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Some Aspects on the Directing and Releasing Influence of Wind Conditions on Visible Bird Migration[1]

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A survey of recent literature on bird migration reveals a lack of unanimity in the opinions of different authors concerning the factors releasing bird migration and the general effects of wind conditions upon visible bird migration. Disregarding the profound factors of a physiological nature, such as metabolic changes etc., several meteorological factors have been assumed to play more or less important roles for bird migration and its release, as will appear after even a brief review of modern literature. For lack of space, this review cannot be carried through on this occasion.

However, the data upon which the different hypotheses are based have been collected under widely different circumstances. First, there may be a rather sharp limit between diurnal and nocturnal migration. Second, the geographical positions of the bird stations from where most of the underlying material comes are widely different, and so is the topography of their environments. The result obtained is of course also deeply affected by the specific composition of the migrating birds. In this communication, the discussion refers to diurnally migrating birds, such as pigeons, birds of prey, and certain passerines.

A purpose of this paper is to call attention to the importance of the geographical position of the observation locality and of the wind conditions for the results obtained in studies on bird migration. This will be attempted through considering a model situation, *i. e.* an imaginary, schematic geographical area without minor topographical features, with all the coasts cut sharp, and without islands in sight from the coast-line. Far away, off the west coast of the land-mass, we shall, however, introduce a small oceanic island. We shall consider the bird migration at three separate localities, *viz.* A) on the small oceanic island, B) at the south-west corner of the land-mass, and C) at an arbitrary locality in the central part of the area.

The birds migrating through this area are to be regarded as completely uniform: we shall imagine all to possess a south-westerly primary direction = standard direction (*cf.* GEYR VON SCHWEPPENBURG 1949), *i. e.* when not influenced by any topo-

[1] Report from the Falsterbo bird Station No. 6.

graphical or atmospherical or other similar factors, they will keep a south-westerly course. They are further assumed to be affected by the only guiding-lines existing, *i. e.* the coasts.

Which external factors need be considered to be of importance for the course of the migrating birds over the area? First, there are the coasts. The flight-paths will converge towards the south-west corner because of the guiding-line effect, as may be exemplified from investigations in many parts of the world. Second, wind conditions will deeply influence the flight-lines. No variable factor has, according to my opinion, so far been discovered to be comparable to wind in importance for the course of migrating birds, and I shall hence restrict myself to a consideration of this factor.

It is true that birds tend to counteract the influence of wind upon their flight-paths. This reaction reduces somewhat the deviating effects of wind, but assuredly it does not render wind conditions insignificant for the course of migrating birds (see *e. g.* RUDEBECK 1950).

Let us now consider the passage of the migrating birds over our schematic area under a selection of different wind conditions. The facts on which the following discussion is based have only partly been published, in several different contexts. The sources cannot possibly be reviewed in this brief communication. I would like, however, to draw the attention to three investigations of great interest in this connection, *viz.* the account of the behaviour of the birds of prey on passage over south-west Scania (Skåne, SW. Sweden) by RUDEBECK (1950), the researches of Dutch ornithologists on the migration of the Chaffinch *(Fringilla coelebs)* over the Netherlands (DEELDER 1949), and some recently published observations on the course of migrating birds over the Danish Islands (BRUUN & SCHELDE 1957). The relevant facts are schematically represented in Fig. 1.

1. In *calm weather* only topography will affect the flight-lines over the area. The theoretical uniform distribution will be disturbed only by the guiding-lines of the coasts. Hence, there will be a concentration of migrating birds in the south-west corner. The absolute figures will be much higher at B than at A and C. Since in calm weather migration will generally proceed at some altitude, numbers are to be expected to be only moderately high at B, for as is well known, birds flying high are less influenced by guiding-lines than are low-flying birds.

2. With *head-wind* of moderate strength migration will attain maximal intensity at B, and the same would apply also to C under the assumption that head-wind has a directly stimulating effect on the release of bird migration. Guiding-line efficiency will be very strong, because the birds fly rather low. At A, consequently, there will be very few birds. With rising wind velocities migration will be still stronger at B in comparison to A and C, but the absolute figures will gradually decrease. This is because strong winds gradually inhibit the migration, whilst guiding-line efficiency will be still stronger. With falling wind velocities conditions will gradually approach those prevailing in calm weather.

