Visual diurnal migratory movements

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(Med et dansk resumé: Synlige dagtrækbevægelser)

CONTENTS

INTRODUCTION

Migration is composed of various reactions. It is nescessary that these reactions be recognized if one is to view them in proper perspective as part of a system. When viewing migration from the point of view of a whole, composed of various parts, the proposal of ULFSTRAND (1960) to apply ethological terminology to avian migration seems logical. The following discussion thus incorporates currently accepted ethological terminology wherever possible.

This paper is mainly based upon observations made by the author at geographically diverse sites in Denmark. Included are data from 600 days (mostly spring) at Knudshoved, East Funen. 120 fall days at Hesselø Is. in the Kattegat, 50 spring days near Blåvand, West Jutland and 17 days in spring from Ringsted, Mid-Zealand. Thus the author himself made his observations of diurnal migratory movements both on sea shores, at an isolated island, and inland.

Observations began just before sunrise and lasted two to six (usually three to five) hours. Observation techniques were discussed in detail by RABØL (1964 and 1965).

During the observations almost any movements irrespective of species, season, direction and "goal directiveness" in the movement have been conceived and noted as a migratory movement. Exceptions herefrom are only distinct movements in breeding area and activities during which a bird moves about constantly within sight. It goes without saying that this practice may involve the risk of including non-migratory movements, e.g. foraging and flight movements and movements in winter quarters etc. Often there are no distinct limit between migratory movements on the one side and the said movements on the other side, and even if there were, the observer is, as a rule, unable to distinguish them from each other. By the above mentioned procedure the observer is compelled to be objective in his registration of e.g. the number of birds migrating in different directions which naturally is the basis of a analysis of the influence of the external factors on the migration.

As regards the exact meaning of the ethological terms used the reader is referred to e.g. Thorpe (1964).

MIGRATORY DRIVE CONCEPT

Behaviour during migration involves a chain of instinctive actions. An *instinctive action* can be regarded as the product of a *drive* (a definite state of internal activity) and one or several *sign stimuli* which can release and/or direct the drive (e.g. Fabricius 1961).

The drive which is the basis for migratory behaviour can be called the *migratory drive*. In order for this drive to be converted to a migratory movement, it must be exposed to a suitable external stimulus. This stimulus directs the movement.

The previously introduced term *migratory force* (Rabøl 1964) is defined as a migratory drive plus one or more sign stimuli, in other words, the total causality of a migratory movement. It is symbolized by a vector the direction of which is determined by the sign stimulus and the length of which depends upon the intensity of the migratory drive (Fig. 1).

Rabøl (1964) uses the *migratory force* concept in a wider and partly different sense than that stated here. When calculating the average direction of migration also the number of individuals in a certain direction was symbolized by a so-called migration force, so that the number of individuals was indicated proportional to the length of the force (the vector).

Of directing external factors which can cooperate with the migratory drive can be mentioned *the sun and the stars*, *the direction of the wind* and *the topography*. The two first-mentioned may occasion a goal migratory force, the two others a *headwind migratory force* and a *topographical mi-*

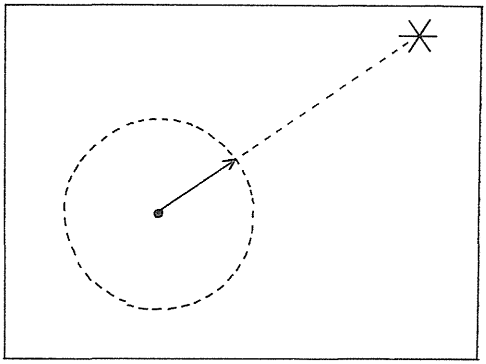

Fig. 1. An instinctive action (e.g. a migratory movement – the arrow) conceived as a product between a drive (the circle which may vary in intensity) and a sign stimulus which releases the drive and directs its conversion to the instinctive action.

Fig. 1. En instinkthandling (f. eks. en trækbevægelse – pilen) opfattet som et produkt mellem en drift (cirklen – der kan være variabel i størrelse) og en nøglestimulus, der virker udløsende på driften og retningsgivende på dennes omsætning til instinkthandlingen.

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* I do not regard the different migratory reactions as fixed action pattern but rather as appetative behaviour (containing both fixed motor pattern and taxis). The use of the concept of sign stimulus is maybe therefore unfortunate. In the ethology a sign stimulus is normally used for only an external stimulus releasing (not directing) a fixed motor pattern. The whole problem is however too complicated to be discussed in further details here.

gratory force (Rabøl 1964). The goal migratory force gives rise to the standard migration (see below), and in my opinion it is not reasonable to definitely separate this from e.g. the headwind migration or leading line migration. The difference between these three forms of migration is to be found mainly in the external influence and less in the migratory drive, although the intensity of this probably decides which of the present stimuli manifest themselves (see later).

Lack (1960a) mentions that the designation migratory urge (= drive) has been used both for 1) "internal factors" and 2) "a result of external and internal factors". The first evidently corresponds to the here mentioned migratory drive, while the latter may correspond to a goal migratory force.

The standard direction is generally considered in the literature as a definite direction which a migrant will take (dependant on the species), when the migratory drive alone is operating, and when there are no disturbing influences from the surroundings (e.g. van Dobben 1953 and Christensen et al. 1961).

This concept of the standard direction as a uniform (or almost uniform) direction for all individuals of a species (a population) is however of a too small plasticity to be useful for ethological considerations. As concluded by Jacobsen (1963) there will of course be a genetically determined distribution of the migration directions around the average goal migration direction, the standard direction. – This distribution is furthermore a question of age and maturation (e.g. Williamson 1963). The juvenile birds have a much greater distribution around the standard direction than the old birds, possibly we may sometimes speak of random dispersal (Williamson, Nisbet 1962). When migration has started, the distribution round the standard direction may be further increased, e.g. by overshooting (of the breeding area or the winter quarter), migrational drift, reversed migration or redetermined migration etc. All these and more factors give a considerable distribution round the standard direction (Fig. 2). Note (Tables 4–5) how great is the dispersal on the inland localities without pronounced leading lines, even on calm days, when a head-wind migratory force has no possibility to manifest itself. Also Dorst (1962) in the chapter "Orientation of migratory birds" mentions experiments made by Sauer Kramer and Matthews (both sun- and star-orientation as well as homing experiments). These experiments show a distinct distribution (like Fig. 2) around the average migration direction.

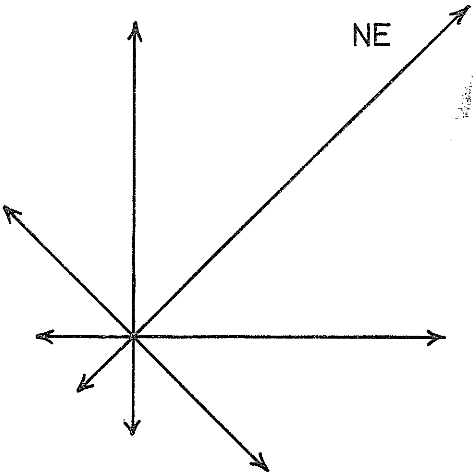

Fig. 2. Variation of the goal migratory forces (spring) around a standard direction towards NE. Compared with the NW and SE sector the SW sector should reasonably be greater than shown due to real reversed migration.

Fig. 2. Spredning af måltrækkræfterne (forår) omkring en normaltrækretning mod NØ. Sammenlignet med NV- og SØ-sektoren skal SV-sektoren rimeligvis være større end vist på grund af forekomst af ægte omvendt træk.

The designation goal migratory force here means the product of the migratory drive and a sign stimulus issuing from the sun and the stars (possibly earth magnetism, e.g. MERKEL et al. 1965). That the result hereof, the migratory movement, often goes in a "wrong" direction compared with the standard direction is ascribed, among other things, to the above mentioned factors.

Goal migratory force may be an unfortunately chosen designation, because e.g. DORST (1962) points out the existence of both *true goal orientation and one-direction orientation.* The random dispersal met with in the juvenile birds of certain species is not in its true sense goal directed. The advantage of a brief designation of something which is uniform in principle may make up for the linguistic incompleteness of the term.

There is complete agreement in the literature that the migratory drive, like other drives, may vary in intensity. The less the weather conditions and the landscape below are able to mark migration (both direction and intensity) the greater is the migratory drive. Generally the migration takes place in a normal way (dependant on the species) with its greatest intensity at certain hours, at which time the migratory drive is said to be strongest. LIND (1965) writes that – generally speaking – instinctive behaviour (and thereby the underlying drive) need not act according to the all or none rule, but, generally, a variation in intensity can be ascertained.

It is also a general experience of the observers that a sudden worsening of the weather conditions or an amelioration may cause a steep fall or sudden rise in the numbers of migrating birds, which is a complicated function of e.g. the migratory drive. Unfavourable weather conditions throughout a longer period of time also obstruct migration only for a short time. Evidently, the migratory drive accumulated gradually to a certain level at which migration starts. Both these observations imply the presence of a variable migratory drive.

It should be pointed out that often changing migration directions should be seen as a transition between the influence of the different stimuli on the migratory drive. What stimulus is at work depends on the migratory drive, and here not only the intensity of the drive is of importance, but also the time elapsed since a sign stimulus was last in operation (e.g. WILLIAMSON (1962) mentioned for leading line migration, and LIND (1965)). Finally, it is of course important whether a stimulus on the whole has a possibility to influence the migratory drive (which e.g. is not possible in the case of a leading line across open water or at great altitude).

THE WIND

The influence of wind on migration is obvious and has often been discussed. However, there is not yet any clear understanding of the drift caused by wind, the head wind migration and the down-wind migration seen in close relationship.

DORST's statement (1962) is thus typical: "In any case, no general rule applies to the relationship between migrations and wind . . .". It fits only in the very strict sense that a definite active reaction form should exercise its influence at any given migration movement, and it is overlooked that the passive drift caused by the wind is nearly always in operation. Dependant on the migratory drive and the available stimuli one could however also speak about rather fixed active reaction forms in relation to the wind.

The influence of wind on migration may be divided – as indicated above – into a passive drift and an active response.

The first is what is normally understood by *migrational drift* (not in the special sense used by Williamson 1955, see later). The wind may partly shorten, partly protract a migration according as it blows as headwind or right with the *heading* (Lack and Williamson 1959). If the direction of the wind forms an angle with the heading, the *track* (Lack and Williamson, 1959) will be a resultant between these two directions dependant, among other things, on the bird's own speed, the wind force and the intersection angle.

The birds may also actively take a definite flight direction in relation to the direction of the wind (at any rate at low altitudes). They may fly right against the wind or straight with the wind, or take such a direction obliquely against or with the wind that the track goes in the goal migratory direction or along a leading line.

Here should only be discussed in some detail *active* wind-migration (i.e. migratory movements where the direction of the wind participates as a sign stimulus). According to Rabøl (1964) active wind migration against or with the wind may be the immediate expression of a *head-wind migratory force* and a *down-wind migratory force* resp.

Conclusively it is pointed out that the general view that a bird, according to its species, "prefers" either down-, head- or side-wind (e.g. Saxtorph 1917), Salomonsen 1953) must be rejected as a general rule. The reactions to e.g. the wind depends on the migratory drive (see earlier) and not, or in a smaller degree, on the species. The same individual may thus – depending on the migratory drive and the external circumstances – be said now to prefer downwind, now headwind, and in other situations pays no attention to the direction of the wind in the sense that it just travels along a leading line towards its goal, or in a given compass direction.

