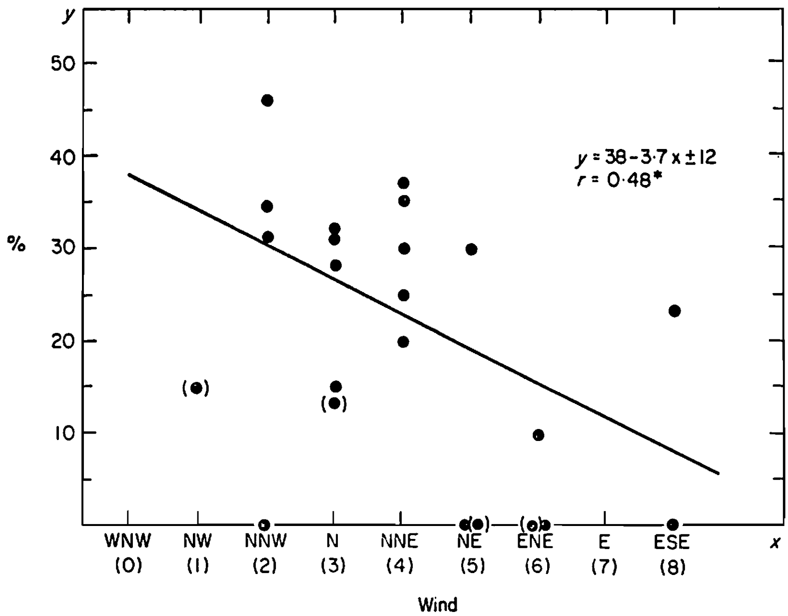

FIGURE 15. Proportion between echoes arriving over a 40 km wide transect in the western inland of Skåne and echoes arriving over the whole width of Skåne in relation to wind direction. Proportions calculated from <100 echoes are bracketed and omitted from the regression analysis. The correlation is significant ($P < 0{\cdot}05$).

Over the sea conditions are different, and the direction of Wood Pigeon flocks was affected by previous track directions over the land and by true wind deflection (drift). The observations fit the hypothesis that the amount of drift was linearly proportional to the angle between the bird's heading and track direction. The difference in behaviour may be explained by the lack of visual orientation cues (other than celestial) over the sea. Dependence on such cues for the detailed choice of flight paths was also suggested by the behaviour of the Wood Pigeons when fog prevented them from seeing the terrain overflown.

After the passage of a cold front the migrating birds have the benefit of strong tailwinds (cf. Svärdson 1953, Nisbet 1975, Lack 1969). Especially when performing long journeys over sea the advantages of a high ground speed seem obvious. Northerly winds are not frequent in southern Scandinavia, and birds often will have to wait a long time for such conditions. Both Wood Pigeons, as described above, and other birds (e.g., Drury & Keith 1962, Alerstam & Ulfstrand 1972, Alerstam *et al.* 1973) move in large numbers on these relatively infrequent occasions, and the vast majority of the population involved may migrate on one or a very few days. Too strict dependence on tailwind conditions, however, might lead to intolerable delay, and the Wood Pigeons on some occasions departed without the benefit of northerly winds (the corridor cases). Rudebeck (1950) demonstrated that for soaring birds of prey the threshold for migratory departure at Falsterbo would sink during periods of unfavourable weather, and in many birds low-altitude migration into headwinds was frequent.

Wood Pigeons only undertake the longest sea-crossing during their whole migration, viz. that across the Kattegatt, in strong tailwinds. Their behaviour when arriving at the coast in many instances clearly revealed their reluctance to depart from land. The guiding line effect reduced the extent of sea to be crossed by the birds. We have pointed out one possible drawback of flying over the sea, namely the less accurate compensation for wind displacement.

ACKNOWLEDGMENTS

This paper is based on work carried out as a joint undertaking by the Swedish Air Force, the Swedish Civil Aviation Board, the Department of Animal Ecology at the University of Lund, and Skåne's Ornithological Society including Falsterbo Bird Station. The authors are grateful to all these authorities and institutes and many of their officers for support and advice. We wish to thank all the field observers, the aircraft pilots, and the radar operators for their careful work. We are particularly indebted to Mr Gunnar Roos, research leader at Falsterbo Bird Station, for valuable information and much assistance.

SUMMARY

The migration of Wood Pigeons in southern Scandinavia was studied from 21 September to 10 October 1971 and from 16 September to 15 November 1972 using radar stations supplemented with observations from an aircraft and a network of ground observers. By far the largest quantities of Wood Pigeons migrated after cold front passages with northwesterly to northeasterly tailwinds. Most birds departed on a few days, apparently as a consequence of strong preference for tailwind situations.