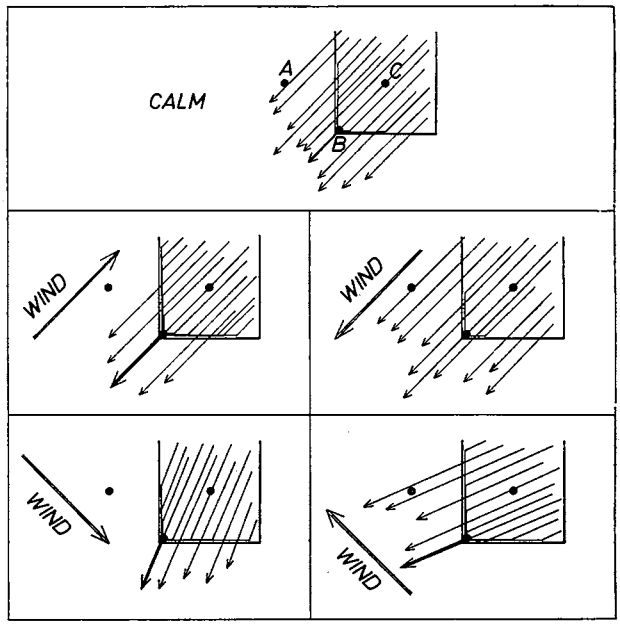

Fig. 1. Schematic representation of the course of bird migration over the imaginary land-mass. See text.

3. With *tail-wind,* conditions change fundamentally. Guiding-line efficiency will be low because of the rising average height of the migrating birds. The birds will thus pass out over the sea on a more »broad-front» migration. Comparatively low figures will be recorded at B, and also at C figures will be lower than with head-wind. A, on the other hand, will get relatively high figures. With rising wind strength migration intensity drops more or less quickly, whilst with falling wind velocities, conditions of course gradually approach those prevailing in calm weather. It should be borne in mind, though, that it is under these circumstances that birds are most likely to be overlooked. It is very difficult indeed to assess the importance of this source of error.

4. Let us now consider a situation with winds coming in from the *north-west, i. e.* at an angle of 90° in relation to the primary direction inherent in the birds. The paths of the migrants will be affected by this wind, hence the migration is deviated. Additional to this effect is the circumstance that the birds will strike the coast-lines at new angles, a fact of great importance for their reactions. The combined effect will be that there will be very few if any birds at A and moderate numbers at B and C. Strong winds will of course have greater effect, whilst very light winds will cause little disturbance.

5. Side-winds from the opposite direction, *i. e.* the *south-east,* will in principle cause similar effects. A sharp difference in the resulting distribution of the migrating

birds is, however, that relatively many birds are to be expected on the island observatory. From the view-point of an observer on this island, this may be described as a kind of drift migration (*cf.* WILLIAMSON 1955 and other works).

Let me take but one example, partly from RUDEBECK's (1950) work at Falsterbo, partly from a previous study by the present author (ULFSTRAND 1958). In years with predominant south-easterly to easterly winds during the migration period of the Honey-buzzard *(Pernis apivorus)* this species obtains relatively low annual totals at the bird observatory at Falsterbo (Scania, Sweden), but in autumns with persistent westerly to north-westerly winds the annual figures are much higher. It was shown by RUDEBECK *(op. cit.)* that this is because in the former case the birds are drifted off their path and pass over Zealand (Sjaelland, Denmark) to the west of Öresund instead. It appears that southerly and south-easterly winds have a much stronger deviating effect than northerly and north-easterly winds. This can probably be explained through the different topographical properties of the Scanian coasts. The west coast is indented by many bays and there are a number of capes protruding towards the west and south-west. Also the migrating birds will normally be able to see the opposite coast before leaving Swedish land. The south coast, on the other hand, is cut sharp and there are neither bays nor promontories, and finally the distance to the coast on the far side of the water surface is much greater. The opposite land is most often out of sight for the migrating birds when they are passing over the Scanian coast-line.

Let us summarize the above discussion and see how migration intensity will vary at the three observatories during a series of days with different wind conditions. The suggestions made above are plotted in Table 1, in which migration intensity is represented by a scale ranging from zero to five.