Downwind migration

Williamson's (e.g. 1955) "migrational drift theory" (which normally is not what is understood by migrational drift – see earlier) mentions – in my opinion – a downwind migratory force. The theory says that birds above open water, in cases where means of orientation by the sun or the stars are missing, go down to low migratory altitudes and perform an active downwind movement (visually determined by the waves) in their attempt to get away from an inhospitable zone as quickly as possible.

Lack's (e.g. 1963) radar investigations of the migration at high altitudes (England) show a general tendency to downwind migration in the autumn and notably in winter. On the other hand, this phenomenon is of no or small importance to the progress of the spring migration. These differences which are dependant on the season should probably be considered as the result of e.g. a different migratory drive, so that downwind migration takes place when the migratory drive is relatively low. How active this downwind migration actually is (whether the downwind is a sign stimulus) is however very difficult to say. Hassler et al. (1963) mentions a clear tendency to migrate in the standard direction with the wind (North America). Here the birds evidently determine the direction of the wind from the ground, and migration starts when the direction of the wind and the goal migratory direction almost coincide. A great deal of the downwind migration described by Lack should probably be conceived in a similar way, and he thus speaks about a real downwind-migratory force which intensifies a goal migratory force. As the wind direction – in my opinion – normally can hardly be determined by a flying bird without visual coordination with the "movement" of the landscape below (see later), a downwind migration at higher altitude is hardly in its proper sense an active downwind migration (even if it started as such), and most probably it is

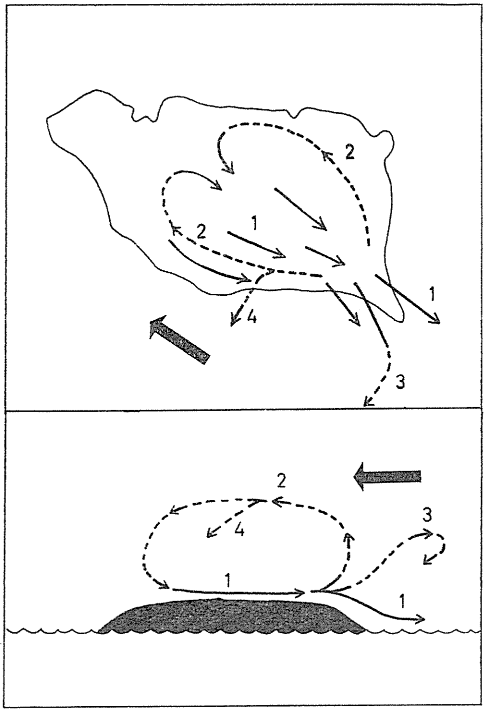

Fig. 3. Hesselø. Migratory movements in the autumn. The lowermost figure shows the island in profile seen from the south. The thick arrow indicates the direction of the wind. A fully drawn arrow indicates migration below 30–40 m, a broken arrow shows migration above this altitude. *1* is headwind migration at low altitude, *2* is downwind migration at higher altitude influenced by drift. *3* shows headwind emigration at low altitude, which during rise in altitude of migration gradually bends and passes into standard migration. *4* indicates standard migration issuing from the drift-migration. The dominating headwind migration at low altitude is seen as the antagonist to the dominating downwind migration at higher altitudes influenced by drift.

Fig. 3. Hesselø. Efterårstrækbevægelser. Nederste figur viser øen i profil set fra syd. Den kraftige pil angiver vindretningen. Fuldt optrukket pil er træk under 30–40 m., stiplet pil viser træk over denne højde. 1 *er lavt modvindstræk.* 2 *er et højere afdriftpræget medvindstræk.* 3 *viser lavt modvindstræk, der under stigning i trækhøjde efterhånden afbøjes og går over i et normaltræk.* 4 *angiver normaltræk udgående fra afdriftstrækket. Man ser det overvejende lave modvindstræk som antagonisten til det overvejende højere afdriftprægede medvindstræk.*

rather a considerable passive unification with the wind of the migration at great altitude (migrational drift) – irrespective of how it started and irrespective of the heading at great altitude.

The visible diurnal migration (apart from WILLIAMSON's "migrational drift") normally does not represent an isolated active downwind migration, even if the birds, just at low altitude, would have the best possibilities of determining the direction of the wind. A passive drift with the wind can, however, often be seen during emigration attempts and following rise in the migratory altitudes. At Hesselø (Fig. 3 and Fig. 14) a tendency was noted to the effect that a migration at higher altitude may follow the downwind coast line. The phenomenon however seems to be subordinate to the simultaneous headwind migration at lower altitude, and is otherwise a passive form of downwind migration, a wind drift directed in some degree only by the leading line. How general this observation is is not known.

A few times I have also seen spring migration of Skylark (*Alauda arvensis* (L.)) in the standard direction in downwind, evidently under simultaneous influence of a downwind migratory influence (Table 5, 21/2 1966) which has contributed to a rapid expansion. (HASSLER et al. 1963) mention the same function for the downwind migration).

It should be pointed out once more that a distinction between an active and a passive downwind migration especially on the radar screen cannot be made.

Headwind migration

Headwind migration seems everywhere to be a widely distributed reaction form during the visible diurnal migration. Strange enough, the literature contains very few attempts at an isolation of what could be called a headwind migratory force (RABØL 1964).

There are several reasons for this:

1) The headwind migration is nearly always regarded as a secondary phenomenon associated with the leading line migration (or e.g. the island attraction, see later). Here it is however largely overlooked that a leading line generally acts equally much in both directions.

2) If migration in one direction takes place almost opposite to the standard migratory direction it is generally called *reversed migration*, a designation which in itself is only descriptive and does not explain anything. What might be called *real reversed migration* (Umkerzug – Ruckzug) can be defined as the result of a goal migratory force which for some reason or other has been temporarily reversed 180 degrees. The problem should not be further discussed here, it is only pointed out that not all reversed migration is real. WESTERNHAGEN (1953) thus mentions that headwind migration secondarily may intensify a real reversed migration. KOCH (1934) says that the reversed migration described by him ("cursus retroversus") is due to positive anemotrophy. These examples and RABØL (1964) among others show that a wind may release a migratory force directed against the wind, a headwind migratory force.

As another indication of such the reader is referred to Figs. 4–5 and to the Tables in this paper.

3) There seems to be a pronounced emotional scepticism towards the presence of an active headwind migration partly because it seems to claim too much energy and partly does not fulfil a direct function.

The headwind migration however serves the important purpose to be a compensating factor which counteracts the migrational drift. It is so to speak the antagonist to this latter in the complex which is called bird migration.

WILLIAMSON (1962) writes that the only way in which the birds can compensate for drift by the wind is by leading line migration, and that this therefore should be regarded as advantageous on an average, so that not every migratory movement along a leading line is necessarily advantageous. This view is however only partly correct, simply because similar logical agreements could be maintained as an explanation of the function of the headwind migration which has also been the case recently (RABØL 1964 and BERGMAN 1964).

That headwind migration claims more energy than downwind migration to cover a distance which, viewed from the ground, is the same, is of course right. But headwind migration does not claim too much energy and is not inadequate for the migration as a whole on account of the function sketched here.

Migration against the wind without the influence of a headwind migratory force (passive headwind migration) no doubt also occurs (Fig. 6, Fig. 7, and Fig. 16). The thorough investigations at Hesselø are mentioned below. If a bird from the sea is heading towards the island, and its flight direction is not right with the wind, it will generally arrive at the island in headwind (Fig. 16) irrespective of the direction of the wind or its standing point. The phenomenon has been found to be extremely common (irrespective of the wind direction), but it always seems evident that a headwind migratory force intensifies the topographical attraction.

Furthermore the headwind-immigration to Hesselø generally continues across the island into a headwind-emigration from the opposite coast (Fig. 7). This may however partly be explained as inertia (RUDEBECK 1950) of the migration after the attraction to the island had ceased. However, the migration from Hesselø also starts early in the morning before an immigration reaches the island, generally as an emigration or coastal migration

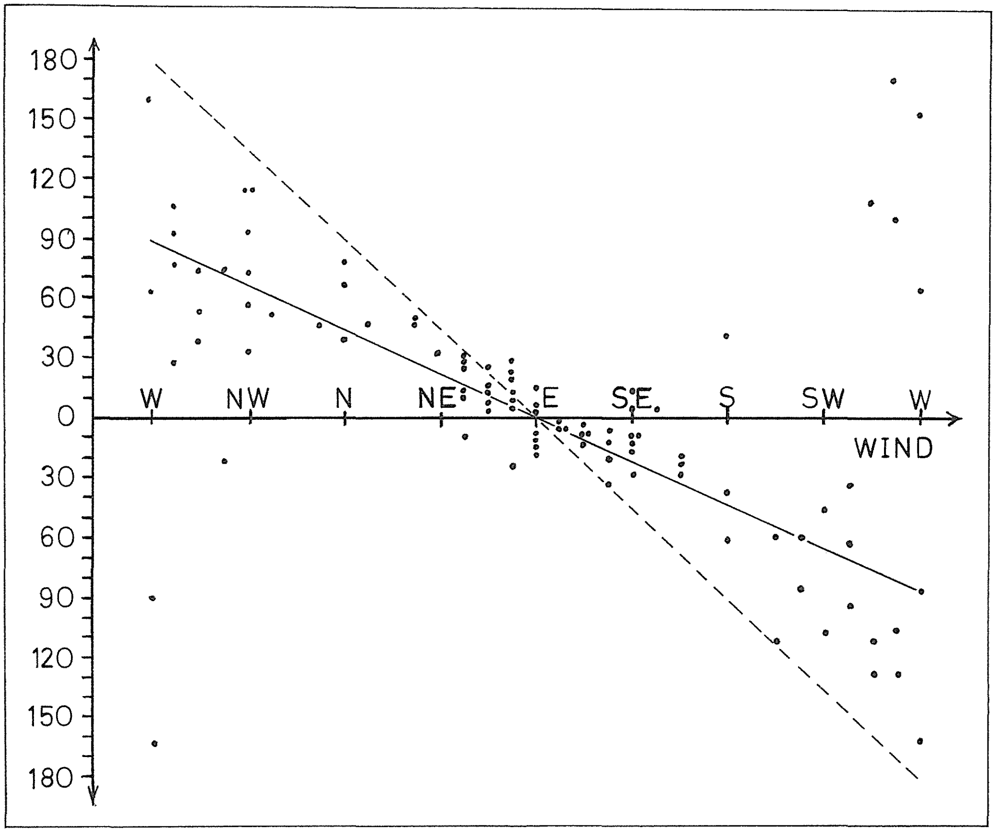

Fig. 4. Skylark *(Alauda arvensis)*. Knudshoved. Spring. Difference in degree between average migration direction and wind direction. Each dot indicates an observation day. The material derives from Table 1 and from Rabøl (1964 – Table 1). Above the abscissa the wind direction lies to the left of the average migration direction and below the abscissa to the right of it.

Note the turning point round E in accordance with the fact that the resultant between the average goal migratory direction (NE) and the average topographical migratory direction (ESE) is directed more or less towards the east.

The fully drawn line shows the deviation when the headwind migratory force and the above mentioned resultant are of equal length. We find an empiric distribution approximately round this line.

The distribution clearly shows the presence of a headwind migratory force. If such did not occur, the dots would be distributed round a line going from + 180° over 0° (E.) to ÷ 180° (the broken line).

