"Headwind migration"

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(Med et dansk resumé: Modvindstræk.)

In his publication "Fugletrækket ved Knudshoved" (1964, hereafter referred to as I) Rabøl gave a detailed account of his observation technique, his results and his interpretation of day-migration. In a later paper "Visual diurnal migratory movement" (1967, II) he has attempted to give a more comprehensive interpretation of his now still more extensive and valuable material. For this purpose he has developed a model of migratory behaviour, and from comparison between model and observations he concludes that the existence of the postulated types of behaviour has been proved; this especially applies to the so-called "headwind migration", the establishing of which appears to be his most important aim.

Migration into the wind has previously been observed and the interpretation has caused much controversy (cf. Dorst 1961), however, Rabøl does not refer to such discussion and states his conclusions rather categorically.

In our opinion Rabøl's model as well as his conclusions are open to serious criticism, which we shall set forth in the following.

RABØL's MODEL

Rabøl recognizes three basic, *indivisible* types of migratory behaviour, viz. "goal migration", "topographical migration" and "headwind migration". It is his opinion that nearly all visible flight movements can be split up into these three components. There is one more factor included in the model, "inertia", this is explicitly mentioned II, p. 79, 1.7 f.b. and is hidden in the deduction of the direction of the "topographical migratory force" at Knudshoved (I, p. 55, 1.25). The inertia may be conceived as a tendency to prolong a flight with unchanged course after the sign stimulus has ceased to be in action.

Below the three "indivisible" types of behaviour and the problem of their combination will be discussed in more detail.

The three types of migratory behaviour.

Rabøl is rather clear in his specifications of the sign stimuli releasing the different types of migratory flight.

When performing "goal migration" the bird heads for a remote and invisible goal

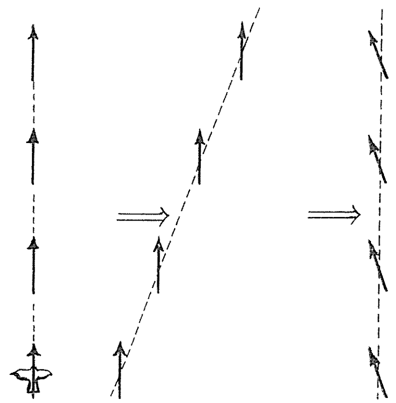

Fig. 1. Flight in a fixed compass-direction ("goal migration"); *a* in calm weather, *b* in a crosswind, uncompensated, and *c* in a crosswind with compensation for drift.

Fig. 1. Fuglens flugt i en fixeret retning („måltræk"); a i vindstille, b i sidevind uden kompensation, c i sidevind med kompensation for afdrift.

behind the horizon, the sign stimulus being "stars and sun", determining the direction towards the goal. RABØL points out that in a migrating population there is a considerable spreading of the individual instinctive compass directions, II fig. 2.

In fig. 1 are shown some situations relating to birds flying in a fixed compass direction, in calm weather and in crosswind. Fig. 1 b shows the well-known phenomenon that a bird flying in a crosswind receives a lateral displacement (drift). It may compensate for such drift while flying by choosing a slightly different course, fig. 1 c. In this case its track will get the intended direction, but this situation corresponds to a combination of "goal migration" and intentional flight into the wind, not to the pure "goal migration".

The "topographical migration" is defined as flight towards a "topographical unit", which may be any prominent structure in the landscape, the simplest picture being that of a bird flying towards a small island. Such flight presupposes that the bird unceasingly maintains a course (heading) pointing towards the island, and if there is a wind the track will become curved, the heading tending to become more and more against the wind, cf. fig. 2 b. This is a consequence of simple physical laws. An analogous example, which may be more familiar to the reader, is a swimmer in a river heading for a pole fixed to the bottom; the swimmer's track will be quite similar to fig. 2 b. We are not concerned with the problem whether the bird (or the swimmer) could

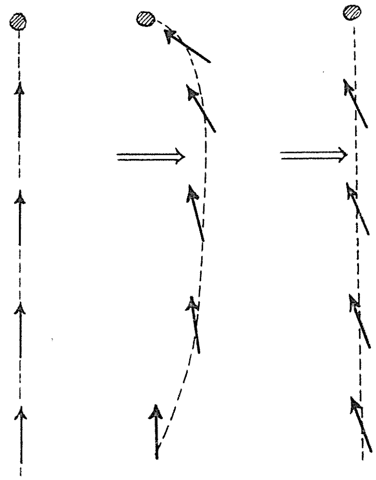

Fig. 2. Flight against a fixpoint ("topographical migration"); *a* in calm weather, *b* in a crosswind, uncompensated, and *c* in a crosswind with compensation for drift.