With northwesterly winds a proportionately high migratory activity was recorded in the Kattegatt area. With northeasterly winds activity was higher in the Baltic area. This allowed the Wood Pigeons to make maximal use of the tailwind component, and their ground speed usually exceeded 80 km/h. The calculated mean air speed was 60 km/h. Their dependence on tailwind was particularly strong when the birds were engaging in long sea-crossings, such as across the Kattegatt.

Different coastlines affected the geographical pattern of migration in different ways. Frequently Wood Pigeon flocks flew almost parallel to the coast but some distance off shore, until they finally departed. The deflective force of coastlines was greatest when the birds' ground speed was low, that is, under headwind conditions or in calm weather.

Mean track directions measured over two areas in northern Skåne, called Inland W and Inland E, situated about 60 km apart, differed by 11°, those over the western area being directed more to the south than those over the eastern. No significant correlation with wind directions was found in these areas. Combining data from the whole land area, however, track directions were found to vary from day to day in significant correlation to the wind direction.

Mean track directions over the Baltic agreed with those over Skåne, but both differed significantly from those over the Kattegatt. Both over the Baltic and over the Kattegatt directions were significantly correlated with wind directions, and showed greater variation than track directions over land. Daily track differences over the Baltic resulted both from differences taking place over the land, and from real wind deflection (drift). Both over the land and over the sea heading directions were correlated with wind directions, suggesting compensatory efforts on the part of the birds.

On three days extensive fog covered much of the study area. Wood Pigeons continued to migrate, but certain aberrations in their behaviour were noted.

Over land migration was relatively heavier in the west with northwesterly winds and in the east with northeasterly winds. The correlation demonstrated between wind direction and the mean track direction was based upon the fact that populations with different inherent primary directions made up different proportions of the migrating cohorts under different wind conditions (pseudo-drift).

The incomplete compensation for wind deflection over the sea is ascribed to the lack of visual orientation cues. The more accurate orientation possible over land suggests one reason for the birds' reluctance to flights across the open sea.

When mean track directions of Wood Pigeons in different parts of southern Scandinavia were related to the migratory goals of these birds, it was found that they have to change their primary direction in the course of their journey from breeding to wintering areas.

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APPENDIX

The track directions and headings for three areas are plotted against wind bearings in Figures 7–9. We feel justified in using linear regressions in the analysis of the data for the following reasons:

i. When the wind speed and the birds' true air speed are the same, the influence of wind on the direction of the birds is directly proportional to the angle between the wind and the heading vectors. During the study periods, wind velocities between 20 and 40 km/h dominated. Since the true mean air speed of the pigeon flocks was 60 km/h, wind and true air speeds may legitimately be regarded as of the same magnitude, and the inaccuracy involved in the assumption of a linear regression is relatively unimportant.

ii. Since we have no reason to suppose that wind speeds are in any way correlated with wind directions, we feel justified in using a linear regression of track direction on wind direction and to ignore provisionally the effect of the wind speed.

iii. Still we wish to explore the consequences of including the wind speed as a factor in the calculations. One way is to use the regression of track directions on the crosswind (to the birds' track direction) component. Another way is to plot track directions on the angle between the birds' heading and track direction; this angle corresponds to the amount of drift when the bird flies on a fixed heading and to the amount of compensation when keeping a fixed track direction. The latter procedure takes the birds' true air speed into account; this is an advantage although, in this particular case, the air speed is probably constant. Using the same data as in Figures 7(a), 8(a) and 9(a), we have arrived at the following equations (y = track direction, x = track direction minus heading direction; thus x will be negative when heading direction is to the right of track direction and positive when heading direction is to the left.):

Inland	$y = 208{\cdot}0 + 0{\cdot}16x \pm 3{\cdot}7$ ($r = 0{\cdot}54$, $P < 0{\cdot}05$)
Baltic	$y = 211{\cdot}7 + 0{\cdot}36x \pm 7{\cdot}9$ ($r = 0{\cdot}68$, $P < 0{\cdot}01$)
Kattegatt	$y = 191{\cdot}7 + 0{\cdot}26x \pm 5{\cdot}2$ ($r = 0{\cdot}59$, $P < 0{\cdot}05$)

The important finding is that the relations between the regression coefficients in these equations are closely similar to those between the corresponding coefficients in Figures 7(a), 8(a) and 9(a). Thus, the addition of wind speed in the calculations failed to advance the analysis beyond the stage attained in Figures 7–9. Furthermore, the wind speed data are less satisfactory than the measurements of direction and introduce an error in the calculations leading to, in this case, a lowering of the levels of significance. We have therefore based our discussion on relationships between flight directions and wind directions exclusively.

Report no. 61 *from Falsterbo Bird Station, Thomas Alerstam & Staffan Ulfstrand, Ecology Building, Helgonav.* 5, *S*-223 62 *Lund, Sweden*