Fig. 4. Sanglærke (Alauda arvensis). *Knudshoved. Forår. Afvigelse i grader mellem gennemsnittrækretning og vindretning. Hver prik står for en observationsdag. Materialet stammer fra Tabel 1 og* Rabøl *(1964 – Tabel 1). Ovenfor abscisseaksen ligger vindretningen til venstre for gennemsnittrækretningen og nedenfor abscisseaksen til højre for.*

Bemærk vendepunktet omkring Ø i overensstemmelse med, at resultanten mellem den gennemsnitlige måltrækretning (NØ) og den gennemsnitlige geografiske trækretning (ØSØ) er rettet ca. mod Ø.

Den fuldt optrukne linie viser afvigelsen, når modvindstrækkraften og den ovenfor nævnte resultant er af ens størrelse. Man finder en empirisk fordeling nogenlunde om denne linie. Til sammenligning viser den stiplede linie, hvordan prikkerne ville fordele sig, hvis en modvindstrækkraft ikke fandtes.

Fordelingen turde klart vise tilstedeværelsen af en modvindstrækkraft. Fandtes en sådan ikke, skulle punkterne falde omkring en linie gående fra + 180° over 0° (Ø) til ÷ 180°.

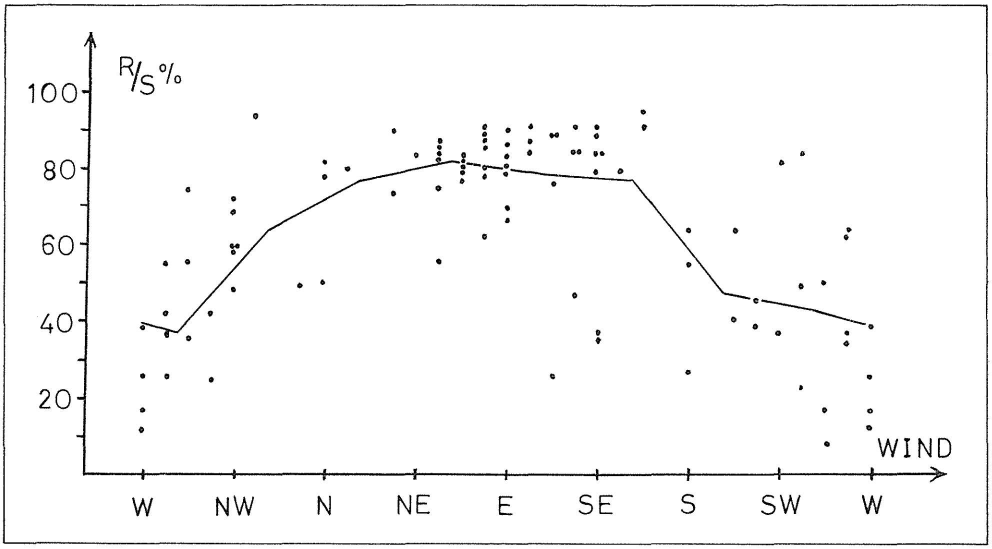

Fig. 5. Skylark (*Alauda arvensis* (L.)). Knudshoved, spring, R/S percentage (RABØL 1964) plotted as function of the wind direction. Same material as Fig. 4. The line drawn shows the average percentage in the 8 sectors, each being 45°. We note that there is greatest accordance round the east with headwind migratory force, average goal migratory force and average topographical migratory force progressing in almost equal directions. The R/S percentage is smallest around the west, because the headwind migratory force here is directed almost oppositely to the two others.

Fig. 5. Sanglærke (Alauda arvensis). *Knudshoved. Forår. R/S-procenten* (RABØL *1964) afsat som funktion af vindretningen. Samme materiale som Fig. 4. Den indtegnede linie viser den gennemsnitlige procent i de 8 sektorer på hver 45°. Man bemærker størst overensstemmelse omkring Ø med modvindstrækkraft, gennemsnitlig måltrækkraft og gennemsnitlig geografisk trækkraft forløbende i omtrent ens retninger. R/S-procenten er mindst omkring V, fordi modvindstrækkraften her er omtrent modsat rettet de to andre.*

against the wind (see however Fig. 3). This also holds good for other migration places, thus expressly mentioned from the coast of North Zealand (CHRISTENSEN and ROSENBERG 1964).

Conclusion: The headwind migration is both a very widespread and isolated phenomenon during the visible diurnal migration, and furthermore, it may have the very important function to counteract the drift caused by the wind.

TOPOGRAPHY

During the visible diurnal passage the migratory directions of the birds may reflect a considerable influence of topographical factors. Two forms of topographical passages can at any rate be distinguished viz. *leading line migration* and *topographical attraction.*

Leading line migration

Leading line migration (and notably coastal migration) has often been described. Normally, the leading line migration along a seashore is conceived only as a deviation of a normal passage due to

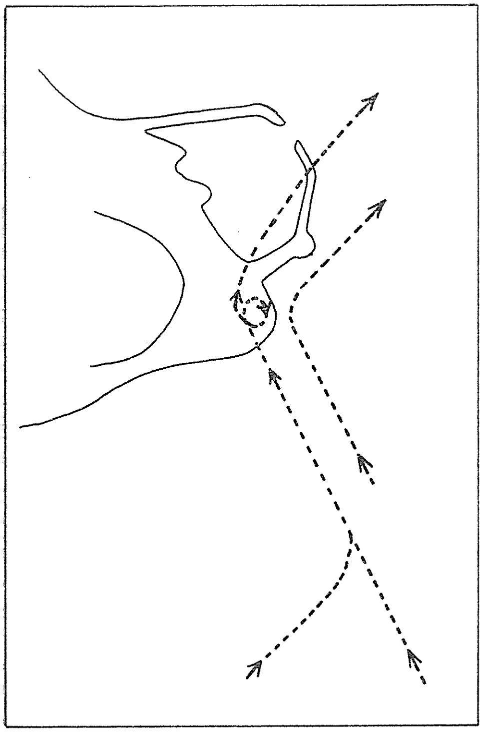

Fig. 6. Attraction and parallel displacement of migratory movements at Knudshoved (spring) mostly with winds in the section between west and north. Notably Skylark.

Fig. 6. Tiltrækning og parallelforskydning af træk ved Knudshoved (forår), mest med vinde mellem V og N. Især Sanglærke.

aversion to emigrate across open water. This might be called *passive leading line migration*. Most other forms of leading line migration (a number of types described by Vleugel and Westerhagen 1957) however could not be explained as caused by aversion and might be called *active leading line migration*. Williamson (1962) and Van Dobben (1953) among others also give examples of active coastal leading line migration. Van Dobben thus writes: "... the guiding line effect is not exclusively caused by aversions. There seems to be also a preference for clear topographical lines" (Fig. 8). The guiding line passage shown in Fig. 8 however need not exclusively be an active guiding line migration. In Fig. 8 (above) the coastal passage may be passive with a goal migratory force to the SE, and correspondingly (below) a goal migratory force to NW.

A sharp distinction between an active and a passive leading line migration cannot be made, either in practice or in theory. In both cases the leading line enters as a sign stimulus (although fear of water intensifies the effect in passive migration), and a leading line migratory force may be said to be present.

Which way along the coast the passage will go depends on what agrees best with the direction of the goal migratory force and/or the headwind migratory force (see later).

Williamson (1962) mentions the general experience that the association with a leading line is greater the more unfavourable the weather conditions are, and that the association with the leading line is much weaker after a short passage across water than after a longer passage across the sea. This may be said partly to be due to a low migratory drive or partly to the non-use of the leading line as sign stimulus for a longer period of time.

It may be reasonable to point out the inertia mentioned by Rudebeck (1950) in the leading line migration. If e.g. there is a sharp bend of the coast, the passage is often continued in a straight line across the sea in the hitherto followed direction of the coast line (Figs. 9, 10, 11, 12), even if this does not point in the standard direction. The conditions near Blåvand (above mentioned figures) distinctly show this common phenomenon which may be said to be due to a constant leading line migratory force. – This however is hardly of stable direction over a longer distance, if it deviates too much from the goal migratory direction. It is however often stable within sight (Knudshoved, Hesselø).

Topographical attraction

This notion may be defined as a topographical migratory force acting towards some topographical unit.

To a bird out at sea it may be a force attracting it towards the nearest shore (Figs. 6 and 16). Also inland we may speak of topographical attraction, e.g. to a wood. The literature contains many examples of topographical attraction, e.g. LACK (1959) who mentions that Starlings (*Sturnus vulgaris* (L.)) often fly at right angles to the coast, although it is known that their migration direction across the sea was a different one. VAN DOBBEN (1953) shows by means of a drawing of the island of Vlieland how the migrating birds – when approaching the island – change their migration direction and fly approximately at right angles to the coast.

The distinction between the two kinds of topographical migratory forces (leading line migration and topographical attraction) should only be regarded as a practical division. There is only a difference in degree, and the attraction is the basic element.

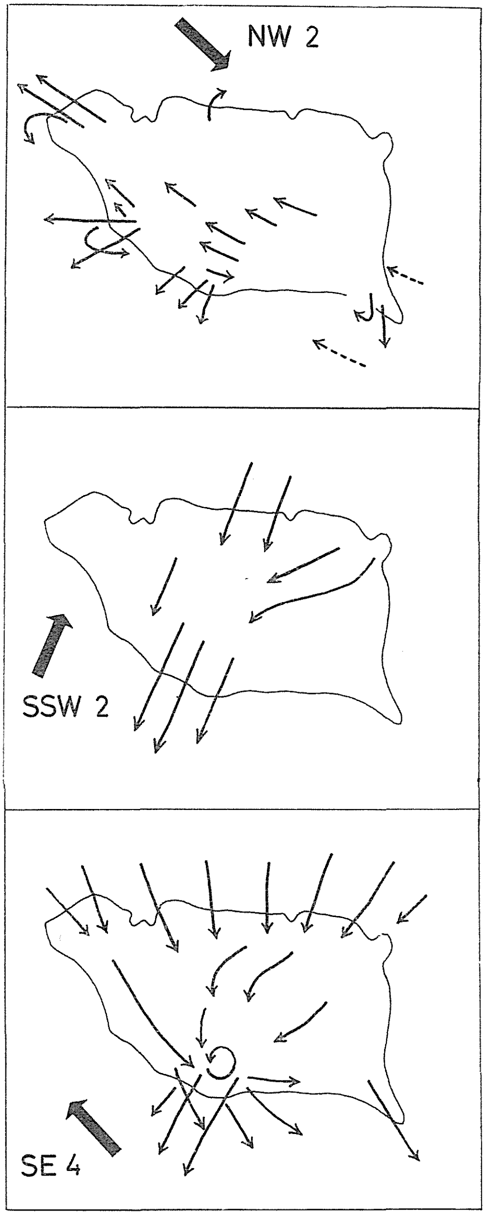

Fig. 7. Chaffinch (*Fringilla coelebs* (L.)). – Hesselø autumn 1964. Direction of wind indicated by the thick arrow. Migratory movements in the days 22. 9., 27. 9. and 12. 10. Number of migrating birds slightly below 1000, more than 2000 and not less than 5000 resp. The number and size of the arrows are indicated proportionately to the dimensions of the migration at the different places on the island. Note the tendency to headwind migration, which in connexion with the attraction towards the island should be regarded as a compensation for the wind drift which operated over open water (see also Fig. 16).