Fig. 2. Fuglens flugt imod et fixeret punkt (topografisk træk), a i vindstille, b i sidevind uden kompensation, c i sidevind med kompensation for afdrift.

proceed to the fixpoint along a straight track by compensation for the drift, cf. fig. 2 c, for in this case we would have a combination of intentional flight into the wind and "topographical migration", and not the latter in its pure form. We therefore conclude that "topographical migration against a point" leads to flight into the wind as shown in fig. 2 b.*)

As to the "headwind migration" it should be noticed that RABØL maintains that flying birds determine the direction of wind through observation of the "movement" of the landscape (II, p. 77, l. 9 f.b.), and the "headwind migration" is therefore a behaviour characterized by flight into the wind released by "moving" topography.

It is now evident that "headwind migration" is released by topographical units which are seen to move, but such topographical units which release a "topographical migration" will also "move", when there is a wind. Moreover, "topographical migration" leads to flight against the wind. It is therefore hard to avoid the conclusion that RABØL's "topographical migration" and "headwind migration" are identical behaviours.

Combinations of behaviours

In his first paper (I) RABØL made extensive use of vector-combinations of the three types of behaviour. In his last paper (II) he admits, however, that simple vector-combinations may not always be the correct approach (II, p. 86 l. 21). Nevertheless vector-combination has been used in procuring the material in II fig. 4, and its interpretation in terms of the three proposed instinctive behaviours requires vector-resolution. The concept underlying this procedure is, that the actual flight direction of the individual bird is a resultant of the three "migratory forces", and hence that the "average migratory force" is the resultant of the three migratory forces taken for all the observed population of migrating birds (I p. 55). The average migratory force is derived from the observations by adding vectors, which represent the relative numbers of birds seen flying in each compass-direction. RABØL's II fig. 4, which demonstrates the variation of the direction of the "average migratory force" with the wind direction, forms a main "proof" for the existence of the "headwind migration", and it can therefore be concluded that at least one condition for this proof is uncertain see also II, p. 88.

A point which deserves further consideration is RABØL's concept that a behaviour of a bird can be described as a simultaneous combination of other "basic" behaviours. This idea of combinations is intimately connected with RABØL's migratory drive concept (II, p. 74). It is assumed here that the different types of migratory behaviour are all caused by one and the same drive, and such assumption would give some justification for combination of the different behaviours, because in reality there is only one behaviour ("motor pattern") and the combination is a combination of the stimuli. However, there are several objections to be made against RABØL's concept. Firstly, the idea, that the drive is non-directed (fig. 1, II) is wrong, for it must be embodied in the bird itself, in what is called the instinct, how it shall react to a stimulus, not only that it shall react. This may, however, be a lapse on behalf of the author, but the peculiar consequence is, that one and the same migratory

*) According to RABØL (II p. 83) the basic element in all kinds of topographical migration is attraction. We have restricted our consideration to the simplest case (attraction toward a single topographical unit) but we want to point out that the picture is different with the respect to crosswind-displacement if flying birds navigate by means of two or more "topographical units" as landmarks. In that case they may maintain a linear track.

drive becomes the mechanism, by which the bird reacts in different and characteristic ways on each of three stimuli. Secondly, the idea that the three sign stimuli "sun and stars", "topography" and "headwind" are equivalent with respect to the migratory drive, as they release the same drive, and as the size of the "migratory forces" only depends on the intensity level of the drive, is contradicted by the information (II p. 76 l. 18) that effects from weather conditions and landscape are reduced, when the migratory drive is strong, *i.e.* the sign stimuli are not equivalent at all intensities of the drive. This inconsistency would disappear by postulating the existence of three "drives" of "instincts", corresponding to each of the different types of behaviour, but in that case it would be much more difficult to justify combinations of the instincts, because they are conflicting. As "instincts" are abstractions from behaviours and their relationship to certain stimuli, it is also logical to attribute each type of reactionpattern its own instinct.

