Headwind-migration. Answer

By

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(Med et dansk resumé: Modvindstræk. Svar.)

Before I answer I should first stress the hard core in the criticism.

CHRISTENSEN and JACOBSEN (C & J) states I have one *cause* (a head wind migratory force) *too much* in my migratory behaviour model.

They think the headwind migratory force can be divided in topographical – and/or goal migratory components – or at least they think I have not clearly showed this is *not* the case.

C. & J. states that I "recognizes three basic, *indivisible* types of migratory behaviour –". I think the designation, *stimulus-different*, is better since it allows a possible stimulus-combination. I further recognize a fourth type, down-migration, not mentioned by C. & J.

I do not think there is one more factor, "*inertia*", included in my model. This designation is not on the same level as the other ones. There is no true directed flight without actual directing stimuli. That a bird continues to emigrate in the same direction after having followed for a time e.g. a coastline is a result of e.g. keeping the same "angle" to the turbulent wind, to the waves or to the sun (only a few possibilities to be mentioned).

In RABØL 1967 (II) I do *not categorically* say that all the headwind-migrations should be regarded as *visual* determined by "mowing" topographical cues. I cite myself, II p. 86: "*Possibly* headwind migration should only be regarded as a unification of the topographically possibilities.", II p. 86: "– headwind migratory force may *perhaps* manifest itself only as a consequence of visual sensations" and II p. 77 1.9 f.b.: "As the wind direction – in my opinion – *normally* can *hardly* be determined by a flying bird without visual coordination – –". At the time I wrote II nearly all authors (NISBET 1955 and DRURY and NISBET 1964 as exceptions) postulated very categorically that a flying bird could not *feel* the wind (among them HESSELBJERG CHRISTENSEN pers. comm.). In the same context C & J in the chapter "RABØL's conclusions" write: "– – when stated in modern texts it is usually implied, that a bird determines its flight-direction without regard to the wind-direction". But this often do not holds true in *recent* texts concerning both visible- and radar-migration (e.g. GRUYS-CASIMIR 1965, EVANS 1967 and BELLROSE 1967). Especially BELLROSE postulates that the turbulent wind could be used and is important as an orientation-reference.

To my cautious visual-skewed headwind-stimulus model in II I now want to add the turbulent stimulus. Possible both in connection or only one of these in a time can act as directing stimuli. In any case I think it is defensible to call the observed headwind-migration for the result of a headwind migratory force or a positive anemo-taxis. A somewhat identical discussion has been undertaken with respect to the rheo-taxis of fishes (Fraenkel and Gunn 1940).

In this context I want to stress that also within solar- or stellar orientation the migratory directions are often established through a topographical- or wind-turbulent factor. The first can be e.g. directions determined from the sun-azimuth (the sun-projection at the horizontal level – e.g. Schmidt-Koenig 1965). The other could be the fixpoint-windturbulence relations discussed by Bellrose (1967). Under the heading, "inertia" I also showed that astronomical or windturbulent stimuli could be "vicarious" for a topographically directed stimulus.

C. & J. state me as having admitted in II that simple vector-combinations may not be the correct approach. They refer to the following statement: "If several sign stimuli do not differ to much from each other in direction they may coorperate, 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". It is difficult to see how this obviously rather *special* case in which vector-combinations cannot be used, can invalidate the concept of vector-combinations in general. I have further in countless other contexts written as e.g. II p. 86: "A migratory direction has *one or several* of the said sign stimuli and a migratory drive as its immedeate cause".

It is possible that a great deal of headwind migration *starts* as a flight (a passive rectification) towards a topographical unit, e.g. Hesselø or Knudshoved. But an emigration against the wind could not has "inertia" as the proximate cause. "Inertia" could not be a cause. Further much emigration against the wind can often not be regarded as goal migration – e.g. II Fig. 7. This figure shows Chaffinches *(Fringilla coelebs)* emigrating "SE" and "NV" in autumn. The standard direction is approximately SSV and very probable there is only a very little direction-variation round the SSV-mean. The only plausible directing stimulus in the emigration should be the headwind determined either visually or by the wind-turbulence. The bending of the emigration shown at Fig. 1 also is difficult to explain soundly without operating with a headwind migratory force.

I next want to deal with C. & J.'s objections against my migratory drive and migratory force concept.