Fig. 7. Bogfinke (Fringilla coelebs). *Hesselø. Efteråret 1964. Vindretning angivet med kraftig pil. Træk på dagene 22. 9., 27. 9. og 12. 10. Antallet af trækkende fugle henholdsvis lidt under 1000, mere end 2000 og mindst 5000. Pilenes antal og størrelse er angivet proportionale med trækkets størrelse, de forskellige steder på øen. Bemærk tendensen til modvindstræk, der i forbindelse med tiltrækningen mod øen er at betragte som en kompensation for den vinddrift, der er sket over åbent vand (se Fig. 16 også).*

HEADWIND MIGRATION AND TOPOGRAPHICAL MIGRATION

A correlation between headwind migration and topographical migration will be briefly made.

1) The direction of the wind may be compared to a leading line. It does not however operate in the same way in the two directions, which a leading line generally does.

2) The general rule applies to a straight coast line that migration will be greatest in the direction along that coast which runs most against the wind. (Table 2. Christensen et al. 1964). The tendency is contrary to the season, but of the standard goal direction approximately coincides with one of the coastal directions the migration may however be greatest in that direction – irrespective of the direction of the wind.

3) At the end of a peninsula (e.g. Knudshoved Fig. 17) or a pronounced bend of the coast (e.g. Blåvand) the general rule applies that the migration towards the bend of the coast is relatively greatest along that coastline which runs most against the wind (or least with the wind), whereupon the migration will turn and continue along the other coast (or change into emigration), approaching the wind. Figs. 9–12 (Blåvand) show this tendency. See also Fig. 13. Similar cases are often described in the literature, e.g. Jenkins et al. (1955 Blåvand, note here how similar the autumn migration (Figs. 3–6) is to the spring migration under the same wind conditions, Lack and Lack (1952 – Lands End), Bruun et al. (1957 – Stigsnæs)).

4) Exposed to the wind – evidently that of the possible topographical sign stimuli manifests itself which fits with

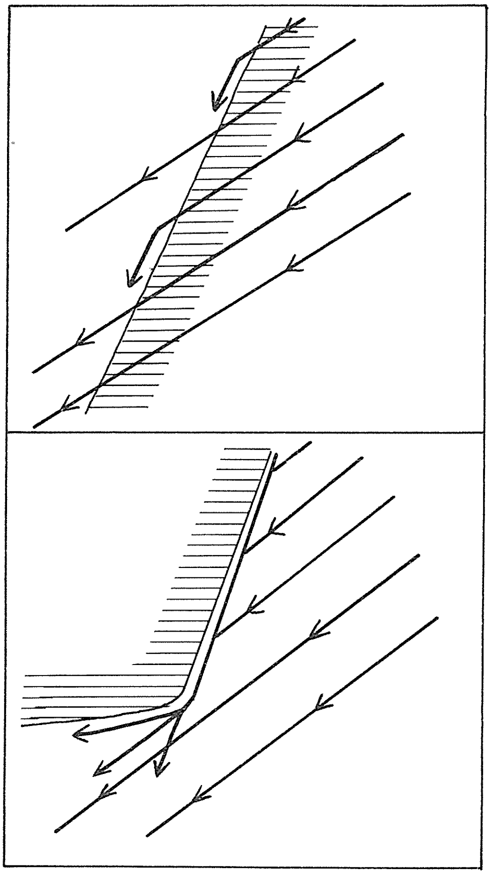

Fig. 8. Examples of active leading line migration, i.e. leading line migration which cannot be explained by aversion to emigration over open water. Above immigration from the sea (hatched) of which a number thereupon follows the coast. Below migration following the coast continuing to some degree even if the coast bends away from the standard direction.

Fig. 8. Eksempler på aktivt ledelinietræk, d.v.s. ledelinietræk, der ikke kan forklares ved aversion mod udtræk over åbent vand. Øverst indtræk fra vandet (skraveret), hvoraf en del derefter følger kysten. Nederst kystfølgende træk, der i nogen grad fortsætter, selv når kysten drejer bort fra normaltrækretningen.

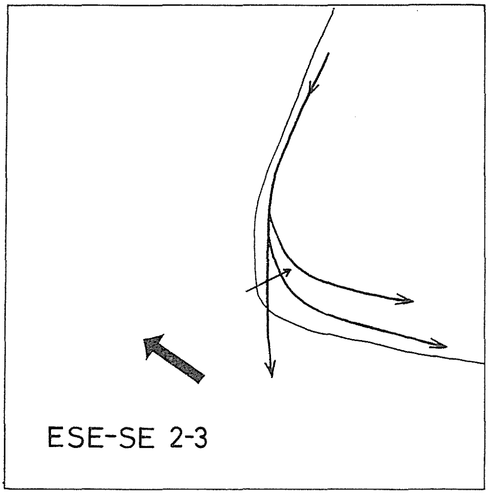

Fig. 9. Linnet *(Carduelis cannabina)*. Blåvand. 17. 4. 1964. Total 286.

Fig. 9. Tornirisk (Carduelis cannabina). *Blåvand. 17. 4. 1964. Ialt 286.*

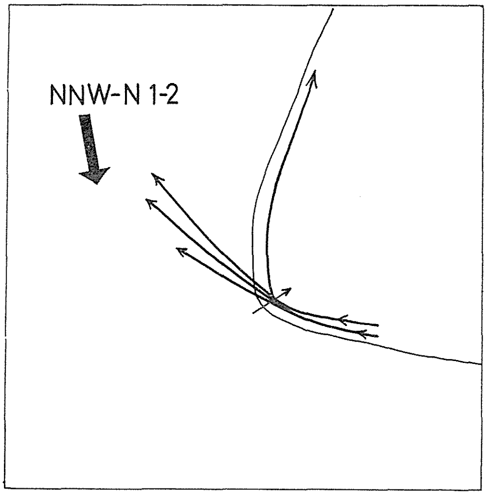

Fig. 11. Linnet *(Carduelis cannabina)*. Blåvand. 6. 4. 1964. Total 111.

Fig. 11. Tornirisk (Carduelis cannabina). *Blåvand. 6. 4. 1964. Ialt 111.*

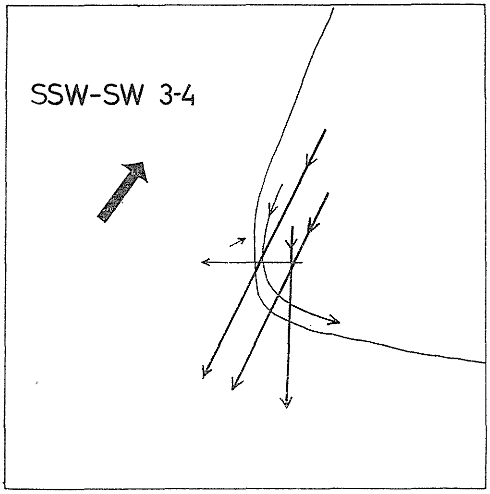

Fig. 10. Linnet *(Carduelis cannabina)*. Blåvand 12. 4. 1964. Total 171.

Fig. 10. Tornirisk (Carduelis cannabina). *Blåvand. 12. 4. 1964. Ialt 171.*

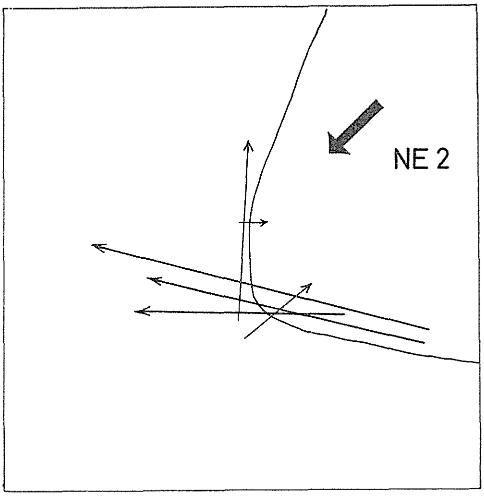

Fig. 12. Linnet *(Carduelis cannabina)*. Blåvand 5. 4. 1964. Total 88. Note the tendency in Figs. 9–12 to follow the coast line which gives the greatest headwind migration.

Fig. 12. Tornirisk (Carduelis cannabina). *Blåvand. 5. 4. 1964. Ialt 88. Bemærk tendensen på Fig. 9–12 til at følge den kystlinie, der giver mest modvindstræk.*

headwind migration. *Possibly headwind migration should only be regarded as a unification of the topographical possibilities.* There is no longer any free "choice". Topographical dependance during migration is a pure visual feature and in a similar way the *headwind migratory force may perhaps manifest itself only as a consequence of visual sensations.* This seems, among other things, to be indicated by the missing capability of correction for drift by the wind during the higher visual diurnal migration and the absence of headwind migration (apart from accidental occurrencies) during the high migration observed by radar (LACK).

GOAL MIGRATION, HEADWIND MIGRATION AND TOPOGRAPHICAL MIGRATION

A migratory direction has one or several of the said sign stimuli and a migratory drive as its immediate cause. That the migration pattern often appears to be so variegated as is the case, is, among other things, due to the fact that some individuals react to one stimulus and other individuals to another.

If several sign stimuli do not differ too much from each other in direction they may cooperate, however (judging from the observations) hardly with a simple vector-resultant as result, but rather, so that only one of the given stimuli determines the direction, e.g., as mentioned above, migration along a leading line, if this fits approximately in direction with headwind migration and/or goal migration. – In such a case the migration pattern may be pronouncedly uniform (e.g. the autumn passage along the Dutch coast with southwesterly wind (VAN DOBBEN 1953).

In an earlier paper (RABØL 1964, Table 12) it has been shown in a number of cases (spring) how significant was the standard migratory force (i.e. the average migratory force to the NE), the headwind migratory force and average topographical migratory force (towards ESE) for the progress of the average drift migratory direction for Skylark at Knudshoved. The headwind migratory force gradually appeared to be the most significant of the operating migratory forces. There is however a very considerable variation round the average of the goal migratory forces as well as of the topographical migratory forces (notably inland and at coasts or point which do not point in the standard migratory direction). This involves that the standard migratory force and the average topographical migratory force will have less influence on the progress of the average migratory direction than a goal migratory force and a simple topographical migratory force have on any migrating bird, since the headwind migratory force in both cases is on the whole a simple force. (During the visible diurnal migration this latter is reduced only in a small degree by the reversely directed downwind migratory force or the more or less passive drift with the wind). This consequently implies a less general influence of a headwind migratory force previously postulated.

By means of a model (Fig. 15) some examples are given of the interaction of the different migratory forces. In a random area there is a population of birds with a sufficiently great migratory drive for releasing migration. There is a dispersal of the individual goal migratory forces round the standard direction towards NE (spring).

The situation *in calm:* the number of migrating birds at the four corners (Fig. 15) will be directly proportional to the number of birds which have goal migratory forces within the angle sectors N–E, E–S, S–W, and W–N respectively. For it is assumed that for a group of birds with equal goal migratory forces, migration at right angles to the coast will result (besides in a certain emigration) in an equally large migration in each of the two directions along the coast. If in Fig. 15 the migration at the SW and NE quarters is compared, an oppositely directed reaction would be expected, partly for topographical reasons and partly as a consequence of different goal migratory forces in the birds which reach the two corners with an average emigration direction towards SW and NE respectively.

The situation: *Exposed to the wind.* An acute angle between a goal migratory force and a coast line may mainly give a leading line-headwind migration obliquely backwards. The average dividing angle for an equally large migration in the two directions along the coast (Table 2) will in such a case be an acute angle (in Fig. 15 e.g. the angle OCA with a westerly wind).