While these remarks do not necessarily show that RABØL's interpretation of his fig. 4 is wrong, it would appear that its value as a "proof" of the "headwind migration" is highly dubious.

RABØL's CONCLUSIONS

Since RABØL's model is inconsistent, it is of little value to compare it directly with observation data. It is possible, however to maintain the idea of an intentional flight into the wind, different from the "topographical migration", by postulating another sign stimulus for the release of the "headwind migration". Atmospheric turbulence has been suggested previously (NISBET 1955).

Although RABØL's interpretation of his observation data is not acceptable it remains to be explained that they (including his II fig. 4) in fact demonstrate a tendency to headwind flight. It is very likely that an amended model would appear to be consistent with the observation material. This does still not mean that the model is correct, unless all other conceivable explanations have been eliminated.

Already Emperor FRIEDRICH II (1194–1250) observed that birds flying headwind generally fly lower than birds flying downwind (STRESEMANN 1951). This observation has often been confirmed more recently, but when stated in modern texts it is usually implied that a bird determines its flight-direction without regard to the wind-direction, but that it chooses its flight-altitude according to the wind-direction relative to the flight-direction (cf. e.g. LACK 1960 p. 178 and 191). This would also be an obvious explanation, considering that the wind usually is stronger in great altitudes than in small altitudes.

RABØL assumes that there is a marked spreading in the directions of the goal migration within a given population of migrants (II fig. 2), and it therefore follows that at any locality and at any point of time, there are some migrants which happen to perform "goal migration" against the wind. Even if these are comparatively few, they may contribute disproportionately more to the visual migration than the more numerous migrants that have other standard directions, since the latter are less likely to be within visible range.

The phenomenon appears to create a background of headwind flight, which must be eleminated before an instinctive headwind migration can be isolated. It may be the sole and sufficient explanation for RABØL's inland observations of birds flying headwind. It may also yield the appropriate explanation of the leading line migration against the wind, assuming with RABØL that influences from the topography, in this case the "leading line effect", are strongest, when the birds fly low. Though he is aware of the principle (I p. 97) he does not mention that he has considered this possibility, and he makes no correction for the phenomenon. It is also difficult to see how it could be done.

RABØL will perhaps maintain that the phenomenon observed by FRIEDRICH II is interpreted in a new way in his concept of "headwind migration": "birds flying low fly against the wind" instead of "birds flying against the wind fly low" (cf. I p. 57). However, such new and less obvious interpretation does not deserve much attention as long as the old and more obvious one has not been shown to be insufficient or wrong.

There is the further complication in RABØL's observation material that the cases where "headwind migration" is most in evidence are from localities with a considerable "topographical migration". RABØL has realized that the birds may approach the island of Hesselø in a headwind, cf. his II fig. 16 and fig. 2 b above, and he admits that this fact in combination with "inertia" may explain why the emigration from Hesselø mainly proceed headwind. However, he does not accept it as a full explanation, and he does not at all consider this possibility for Knudshoved, which is very similar to an island. One may also consider the possibility that there are small "topographical units" on the island or peninsula to which the birds may react and therefore fly headwind when they are crossing such localities and are approaching the opposite coast. The observations at Teglværksskoven (II table 2) are likewise complicated by the fact that there is a small wood, a "topographical unit", right at the observation point.

It appears therefore that none of the author's observations are well suited for the isolation of the "headwind migration" because in each case it must be expected that a tendency to headwind flight manifests itself for some other reason than the instinctive "headwind migration". RABØL can therefore not conclude that such behaviour has been isolated (ascertained, *konstateret*).

DANSK RESUME

Modvindstræk.