TABLE 1

Relative intensity of visible migration at the three observatories A, B and C during different wind conditions. The absolute figures are very different for A, B and C.

	calm	head-wind			tail-wind		NW	SE
		l.	m.	s.	m.	s.	m.	m.
A (island)	xxxx	xx	x	0	xxxx	xxx	0	xxxxx
B (corner)	xx	xxx	xxxxx	xxx	xx	x	xx	xx
C (central)	xx	xxxx	xxxxx	xx	xxx	xx	xx	xx

l. = light wind
m. = moderate wind
s. = strong wind

It is apparent from the table — which is, after all, but a summary of the foregoing discussion — that the pictures obtained at the three different localities are not in complete agreement with each other. Considerable discrepancies exist. Workers at the three stations would arrive at widely divergent conclusions about the relationship between wind conditions and bird migration and about the meteorological

factors releasing bird migration. The insight obtained through the above discussion is that it is very difficult, even impossible to make general decisions on many problems of bird migration from studies at one place only. This is especially true if studies are being carried out at localities situated on prominent guiding-lines or on an isolated island where the birds will appear only under special circumstances. One has constantly to keep in mind this dual aspect of bird migration: what caused the birds to start their migration flight, and what made them pass this or that way? It would appear that the best localities for investigations of these problems are inland places with the most uniform environments possible.

Now, is the imaginary area and its bird migration as described above relevant for real conditions? I believe that that is the case. We may transfer the simplified picture outlined above to several European districts. The model was constructed chiefly on the basis of experiences in the south part of Sweden, which has, however, no observatory »A», a very notable observatory »B» (*i. e.* Falsterbo), and where I have carried out field investigations on a locality corresponding to »C». No doubt, however, our picture may be transferred to the North Sea area with Helgoland as »A» and probably some Danish and German capes showing »B» conditions. Indeed, I think that the whole of western Europe may in a general way correspond to the schematic area outlined above with certain islands to the west of the European continent representing »A». Some promontories on the sea-border will exhibit conditions comparable to our locality »B».

Assuredly, the combined effects of topographical and meteorological factors involve a complex problem. I think that some advance in our concepts may perhaps be gained by considering model situations where different factors are analysed apart from each other. The discussion has demonstrated that the geographical and topographical characteristics of the observation spot and its environment exert a considerable influence on the picture of the process of bird migration obtained.

Several studies have been carried out concerning the influence of wind conditions on bird migration: its course, and how this is affected by the wind. This is far from saying that this aspect has been exhausted. On the contrary, much remains to be done. Now, what might be said in this connection concerning the influence of wind on the release of migration? First, I would like to emphasize once again that generally no broad conclusions on meteorological stimuli releasing bird migration should be drawn from investigations performed at only one locality. This is because of the fact that the bird »avalanches» (SVÄRDSON 1953) as recorded at a bird station of traditional site are but a selection of all the avalanches in the given region. Some will remain unnoticed or be strongly underestimated because of the effects of the wind on the bird stream. For instance, it would appear justifiable to assume a positive effect of head-winds on the migration release in birds of prey at Falsterbo, but such a conclusion is unwarranted (ULFSTRAND 1958). I would not say that head-winds do *not* exert such an influence, only that the material collected at this place alone does not permit definite conclusions. It might be that head-winds merely contri-

bute to the concentration of flight-lines and that they are of no great significance in releasing migration. However, investigations in other localities have demonstrated with some probability that head-winds under some circumstances do have a directly stimulating effect on migration and that is why, in the discussion presented above, I have supposed migration intensity to be maximal with head-winds. A more definite solution of the problem may be obtained from studies at suitable localities, where the concentrating effects of wind are of less importance than they are at, for instance, Falsterbo. Some of the assumptions made by different authors that there is a positive correlation between head-winds and migration release seem to have been unwarranted, for very often the field work was performed where migration is likely to be especially intense with head-winds, but this for purely topographical reasons.

Parenthetically, it should be pointed out that the conclusions arrived at in the above discussion would not be invalidated if it is proved that there is no such correlation between head-winds and migration release.

It is very probable that many factors have contributary effects as stimuli releasing bird migration. Wind may well be one of them. I believe that some advance in our views on bird migration might be gained through an ethological approach to the various problems. It is, I think, quite in agreement with modern ethological considerations that such a complex behaviour pattern as bird migration should be controlled by several releasing mechanisms and that it should be released only under rather special external (and internal) circumstances. If only one factor were to be responsible for the release of migration, the chances for a successful conclusion to migrational adventures would surely be reduced. Only when a certain accumulation of factors all with positive effects is at hand, migration starts. Some of these releasing stimuli are well known: temperature, visibility, thermal air-currents, physiological status and many other factors. All of them cooperate, but sometimes one factor is the chief one, sometimes another. Many other factors are to be assumed to be of importance, such as wind conditions and the presence of species companions in gregarious species. One may turn the problem upside down and direct one's attention in the first place to the factors inhibiting bird migration, an aspect suggested by NISBET (1957). Birds with badly balanced releasing mechanisms will be at a strong selective disadvantage, whilst well adjusted individuals will have much greater chances of survival. To be well adjusted to migrational performances is a matter of life or death for migratory birds.

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