The migration at the *SW corner:* Wind from SW (compared with the reactions in calm) influenced by the coast lines and headwind migration will absorb a greater part of the variation round the standard migratory direction (e.g. in Fig. 15 the goal migratory forces from SE via S to NW). More birds will therefore reach the SW corner than in calm. The situation is the opposite with wind from NE, in which case only birds with goal migratory directions within e.g. the angle EOF will reach the SW corner. The result is therefore smaller migration in NE wind than in calm.

In the above working hypothesis it is even presupposed that the migratory directions inland remain unchanged irrespective of changing wind. My few inland observations of migrating Skylarks (e.g. Table 4 and Table 5) however show that also inland a considerable headwind migratory force is operating. This is not surprising. It would however be strange, if this form of reaction only occurred in connexion with coastal leading lines. To this is however added the oppositely directed drift by the wind (migrational drift) a.o. ULFSTRAND 1960). To which side the *headwind migration: winddrift* shifts during the visible diurnal migration inland is however unknown. At the coasts it has been displaced, as mentioned above, to the advantage of headwind migration. Headwind migration probably dominates during low migration (i.e. migration below 50–100 m), while the drift by wind dominates at greater altitudes.

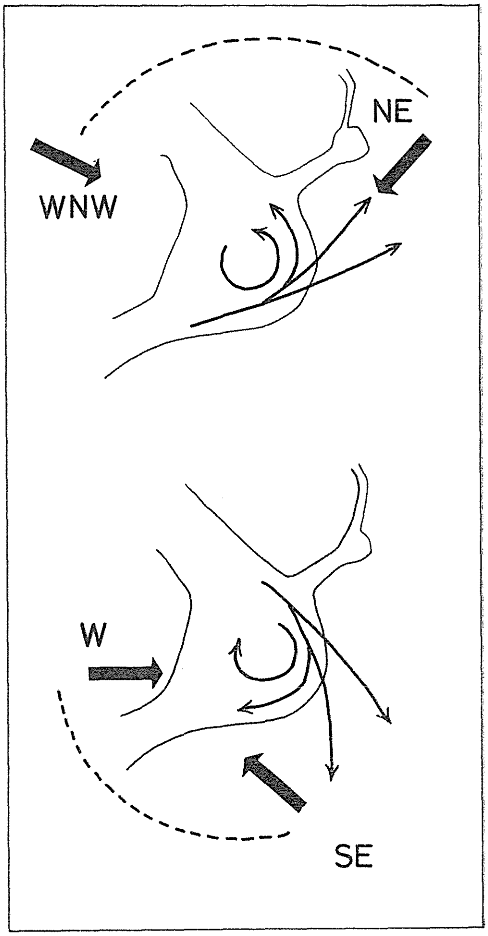

Fig. 13. General migratory movements at Knudshoved with different wind directions caused by interaction between leading line migratory forces and the headwind migratory force. This holds good for spring as well as for the autumn.

Fig. 13. Generelle trækbevægelser ved Knudshoved med forskellige vindretninger forårsaget af samarbejdet mellem ledelinietrækkræfter og modvindstrækkraften. Gælder både forår og efterår.

If a headwind migratory force is not acknowledged and we anticipate that the migration directions inland are only influenced by a standard migratory force (in the "narrow" definition as operating in the same direction) and a drift by the wind, we are, as a matter of fact, unable to explain e.g. an emigration from Falsterbo in spring or a western immigration to Knudshoved at the same season (Rabøl 1964). Such a simple concept does not give the migrating birds sufficient possibilities for reaching these two places. If, on the other hand, we anticipated partly a variation of the goal migratory forces and partly a headwind migratory force in close cooperation with topographical migratory forces (notably at the coast, but also inland) it is quite easy to explain the southwestern emigration e.g. at Falsterbo in spring (e.g. Mathiasson 1960 and 1961).

Finally, it seems reasonable to point out that it is not possible always to give a full explanation of the causes of a given migratory movement. Different sign stimuli may influence a migratory drive of varying intensity. Sometimes only one sign stimulus will operate, at other times several stimuli increase or counteract each other. As a rule, it can be demonstrated what sign stimuli are responsible for a migratory movement, but it may not be possible to determine how much the individual stimulus influence. At best only a rough estimate is possible (see Fig. 18).

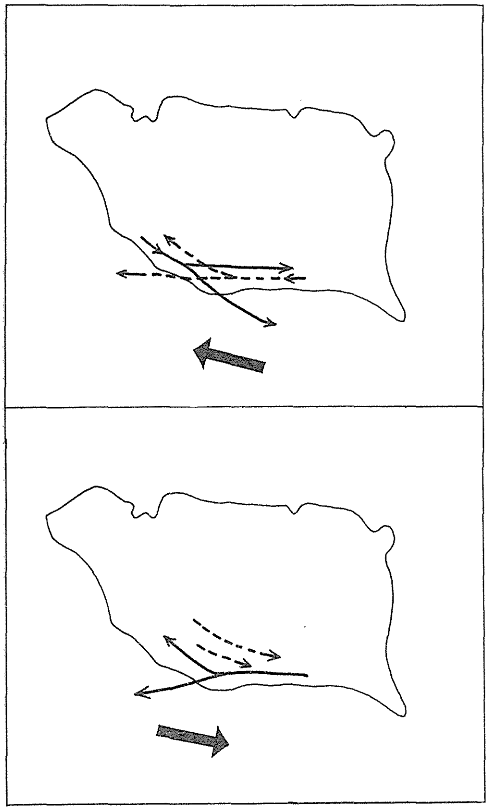

Fig. 14. Hesselø. Autumn. Migratory movements at the SW corner. Migration at low altitude (below 30–40 m) fully drawn. Migration at higher altitude is hatched. The migration at low altitude follows the coast which gives the greatest headwind migration. The more passive downwind migration at higher altitude will drift in the opposite direction.

Fig. 14. Hesselø. Efterår. Trækbevægelser ved SV-hjørnet. Lavt træk (under 30–40 m) er fuldt optrukket. Højere træk er stiplet. Det lave træk følger den kyst, der giver mest modvindstræk. Det højere, mere passive medvindstræk vinddrifter i den modsatte retning.

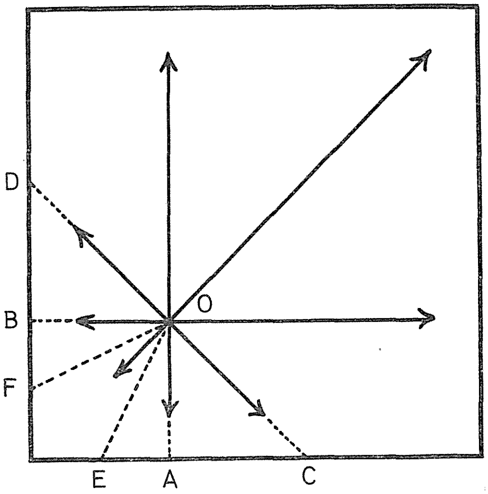

Fig. 15. Variation of the goal migratory forces in a random land area (spring).

Fig. 15. Måltrækkræfternes spredning i et vilkårligt landområde. (Forår).

ALTITUDES OF MIGRATION

A brief comparison between migration at visible altitudes and that above visible altitude is made.

After thorough radar investigations in South England EASTWOOD et al. (1965) conclude that the median altitude for diurnal migration is 1500–2000 feet (5–600 m) (in Fig. 5 is however only stated 1000 feet (300 m)) for the average distribution throughout the year). It is further shown that 80 $^0/_0$ of the diurnal migrants fly at an altitude below 3.500 feet (about 1 km). Since the number of migrants is stated to increase downwards about 30$^0/_0$ of the diurnal migration will probably take place at visible altitudes, i.e. below 200 m which CHRISTENSEN et al. (1964) maintain as necessary to sight a migrating passerine bird.

CHRISTENSEN et al. (1964) state that only about 1$^0/_0$ (about 500.000) of the Swedish and Finnish migrating population (about 50 millions) of Chaffinches (*Fringilla coelebs* (L.)) are seen emigrating at Falsterbo in the Autumn.

Together with spring observations from migration places in Denmark this fact apparently indicates that only a minimal part of the total number of migrating birds fly below visible altitudes.

Many objections can however be made to this calculation.

1) The noted number of birds is confounded with the actual number of migrating birds within visible side and altitude (e.g. ENEMAR 1964).

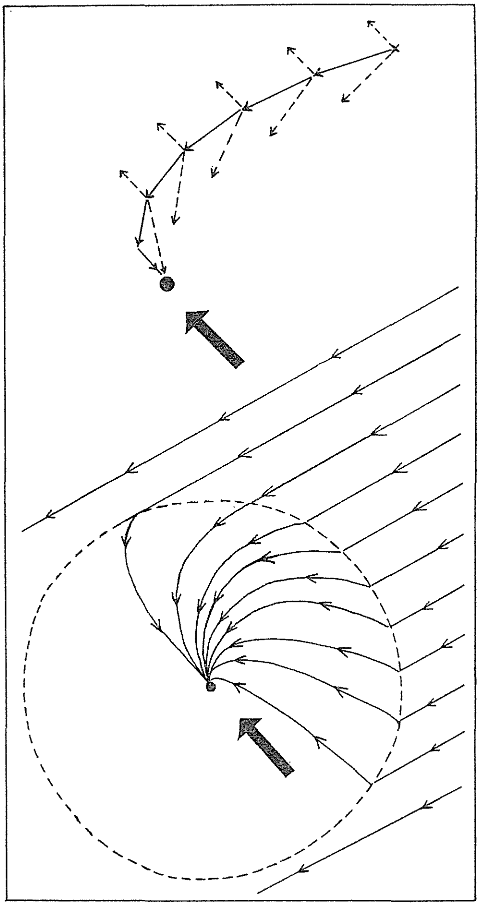

Fig. 16. Migratory routes towards an island. Wind SE. The uppermost figure shows the migratory route for a bird coming from NE. The migration route is constructed, when the bird's own speed is twice the velocity of the wind. The bird comes in approaching the wind. On the lowermost figure the straight lines show a standard migration marked by drift. At a certain distance from the island (the circle) the topographical attraction comes into operation. The migration towards the island will therefore take place in accordance with the uppermost figure, i.e. the migratory routes towards the island will be curved lines, which have that in common that they will reach the island *against* the wind.

Fig. 16. Trækveje mod en ø. Vind SØ. Den øverste figur viser trækvejen for en fugl kommende fra NØ. Trækvejen er konstrueret, når fuglens egenhastighed er to gange vindhastigheden. Fuglen kommer ind tilnærmet mod vinden. På den nederste figur viser de rette linier et afdriftpræget normaltræk. I en vis afstand fra øen (cirklen) træder den geografiske tiltrækning i funktion. Trækket mod øen vil herefter foregå i overensstemmelse med den øverste figur, d.v.s. trækvejene mod øen vil blive krumme linier, der har det tilfælles, at de rammer ind på øen mod *vinden.*

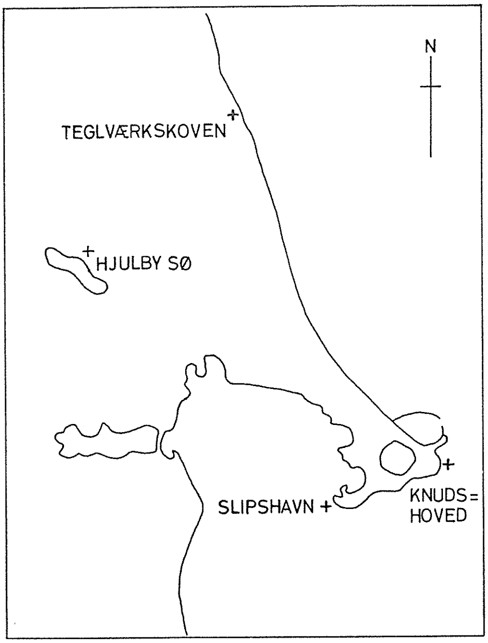

Fig. 17. The observation posts for Tables 1–4.
Fig. 17. Observationsposterne for Tabel 1–4.