I to afhandlinger her i tidsskriftet har RABØL (1964 og 1967, her kaldet I og II) forsøgt at fortolke variationerne i de flugtretninger, han har iagttaget under sine omfattende observationer af det synlige dagtræk, på grundlag af en modelforestilling om trækdriften, der antages at være ophav til tre instinktive trækadfærdsformer. De synlige dagtrækbevægelser betragtes som sammensat af disse tre adfærdsformer „måltræk", „topografisk træk" og „modvindstræk". Dertil kommer fænomenet *inerti*, hvorved forstås at fuglene har en tendens til at fastholde en flyveretning efter at det retningsgivende stimulus er ophørt at fungere. Hans hovedanliggende har været at argumentere for eksistensen af det instinktive modvindstræk, og han konkluderer at have isoleret denne adfærd. Medens de to andre adfærdsformer er almindeligt accepterede, har modvindstrækkets existens været genstand for tvivl og diskussion tidligere (jf. DORST 1961), hvad RABØL dog lader uomtalt. Såvel RABØLS model som hans argumenter for modvindstrækket forekommer os lidet tilfredsstillende og indbyder til de følgende kritiske kommentarer.

„Måltrækket" er rettet mod et fjernt og usynligt

mål, som fuglene orienterer sig imod ved hjælp af stjernehimmel og sol, der altså repræsenterer nøglestimulus for måltrækkets instinktive retningsvalg. RABØL påpeger, at i en given population af trækkende fugle, må man regne med en betydelig spredning på måltrækretningen (II fig. 2). Allerede kejser FRIEDRICH II (1194–1250) opdagede, at fugle der flyver mod vinden flyver lavere end fugle, der flyver med vinden, et fænomen der ofte er bekræftet i nyere tid og forstået således, at det er flyvehøjden, der repræsenterer fuglenes reaktion på vindens retning i forhold til deres flyveretning. Dette reaktionsmønster må i forbindelse med spredningen på måltrækretningen medføre, at der vil være en betydelig baggrund af måltrækkende fugle, der flyver mod vinden nær jorden, hvad der alene kan forklare RABØLS indlandsobservationer og meget vel også forklare ledelinietrækket i modvind, hvis man med RABØL antager, at topografiske stimuli, her ledelinien, særligt har indflydelse på lavtflyvende fugle. Selvom RABØL er bekendt med fænomenet, har han ikke taget højde herfor i sin analyse af materialet

„Topografisk træk" er træk, der er retningsbestemt af stimuli fra landskabet, „topografiske enheder", og det enkleste eksempel er en lille ø, som fuglene søger henimod. En sidevind vil medføre, at flugtruten for en fugl, der flyver mod et bestemt punkt bliver krummet således, at den bliver rettet mere og mere mod vinden (fig. 2 og II fig. 16). Rent topografisk træk indebærer altså en tendens til modvindsflugt. RABØL accepterer, at dette kan være en del af, men ikke hele forklaringen på modvindstrækket ved Hesselø, ligesom udtrækket i modvind også kun delvis forklares ved inerti. Han har imidlertid slet ikke taget denne forklaringsmulighed i betragtning ved analysen af sine iagttagelser fra Knudshoved, der ligner en ø så meget, at det samme fænomen må antages at kunne spille en væsentlig rolle.

„Modvindstræk" er en instinktiv tendens til at flyve imod vinden. RABØL mener ikke, at fuglene kan bestemme vindretningen på anden måde end ved at iagttage landskabets bevægelse i forhold til luftruten og nøglestimulus for modvindstrækket er altså topografiske enheder, der bevæger sig. Topografiske enheder, der udløser „topografisk træk" vil imidlertid bevæge sig på tilsvarende måde, når det blæser, og da det som vist også indebærer en tendens til at flyve mod vinden, må man konkludere, at RABØLS to adfærdskategorier „topografisk træk" og „modvindstræk" ikke kan adskilles, og derfor er identiske.

Modvindstrækkategorien kunne dog opretholdes, hvis man antog et andet stimulus, f. eks. den atmosfæriske turbulens, som foreslået af NISBET (1955).