2) Even at the most intimate (i.e. concentrated) migration place the birds will pass over a much broader front than the observer can possibly survey.

3) Regarding the migration at Falsterbo: Not the total Finnish population migrates via Sweden, so for that reason alone the figure is too high. Furthermore there is a coastline from Oslo to Falsterbo which is several hundred km long with many coastal projections and with Zealand within that distance for more than about 50 km. It is also known that a considerable migration, e.g. of Chaffinches takes place both across the Kattegat (Fig 7), and North Zealand. Of the Finches which arrive at the Swedish westcoast probably only a small number reaches Falsterbo, where the most important leading line for the migration is the much shorter coastal stretch from east (Rudebeck 1950). Taking these sources of error into consideration it seems as if a considerable part of the Scandinavian Chaffinches and diurnal migrants generally fly at visible altitudes. For most species the number will probably be 10–50$^{0}/_{0}$. For some groups, as e.g. birds of prey, the number is upwards of 100$^{0}/_{0}$.

For the direct observation of the bird migration not only radar observations but also the study of the visible diurnal passage are of great interest (Wilcock 1964). And not only of ethological interest (Christensen et al. 1964) but also of a pure ornithological interest. Furthermore, these studies can be carried out by anybody, and they have aesthetical aspects – which radar observations at rate have only in a smaller degree.

CONCLUSION

It is the momentary behaviour and not the final result which has been studied. Radar observations give information of the migration over a larger distance and at greater altitudes than visuel observations can possibly do. Radar also in a much higher degree shows the conversion of the migration drive itself into standard migration. I am however not of the opinion that the "radar migration" for that reason should be considered more "right" than the visible migration. On the other hand, it could be maintained that it takes place under less influence of external stimuli (however, the drift by wind is greater), and that the migratory drive on the whole is greater. Thus visual observation is not a superfluous study compared with the "radar migration". It only gives information of the migration at a lower altitude and with a generally different combination of causes, where the "irrelevant" external stimuli play a relatively dominating rôle. The study of these influences is of the greatest interest, because all forms of migratory movements should be equalized in principle, although the conditions which they elucidate (and which we try to find) may be different. The criterium for a migratory movement is – in my opinion – only the presence of a migratory drive, but not the intensity of this or the nature of the influencing sign stimulus.

The literature contains a great number of descriptive notions, as e.g. reversed migration, retromigration, and reorientation, only to mention three designations, which are closely related as to content. – Subconsciously one often tries to explain an observed migratory movement as a manifestation of one of those designations. This procedure is however tautologic. On the other hand, it is no tautology (there is no getting away from the language) to conceive the background of a migratory movement as being composed of one or several "indivisible" causes termed migratory forces, where the goal migratory force is the primary cause. The purpose must be to get down to as few causes as possible, but so that with a given combination of these, a probable explanation can always be given of the progress of any possible migratory movement.

There are countless possibilities of explaining a migratory movement (see earlier). This does not, however, mean that we should refrain from an explanation of this movement and from an explanation at all. It is only a sober view on the great variability of the combination of causes.

The causes are both the basis of the migratory movements and form part of them. It is of course not the coast line itself or the wind, but influences from these are in some way or other converted to integral factors in the resulting migratory movement. It is ascertained that this is the case, but in this connexion it is only said why in a lesser degree.

The study of the different migratory forces and their importance follows after these forces shave been ascertained. Thus there is no basis for a discussion of a possible function of the headwind migration, before a headwind migratory force has been isolated. If however such force has been demonstrated it most probably also has a function. What function is then open to discussion.

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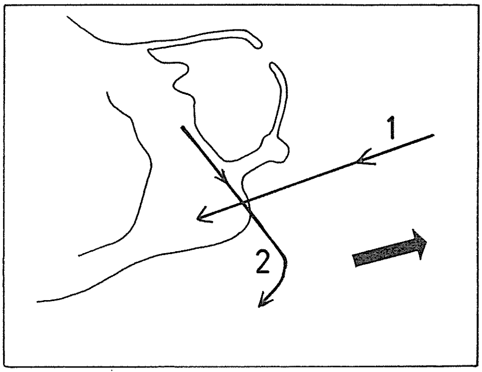

Fig. 18. Migratory movements. Knudshoved. Autumn. Wind WSW. *1* shows immigration. Of importance is especially a goal migratory force, intensified by a headwind migratory force and a topographical attraction near land. *2* shows reversed migration after emigration. The movement starts under influence of notably a leading line migratory force towards SE. Topographical attraction and a headwind migratory force and a goal migratory force cause that the bird will turn and fly WSW in the last instance intensified by a leading line migratory force in that direction.

Fig. 18. Trækbevægelser. Knudshoved. Efterår. Vind VSV. 1 *viser indtræk. Betydende er især en måltrækkraft, forstærket af en modvindstrækkraft og en geografisk tiltrækning nær land.* 2 *viser tilbagetræk efter udtræk. Bevægelsen starter under indflydelse af især en ledelinietrækkraft mod SØ. Geografisk tiltrækning og en modvindstrækkraft, samt en måltrækkraft forårsager, at fuglen vender om og nu går VSV i sidste instans forstærket af en ledelinietrækkraft i den retning.*

SUMMARY

A migratory movement is the product of a migratory drive and one or several sign stimuli such as the sun or stars, the direction of wind, or the topography. This product is called a goal migratory force, a head- or downwind migratory force, or a topographical migratory force respectively. The concept of standard direction, as used here, corresponds to the direction of the average goal migratory force. When seen in a population, this is the result of a genetically determined variation of the goal migratory directions, maturation, and the degree of overshooting, wind-drift, or reversed migration (Fig. 2).

The influence of wind may be considered passive (migratory drift) or active. The latter can be a down-wind migratory force (down-wind migration is, however, often passive) or a headwind migratory force. A headwind migratory force should be considered a compensatory reaction to the influences of wind-drift.

Geographical influence may manifest itself in a topographical attraction or in leading line migration.

Headwind and topographical migrations are closely related. The former is probably directed through visual perception. A bird selects one of the topographical sign stimuli which fits headwind migration. Along a coastline, the migration is generally greatest in the direction which gives the most headwind migration. A corresponding rule applies at coastal projections. 10–50% of diurnal migration is estimated to pass within range of sight, i.e. below 200 m. The value of making visual observations is not to be overlooked.

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DANSK RESUMÉ

Synlige dagtrækbevægelser

Formålet med artiklen er især en beskrivelse af, hvordan fuglenes trækbevægelser kan opfattes og inddeles. Der er forsøgt en mere *etologisk* fremgangsmåde end normalt ses indenfor dette felt.

Der foretages en gennemgang og visualisering af *trækdrift-begrebet*. Endvidere vises tilstedeværelsen af et aktivt, selvstændigt *modvinds-træk*. Der forsøges en inddeling af det *geografiske træk*, og den nære sammenhæng mellem modvindstræk og geografisk træk omtales. Desuden diskuteres *medvindstrækket* og *trækhøjderne*.

Artiklen er tænkt som en afrunding af RABØL (1964) og bygger overvejende på egne iagttagelser, der er sammenlignet med den existerende litteratur om de omhandlede emner. Vedrørende observationsteknik o.l. henvises til RABØL (1964 og 1965).

Vedrørende den exakte betydning af de anvendte ethologiske termer henvises til f. eks. LIND (1965).

Trækdrift-begrebet

En trækbevægelse er en *instinkthandling*. En instinkthandling kan betragtes som et produkt af en *drift* (her trækdrift – en bestemt indre aktiveringstilstand) og en til flere ydre *nøglestimuli*, der er i stand til at virke udløsende og retningsgivende på driften.

Den tidligere indførte term, *trækkraft* (RABØL 1964) må forestilles at bestå af en trækdrift og en (eller flere) nøglestimulus. Den symboliseres med en kraft (vektor), hvis retning er bestemt af nøglestimulusen og hvis længde (størrelse) er et udtryk for trækdriftens størrelse (Fig. 1.). RABØL (1964) bruger begrebet trækkraft i en videre og delvis anden betydning end den her givne.

Af retningsgivende ydre faktorer, der kan samvirke med trækdriften kan nævnes sol- og stjernehimlen, vindretningen og geografien. De to første kan give anledning til en *måltrækkraft*, de to andre til henholdsvis en *modvindstrækkraft* og en *geografisk trækkraft*. Måltrækkraften giver ophav til *normaltrækket*. Dette skilles ikke afgørende fra f. eks. modvindstræk og ledelinietræk. Forskellen på de tre trækformer ligger nemlig overvejende i den ydre påvirkning og mindre i trækdriften, omend størrelsen af denne nok er bestemmende for hvilke af de forhåndenværende stimuli, der gør sig gældende.

Nogle opfattelser fra litteraturen vedrørende trækdriften omtales og kommenteres. Der hersker almindelig enighed om, at trækdriften som andre drifter kan variere i styrke. Jo stærkere den er, desto mindre formår vejret og det underliggende landskab at sætte deres præg på trækket (både dets retning og størrelse). Begrebet *normaltrækretning* diskuteres. Denne kan siges at være retningen af den gennemsnitlige måltrækkraft for en population. Begrebet betragtes gennemgående for strikt – som en samme retning for alle populationens individer. Der er imidlertid en betydelig spredning omkring gennemsnitsværdien (normaltrækretningen), som Fig. 2 antyder. Årsagerne hertil kan være flere, f. eks. genetisk bestemte forskelle, ungfugle-spredning, tilbagetræk efter forlænget træk, vindafdrift o.s.v.

Vinden

Vindens indvirkning på trækket er åbenbar og ofte beskrevet. Imidlertid foreligger endnu ingen klar forståelse af vindafdriften, modvindstrækket og medvindstrækket set i en større sammenhæng.

Vindens indvirkning på trækket kan inddeles i en passiv vinddrift og en aktiv reaktion (d.v.s. trækbevægelser, hvor vindretningen indgår som en nøglestimulus). I sidste tilfælde kan enten en modvindstrækkraft eller en medvindstrækkraft gøre sig gældende.

En *medvindstrækkraft* forstærker øjensynlig ofte en måltrækkraft især for det høje træks vedkommende. Aktivt medvindstræk forekommer dog også i synlig højde, bl.a. postuleret af WILLIAMSON. Enkelte egne observationer f. eks. 21. 2. 1966 Tabel 5 viser også fænomenet. Funktionen af en medvindstrækkraft ligger givet i muligheden for en hurtig (lang) ekspansion af et træk. Især i stor højde vil meget tilnærmet medvindstræk dog nok bedst opfattes som en passiv vindafdrift. Også i det synlige træk (f. eks. under udtræksforsøg) ses ofte en slags passivt tilbagetræk med vinden (Fig. 3 og Fig. 14).

Modvindstræk synes overalt at være en meget udbredt reaktionsform under det synlige dagtræk. Besynderligt nok findes i litteraturen meget få forsøg på en isolering af, hvad der kunne kaldes en *modvindstrækkraft*. Årsagerne hertil er bl.a., at meget træk mod vinden også er ledelinietræk, resultatet af f. eks. ø-tiltrækning (Fig. 16) eller kan komme ind under begrebet omvendt træk. F. eks. Tabel 2 og Fig. 9–12 viser dog former for træk mod vinden, der kun meget vanskeligt kan forklares som andet end resultatet af en modvindstrækkraft (se også senere). Der synes at være en udpræget følelsesmæssig skepsis mod tilstedeværelsen af et aktivt modvindstræk (en modvindstrækkraft), både fordi det virker overflødigt energikrævende og ingen funktion synes at opfylde. Modvindstrækket tjener dog den meget vigtige opgave at være en kompenserende faktor (indskudt i det lave træk), der modvirker vindafdriften. Det er så at sige antagonisten til denne sidste i det kompleks, der hedder fugletrækket.

Geografien

Der skelnes mellem to former for geografisk træk, nemlig *ledelinietræk* og *geografisk tiltrækning*. Her indvirker enten en ledelinie eller en eller anden fremtrædende landskabsenhed (f. eks. en ø, Fig. 6 og Fig. 16) som nøglestimulus.

Modvindstræk og geografisk træk

En korrelation mellem modvindstræk og geografisk træk foretages. Ved en lige kystlinie gælder den almene regel, at trækket er størst i den retning langs kysten, der giver mest modvindstræk (f. eks. Tabel 2). Ved en kystombøjning eller på spidsen af en halvø gælder den nærstående regel, at trækket mod kystens vendepunkt er relativt størst langs den kystlinie, der forløber mest mod vinden (eller mindst med vinden). Se Fig. 9–13. Den nøje sammenhæng mellem træk mod vinden og geografisk træk påpeges. Modvindstræk fastlægges muligvis helt gennem visuel perception; det er en udvælgelse af en af de geografiske nøglestimuli, der passer med modvindstræk.

Måltræk, modvindstræk og geografisk træk

Afviger flere nøglestimuli ikke i retning for meget fra hinanden, kan de samarbejde, dog næppe (efter observationerne at dømme) med en simpel vektorresultant som resultat, men mere således at kun en af de givne stimuli virker retningsgivende. Som eks. herpå kan nævnes træk langs en ledelinie, hvis denne passer tilnærmet i retning med modvindstræk og/eller måltræk.

Ved hjælp af en model (Fig. 15) gives nogle eks. på samspillet mellem de forskellige trækkræfter. Der er en spredning af de individuelle måltrækkræfter omkring normaltrækretningen mod NØ (forår). På grund af denne spredning vil ses træk (udtræk) ved alle 4 landhjørner. Ser vi specielt på SV-hjørnet vil ses flest fugle med „SV"-vind og færrest med „NØ"-vind, medens situationen i vindstille er intermediær. Årsagen hertil er overvejende, at trækket, når det rammer ud på en kyst, følger kysten i den retning, der giver mest modvindstræk. F. eks. det fra Falsterbo kendte udtræk om foråret kan ganske utvunget forklares ved måltrækkræfternes spredning og samtidig indvirken af en modvindstrækkraft.

Trækhøjder

På grundlag af især de engelske radarundersøgelser af fugletrækkets højde (EASTWOOD et al. 1965), skønnes at 10–50% af dagtrækket foregår i synlig højde, d.v.s. nedenfor ca. 200 m (for småfuglenes vedkommende).

Konklusion og diskussion

Forskellige forhold diskuteres. Her skal blot fremhæves, at sammenlignet med „radartrækket" oplyser visuel observation om træk med en delvis anden årsagskombination, hvor de „uvedkommende", ydre påvirkninger spiller en relativt dominerende rolle. Studiet af disse påvirkninger har i allerhøjeste grad interesse, fordi alle former for trækbevægelser principielt må ligestilles, selv om det de oplyser om (og det man søger at finde) kan være forskelligt. Kriteriet for en trækbevægelse er efter min opfattelse blot tilstedeværelsen af en trækdrift men ikke størrelsen af denne eller arten af den indvirkende nøglestimulus.

TABLES 1-5

Table 1. Skylark *(Alauda arvensis)*. Knudshoved.

1) The indicated direction in the column, the average migration direction gives the nearest direction at the average migration direction indicated by degrees.
2) R/S indicates the ratio between the size of the average migratory force and the sum of migrants; it is a direct measure of the agreement of migration in the average migration direction.
3) The next four columns show the aggregate number of migrants in directions within the given compass.
4) See Figs. 4 & 5.

Tabel 1. Sanglærke (Alauda arvensis). *Knudshoved.*

1) Retningsangivelsen i kolonnen. Gennemsnitstrækretning giver den nærmeste retning ved den i grader angivne gennemsnitstrækretning.
2) R/S angiver forholdet mellem størrelsen af gennemsnitstrækkraften og summen af de trækkende individer og er et ligefremt mål for enigheden om træk i gennemsnitstrækretningen.
3) De fire næste kolonner viser det samlede antal trækkende individer i retninger indenfor de givne rammer.
4) Se iøvrigt Fig. 4 og Fig. 5.

Wind *Vind*	Average migratory direction *Gennemsnitstrækretning*	R/S	N-ENE. *N-ØNØ.*	E-SSE. *Ø-SSØ.*	S-WSW. *S-VSV.*	W-NNW. *V-NNV.*	Date *Dato*
N-NNE. 3-4	NE-ENE. 57°	138/173 (80%)	121	48	0	4	5. 4. 1964
NNE-NE. 3-4	ENE-E. 81°	36/40 (90%)	18	22	0	0	25. 4. 1964
NE 3-4	ENE-E. 76°	47/57 (83%)	32	24	1	0	3. 4. 1964
NE-ENE. 5	ENE. 68°	101/124 (83%)	63	45	8	6	29. 3. 1964
NE-ENE. 4-5	ENE-E. 82°	57/77 (74%)	29	40	5	3	18. 3. 1964
NE-ENE. (3)-4	ENE. 67°	92/108 (87%)	69	34	1	4	4. 4. 1964
NE-ENE. 3-4	NE. 46°	102/187 (55%)	94	61	5	27	1. 4. 1964
NE-ENE. 3	ENE-E. 81°	21,2/29 (73%)	9	17	0	3	31. 3. 1964
ENE. 4-(5)	ENE-E. 74°	70/86 (81%)	37	46	1	2	6. 3. 1964
ENE. 4	ENE-E. 84°	30/39 (77%)	13	24	1	1	30. 3. 1964
ENE. 4	ENE-E. 81°	304/371 (82%)	157	201	9	4	16. 3. 1964
ENE. (3)-4	E. 93°	58/70 (83%)	23	45	1	1	7. 3. 1964
ENE. (1)-2	ENE. 71°	22/28 (79%)	17	10	1	0	2. 3. 1964
ENE-E. 4-5	E. 85°	20,8/26 (80%)	8	16	1	1	31. 3. 1963
ENE-E. 4	E-ESE. 100°	85/100 (85%)	23	80	7	0	2. 4. 1964
ENE-E. (3)-4	E-ESE. 98°	106/121 (88%)	19	101	1	0	5. 3. 1964
ENE-E. 3-4	E. 88°	64/102 (62%)	25	61	3	13	28. 3. 1964
ENE-E. 3-4	NE-ENE. 54°	37,5/48 (78%)	29	40	5	3	18. 3. 1964
ENE-E. 1-2	E-ESE. 107°	25/28 (89%)	1	26	1	0	24. 4. 1964
E. (6)-7	ENE-E. 78°	39/49 (79%)	25	24	0	0	13. 3. 1964
E. 5-6	ENE-E. 81°	109/137 (80%)	50	81	4	2	25. 3. 1964
E. 3-4	ENE. 71°	284/316 (90%)	128	188	0	0	22. 3. 1963

Wind *Vind*	Average migratory direction *Gennemsnitstrækretning*	R/S	N–ENE. *N–ØNØ.*	E–SSE. *Ø–SSØ.*	S–WSW. *S–VSV.*	W–NNW. *V–NNV.*	Date *Dato*
E. 3–4	ENE–E. 76°	62/94 (66%)	34	52	6	2	23. 3. 1964
E. 3	E–ESE. 103°	260/304 (86%)	30	264	3	7	1. 4. 1963
E. 2–3	E. 95°	79/115 (69%)	34	69	7	5	19. 3. 1964
E. 2–3	E–ESE. 94°	164/197 (83%)	56	130	7	2	27. 3. 1964
E–ESE. 6–(7)	E. 95°	33,6/40 (84%)	9	30	1	0	30. 3. 1963
E–ESE. 4–5	E–ESE. 97°	242/262 (92%)	54	202	5	1	26. 3. 1964
ESE. 4	ESE. 108°	192/216 (89%)	11	201	3	1	12. 3. 1964
ESE. (2)–3	E–ESE. 104°	112/150 (75%)	31	106	8	5	19. 4. 1964
SW–WSW. 2	SE.. 129°	41/86 (48%)	12	51	7	16	15. 4. 1964
WSW. 3	SE 135°	26/160 (16%)	21	73	20	46	11. 4. 1964
WSW. 2–3	NNW–N. 354°	6/85 (7%)	12	31	14	28	9. 3. 1944
WSW. 2–(3)	ESE. 118°	35/71 (49%)	16	40	9	6	14. 4. 1964
WSW–W. (2)–3	ESE–SE. 129°	196/304 (64%)	22	232	6	44	13. 4. 1964
WSW–W. 1–2	ENE. 65°	48/142 (34%)	45	60	7	30	8. 3. 1964
WSW–W. 1–2	SSE· 150°	13/21 (62%)	0	15	3	3	20. 2. 1964
W. 3–4	S. 180°	15/94 (16%)	13	36	20	25	10. 2. 1964
W. 1	E–ESE. 106°	16,5/63 (25%)	16	28	10	9	20. 4. 1964
W. 0–2	NE–ENE. 59°	86/227 (38%)	115	55	22	35	9. 4. 1964
W–WNW. 5	NNE. 27°	71/128 (55%)	86	15	8	19	2. 2. 1964
W–WNW. 3–4	N–NNE. 13°	65/159 (41%)	80	18	19	42	4. 2. 1974
W–WNW. 3	N. 357°	14,5/57 (25%)	20	13	5	19	12. 2. 1964
W–WNW. 1–3	WNW–NW. 307°	38/107 (36%)	25	13	10	59	7. 4. 1964
WNW. 4	N–NNE. 6°	88/119 (74%)	77	3	1	38	22. 1. 1964
WNW–NW. 3	W–WNW. 282°	19/80 (24%)	16	15	23	26	11. 2. 1964
WNW–NW. 2–(3)	NNE. 20°	64/153 (42%)	78	31	10	34	9. 2. 1994
NW. 4–5	NE. 48°	26/44 (59%)	29	6	4	5	8. 2. 1964
NW. 3–4	NNE. 26°	122/210 (58%)	111	40	1	48	6. 4. 1964
NW. 2	N–NNE. 12°	58/121 (48%)	61	23	2	35	8. 4. 1964
NW. 1	ENE. 68°	156/228 (68%)	119	77	1	31	11. 3. 1964
NW–NNW. 2–3	NNE. 18°	697/739 (94%)	596	12	0	131	23. 3. 1963
ESE. (2)–3	E–ESE. 100°	62,5/70 (89%)	11	58	1	0	21. 4. 1964
ESE. 2–3	E–ESE. 104°	34/136 (25%)	24	63	23	26	24. 3. 1964
ESE–SE. 5	E. 90°	42/90 (47%)	26	48	11	5	26. 2. 1964
ESE–SE. 4–5	ESE. 110°	640/697 (92%)	0	688	9	0	19. 3. 1964
ESE–SE. 3–4	E–ESE. 103°	98/117 (84%)	20	95	1	1	29. 2. 1964
SE. 4–(5)	SE–SSE. 148°	20/58 (34%)	10	26	20	2	27. 2. 1964
SE. 3–4	SE. 139°	42/107 (37%)	18	57	23	9	25. 2. 1964
SE. 3–4	ESE–SE. 120°	180/199 (91%)	12	185	0	2	18. 4. 1964
SE. 3–4	E–ESE. 105°	300/338 (89%)	16	322	0	0	14. 3. 1963
SE. 2	ESE. 117°	58/69 (84%)	11	56	0	2	17. 4. 1964
SE. 1–2	ESE–SE. 125°	168/200 (84%)	7	167	20	6	2. 4. 1964
SE–SSE. 3–(4)	SE–SSE. 149°	19/24 (79%)	0	18	6	0	22. 2. 1964
SSE. 5	SE. 134°	118/123 (95%)	0	116	7	0	16. 3. 1963
SSE. 3	ESE–SE. 127°	990/1085 (91%)	62	1023	0	0	17. 3. 1963
S. 2–3	ESE. 116°	118/187 (63%)	19	137	10	21	16. 4. 1964
S. 0–1	SSW–SW. 219°	414/1611 (26%)	172	474	650	315	11. 3. 1963
SSW. 2–(3)	SE–SSE. 141°	272/433 (63%)	41	275	82	35	10. 4. 1964
SSW. 1–2	E. 90°	20/50 (40%)	8	26	4	12	23. 4. 1964
SSW–SW. 3–(4)	ESE–SE. 125°	87/195 (45%)	47	96	34	18	12. 4. 1964
SSW–SW. 2–3	SSE. 152°	20/53 (38%)	4	31	3	15	26. 4. 1964
SW. 1	ESE. 116°	59/73 (81%)	10	57	5	1	22. 4. 1964
SW–WSW. (2)–3	SSW. 200°	15/68 (22%)	14	17	20	17	3. 2. 1964