RABØLS væsentligste bevisførelse for modvindstrækkets existens hviler på en analyse af Knudshovedtrækket, der for enkelte dage karakteriseres ved en gennemsnitstrækretning, der er retningen for en „gennemsnitstrækkraft", en vektor, der er udregnet på grundlag af observationerne, idet antallene af fugle, som er set flyve i de forskellige retninger adderes som vektorer. Ud fra den antagelse, at den enkelte fugls aktuelle flyveretning er en resultant af de tre postulerede „trækkræfter", d.v.s. instinkter til at flyve i de tre retninger svarende til „måltræk", „topografisk træk" og „modvindstræk", kan man tilsvarende antage, at gennemsnitstrækkraften er en resultant af summerne af de tre trækkræfter i hele den iagttagne population af trækkende fugle. Hvis stimulus for en af trækkræfterne varierer, skulle man kunne spore denne variation i gennemsnitstrækkraften. Dette er grundlaget for analysen i I, men i II har RABØL vedgået, at vektorkombinationer på instinkter eller adfærdsformer ikke altid er den rette vej, selvom han fastholder at en eller anden form for kombination må finde sted. II fig. 4 er ikke desto mindre en fremstilling af gennemsnitstrækretningens variation med vindretningen, og fortolkningen ud fra modellens instinktive adfærdsmønstre forudsætter det samme ræsonnement som i I. Fig. 4 repræsenterer det væsentligste „bevis" i II for modvindstrækkets existens, men forudsætningen for fortolkningen gælder ikke ubetinget.

Nu er det svært at se, at det er tilladelig at opfatte en fugls adfærd som værende sammensat af flere samtidig basale adfærdsformer. Ideen om sådanne kombinationer hænger nøje sammen med modellens forestilling om, at instinktet eller driften bag de tre adfærdsmønstre er et og det samme, trækdriften; adfærdsformerne er i grunden den samme adfærd, blot udløst og retningsbestemt af forskellige stimuli. Dette kunne synes at legitimere kombinationer, men modellen kan ikke accepteres uden videre. For det første er instinktet ikke retningsbestemt, stimulus alene bestemmer retningen (II fig. 1). Heroverfor må indvendes, at fuglens reaktionsmåde på et stimulus, her retningsvalget, er noget fuglen iboende, altså tilhørende det man kalder et instinkt, instinktet bestemmer ikke blot hvad der skal reageres på. For det andet er de tre stimuli „sol og stjerner", „topografiske enheder" og „modvind" ligestillede, for så vidt som de udløser det samme instinkt, ligesom størrelsen af „trækkraften" alene afhænger af driftens størrelse, af intensitetsniveauet; men dette modsiges af, at „topografisk træk" og „modvindstræk" undertrykkes, når driften er stor, – de tre stimuli er altså ikke ligestillede ved alle intensitetsniveauer af driften. Da „instinkter" er abstraktioner fra adfærd og disses eventuelt fastslåede relation til visse stimuli, ville det være logisk at antage et instinkt for hver type af adfærd, så meget mere, som de er tilknyttet hver sit stimulus. Derved ville de nævnte urimeligheder forsvinde; men på den anden side ville det være meget vanskeligere at retfærdiggøre kombination af instinkterne, for så vidt som de er alternative, i konflikt, om de fungerer samtidig.

Selvom Rabøls fortolkning af fig. 4 ikke nødvendigvis er forkert, er diagrammets værdi som bevis for modvindstrækket højst tvivlsom, og som ovenfor omtalt er der ved fortolkningen af den fundne variation med vindretningen ikke taget hensyn til, at de andre former for trækadfærd også kan indebære modvindstræk.

Selvom en forbedret model kunne bringes i overensstemmelse med observationerne, ville den dog ikke kunne anses for korrekt, førend andre kendte forklaringsmuligheder var udelukket. Både „måltræk" og „topografisk træk" fører til en vis overvægt af ikke-instinktiv modvindsflugt indenfor den del af det synlige dagtræk, der er synligt fra jorden, og ingen af Rabøls observationsrækker er derfor egnede til at isolere et instinktivt modvindstræk. Rabøl kan således ikke konkludere, at han har påvist denne adfærdsform.

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