Table 2. Skylark *(Alauda arvensis)*. Teglværksskoven.

Coast line running about NNW–SSE. (Fig. 17), i.e. almost at right angles to the standard direction. The date 26. 3. 1961 however refers to an observation from a N–S.-going coast line south of Nyborg. "NNW." (W–NE.) indicates the number of migrants with migration directions within the sector W–N–W., but mainly NNW. Correspondingly for "SSE." (E–SW.). The column "At right angles" show migrations at right angles to the coast, predominantly ENE. with easterly winds and WSW. with westerly winds. The table clearly shows the general rule that the passage along a coast line is greatest in the direction which is mostly against the wind. Note the somewhat changing reactions, in a wind approximately at right angles to the coast line.

Tabel 2. Sanglærke (Alauda arvensis). *Teglværkskoven.*

Kystlinie forløbende ca. NNV–SSØ. (Fig. 17), d.v.s. omtrent vinkelret på normaltrækretningen. D. 26. 3. 1961 henviser dog til observation fra en N–S.-gående kystlinie sydfor Nyborg. „NNV" (V–NØ) er antallet af individer med trækretninger indenfor sektoren V–NØ, men ganske overvejende NNV. Tilsvarende for „SSØ" (Ø–SV). Kolonnen Vinkelret oplyser om træk vinkelret på kysten, ganske overvejende ØNØ med østlige vinde og VSV med vestlige vinde. Tabellen viser tydeligt regelen, at trækket langs en kystlinie er størst i den retning, der forløber mest mod vinden. Bemærk de noget skiftende reaktioner med vinden tilnærmet vinkelret på kystlinien.

Wind *Vind*	"NNW" (W–NE) *„NNV" (V–NØ)*	"SSE" (E–SW) *„SSØ" (Ø–SV)*	At right angles (ENE and WSW) *Vinkelret (ØNØ og VSV)*	Date *Dato*
NNE. 3–4	82	1	43	5. 4. 1964
NNE–NE. 3–4	24	0	2	25. 4. 1964
NE–ENE. 5	43	40	54	29. 3. 1964
ENE. 4	2	19	5	30. 3. 1964
ENE–E. 3–4	7	26	0	28. 3. 1964
E. 7–8	5	7	0	15. 3. 1964
E. 5–6	94	84	32	25. 3. 1964
E. 4–5	15	2	11	22. 3. 1964
E. 2–3	15	93	13	27. 3. 1964
E–ESE. 4–5	44	207	30	26. 3. 1964
ESE–SE. 5	6	181	1	26. 2. 1964
S. 1	2	10	5	12. 4. 1963
SSW. 3	0	15	0	3. 4. 1961
SSW–SW. 3–4	61	75	8	12. 4. 1964
SW. 2–3	34	17	0	11. 4. 1963
SW–WSW. 4–5	12	78	20	26. 3. 1961
WSW. 3	139	100	12	11. 4. 1964
WSW–W. 2–3	782	87	0	25. 3. 1962
WSW–W. 1–2	72	50	2	8. 3. 1964
W. 2	16	3	0	13. 4. 1963
W–WNW. 3	19	8	0	12. 2. 1964
WNW. 3–5	66	1	9	30. 3. 1961
WNW–NW. 3	104	0	2	11. 2. 1964
WNW–NW. 2	49	12	0	9. 2. 1964
NW. 4–5	77	4	0	8. 2. 1964

Table 3. Skylark *(Alauda arvensis)*. Slipshavn. See Fig. 17. The average geographical emigration direction, which is here almost SW. compared with ESE. at Knudshoved) gives, on an average, a greater R/S percentage in westerly than in easterly winds. We also note a western average migration direction on the four days with westerly winds, which with such wind directions is an exception to the rule at Knudshoved (cp. Table 1.).

Tabel 3. Sanglærke (Alauda arvensis). *Slipshavn. Se Fig. 17. Den gennemsnitlige geografiske udtrækretning, der her er ca. SV. (mod ØSØ. ved Knudshoved), medfører en gennemgående større R/S-procent med vestlige end med østlige vinde. Man ser også de fire dage med V-vind en vestlig gennemsnittrækretning, hvad der med sådanne vindretninger er undtagelsen på Knudshoved (sammenlign med Tabel 1).*

Wind *Vind*	Average migratory direction *Gennemsnitstrækretning*	R/S	N–ENE. *N–ØNØ.*	E–SSE. *Ø–SSØ.*	S–WSW. *S–VSV.*	W–NNW. *V–NNV.*	Date *Dato*
NNE. 3–4	NNE–NE. 31°	184/227 (81%)	207	11	9	0	5. 4. 1964
NE–ENE. 5	N–NNE. 15°	94/120 (78%)	101	14	5	0	29. 3. 1964
ENE–E. 3–4	SSE. 155°	10/29 (34%)	10	1	18	0	28. 3. 1964
ENE–E. 2	NE. 50°	34/141 (24%)	68	32	37	4	27. 3. 1964
E–ESE. 5	NNE. 17°	102/231 (44%)	149	47	42	3	25. 3. 1964
E–ESE. 4–5	ESE. 100°	42/100 (42%)	33	50	17	0	26. 3. 1964
SSW–SW. 3–(4)	W. 265°	56/71 (79°)	13	3	49	6	12. 4. 1964
W–WSW. 3–4	WSW. 243°	128/162 (79%)	4	5	110	43	11. 4. 1964
WNW–NW. 2	WNW. 289°	23/38 (61%)	9	0	12	17	9. 2. 1964
W. 3–4	SSW–SW. 211°	28/34 (82%)	4	1	26	3	10. 2. 1964

Table 4. Skylark *(Alauda arvensis)*. Hjulby Sø. Inland locality (see Fig. 17). Note the influence of the headwind migration force and a distinct variation of the migration directions.

Tabel 4. Sanglærke (Alauda arvensis). *Hjulby Sø. Indlandslokalitet (se Fig. 17). Bemærk indflydelsen af modvindstrækkraften og en klar spredning af trækretningerne.*

Wind *Vind*	Average migratory direction *Gennemsnitstrækretning*	R/S	N–ENE. *N–ØNØ.*	E–SSE. *Ø–SSØ.*	S–WSW. *S–VSV.*	W–NNW. *V–NNV.*	Date *Dato*
NNE. 3–4	NE. 49°	43/50 (86%)	35	15	0	0	5. 4. 1964
E. 7–(8)	NE. 45°	75/75 (100%)	0	75	0	0	15. 3. 1964
E. 3–(4)	ENE–E. 74°	14,5/18 (81%)	9	9	0	0	1. 3. 1964
S. 0–1	N–NNE. 7°	148/212 (69%)	118	12	10	72	11. 3. 1963
W. 1–2	NNW–N. 346°	19,5/53 (37%)	21	7	9	16	8. 3. 1964
W–WNW. 5	NNW–N. 348°	101/115 (88%)	58	2	1	54	2. 2. 1964
WNW–NW. 2–(3)	NW. 319°	46/90 (51%)	33	3	15	39	9. 2. 1964

Table 5. Skylark *(Alauda arvensis)*. – Inland localities. Observation post on open land, 12.3 and 19.3 are from Højrup, Middle Funen. The other observations are from Torpet near Ringsted, Middle Zealand, where observations were made during a period of 17 days in the spring of 1966. Only days with more than 15 migrating birds are however included here. There is a great variation in the migratory directions even on calm days. The other days appear to differ much although the directions of the wind were almost identical.

Tabel 5. Sanglærke (Alauda arvensis). *Indlandslokaliteter. Observationspost i åbent land. 12.3. og 19. 3. stammer fra Sdr. Højrup, Midtfyn. De andre observationer er fra Torpet ved Ringsted, Midtsjælland, hvor der ialt i foråret 1966 observeredes 17 dage. Kun dage med over 15 trækkende fugle er dog medtaget her. Man bemærker stor spredning i trækretningerne selv på de vindstille dage. De øvrige dage fremtræder meget forskellige, selv om vindretningerne har været noget nær identiske.*

Wind *Vind*	Average migratory direction *Gennemsnitstrækretrung*	R/S	N–ENE. *N–ØNØ.*	E–SSE. *Ø–SSØ.*	S–WSW. *S–VSV.*	W–NNW. *V–NNV.*	Date *Dato*
0	NNW. 349°	14,8/39 (38%)	14	5	6	14	4. 3. 1966
0	ENE. 72°	13,6/31 (44%)	8	16	1	6	19. 3. 1966
S–SSW. (2)–3	N–NNE. 15°	320/356 (90%)	313	4	2	37	21. 2. 1966
S–SSW. 2–3	W. 265°	31/101 (31%)	21	10	38	32	28. 2. 1966
S–SSW. 2–3	S–SSW. 186°	20/30 (67%)	1	11	16	2	3. 3. 1966
SW. 5	WNW. 301°	10,1/27 (37%)	9	2	7	9	24. 2. 1966
SW. 2–3	NNE. 22°	0,8/19 (4%)	8	1	8	2	25. 2. 1966
SW. 2–3	WSW–W. 260°	10,4/20 (52%)	3	2	8	7	10. 3. 1966
SW–WSW. 2–3	SW–WSW. 237°	16/37 (43%)	6	4	21	6	8. 3. 1966
SW–WSW. 0–1	SW–WSW. 238°	60/157 (38%)	27	14	84	32	12. 3. 1966

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