The *motor pattern* (in the migratory movement) "originating" from the migratory drive is in itself undirected in space. In the migratory drive is, however, potentiality for selection of appropriate directing stimuli. When these are lacking – e.g. birds showing "zugunruhe" in overcast (Emlen 1967) – the "intention"-movements are un-directed.

What I have called a *migratory force* is the same as e.g. Fraenkel and Gunn (1940) and Lindauer (1964) call a *taxis*. Koehler (1950) distinguishes between a *taxi(a)* – "die gesamte Orientierungshandlung" – and a *taxi(n)* – "die orientierender Wendung". The first is what Fraenkel and Gunn mean with taxis, and the second is what ethologists mean with the concept of taxis. A *migratory movement* is a taxi(a), which again is soluble in a *fixed motor pattern* (the flight) and one or a combination of *taxis(n)*. After Fraenkel and Gunn the different migratory forces can be said to belong to *telo-* or *menotaxis* (compass-reactions).

I cannot see (as C. & J. propose) why it is better operating with three "instincts" (four with the downwind migratory force). It is only a matter of words and I think it is lesser appropriate in "attacking" the

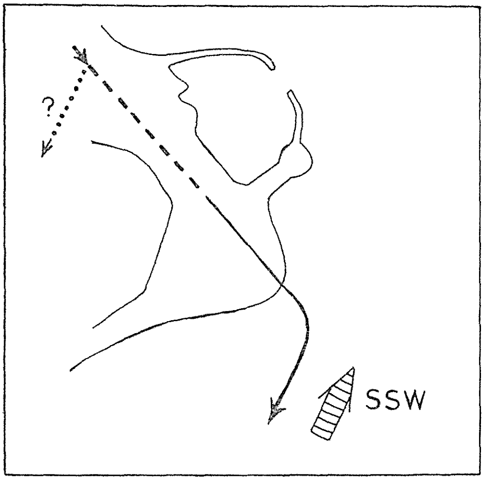

Fig. 1. A common reaction (hatched and fully drawn) Knudshoved, spring. A SE-emigration is converted into a SSW-movement against the wind. It is difficult to see if the goal direction is to the "SW" (reversed migration) why the movement not earlier (the dotted line with?) is bent in that direction. The SSW-movement most probably is directed by the (head)wind.

Fig. 1. Et alm. trækbevægelses-forløb på Knudshoved, forår. Et SØ-udtræk går over i en SSV-bevægelse rettet mod vinden. Hvis fuglens mål-område lå mod „SV" burde fuglen forlængst have fulgt en trækvej symboliseret med den prikkede pil. Derfor retningsgives SSV-bevægelsen sandsynligvis af (mod)vinden.

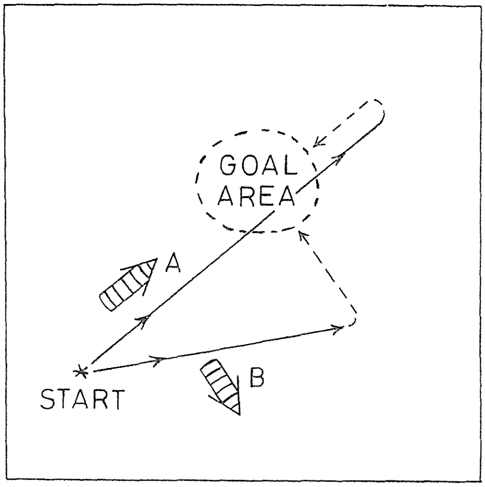

Fig. 2. A goal area is overshooted in a following wind (A) or a displacement occurs under a lateral wind-drift (B). The compensatory goal movements (the hatched lines) are now directed into the wind without the latter being nescessarily needed as a directing stimulus.

Fig. 2. Et målområde overskydes i medvind (A) eller der forekommer en sideforskydning på grund af sidevinds-drift (B). De kompensatoriske måltræk-bevægelser peger nu mod vinden, uden at denne nødvendigvis behøver at indgå som retningsgivende stimulus i trækbevægelsen.

problems since the motor patterns are identical for the different forces. It also seems an appropriate model that "the sign (better directing) stimuli are not equivalent at all *intensities* of the drive" (to cite C. & J.). Both Rabøl (1964) and Gruys-Casimir (1965) maintain that migration more or less right into the wind very often becomes a more prominent reaction with time in the daily movements. From such observations of conversions to different reactions it is often stated that the migratory drive wanes with time. It is may be a rather tentative conclusion but I still think my conclusions II p. 76 last in the chapter "Migratory drive concept" are defensable, among other for the following reasons:

The designation, *drive-intensity*, should shortly be discussed. What do we mean with a high intensity? We mean a great probability or a great amount of "energy" to perform an act. We say the migratory drive (intensity) is strong when the amount of standard migration (in a population) is very high, e.g. migration which follows weather-improvement after a delayed period in bad weather. The delay has caused a great "drift" between the birds "goal-search-image" (the "coordinates" of the actual goal area) and the "coordinates" of the place where the bird is. See fig. 2. The un-equilibrium between both causes a great amount of goal (standard) migration and it is appropriate to say that goal migration and a strong drive is often linked. When the distance between the goal area and the actual position diminishes (through goal migration) some sort of drive satiation comes. The goal becomes further more "diffuse" as if some sort of gridorientation were used (e.g. SCHMIDT-KOENIG 1965). May be it is why topographical- and headwind-orientation can be ascertained to play a greater role than previously and it is defensable to say that they often occur under a rather weak drive (intensity).

The most serious objection against my conception of the headwind migration in C. & J. is the question concerning the relationship between the *flying height* and the migration directions. C. & J. use my fig. 2 in II showing the pronounced variation of the goal migratory forces around the standard direction. This figure was especially produced to reflect the goal migratory forces in Skylark *(Alauda arvensis)*, Denmark and spring. Other birds – especially nocturnal and far-migrating birds – probably has much lesser direction-variations round the standard direction and round the 180°-"wrong" (reversed) direction.

GRUYS-CASIMIR (1965) describes a technique discovering movements from ground up to over 1 km. in height. In her Table IX and fig. 10 p. 218–219 she shows the average migratory heights for the standard migration, Holland, inland, autumn, Chaffinch. The heights in a following wind were greater than in a headwind, but the differences were rather small (most averages in following wind 40–70 m. and in headwind 20–50 m.). Different reactions are probable in other species and in other regions, but I think Skylark, Denmark, spring (the most important species for my interpretations) follow much of the same pattern as the Chaffinch with respect to rather small differences in flying heights under different wind conditions.

My conclusion should be that the effect mentioned by C. & J. is obvious, but probably of minor-importance *without any cooperation* of a notable headwind migratory force. This probably acts better (through visual conduction) in the lower flying heights. I also think birds flying low have on the average a rather weak migratory drive.

Fig. 2 shows headwind migration which is *not* nescessarily a result of a headwind migratory force. A goal area can be overshooted in a following wind or a displacement can occur under a lateral wind-drift. In both instances the compensatory goal movements may occur in directions approximately against the wind. May be fig. 2 shows a common reaction-pattern but I want to stress that many such movements – as movements started as a topographical attraction (discussed earlier) – also beside topographical – and/or astronomical stimuli use the headwind as an integrating orientation cue.

We can very often ascertain an *overcompensation* for the wind-drift (e.g. II fig. 4 and GRUYS-CASIMIR 1965). I think this cannot be explained sufficiently as a reaction only directed of topographical- or astronomical stimuli. The overcompensation is an active answer to a stimulus-configuration in which the (head)wind is a part. Also a mere *compensation* can be said to have a headwind-migration component as C & J mentions under their fig. 1 c ("an intentional flight into the wind"). It is, however, only in regard to migratory movements showing overcompensation that I will talk about an integrating headwind-component, a headwind migratory force.

If I should criticize the criticism I should say that to a fairly high degree it remains only at a semantic level. But there also seems to be a core of reality in the criticism. It is difficult to see why I should prove my conclusions further – even in the case of new and very critical observation-methods.

My model, of course, is open to modifications. I do not think, however, that to a certain level of treatment it is a "wrong" (in-appropriate) model.

DANSK RESUME

Modvindstræk. Svar.

Jeg kunne jo begynde med en kritik af kritikken. *Inerti* er ingen causal forklaring på forløbet af en trækbevægelse. Begreberne inerti og *trækkraft* ligger ikke i samme plan. Der findes ingen vedvarende retlinede trækbevægelser uden en stadig indvirkning (justering) af en eller flere retningsgivende stimuli. Givet et udtræk over vand, der fremtræder som en retlinet fortsættelse af et ledelinietræk (eller en ø-tiltrækning). At fuglen fastholder samme retning har sin causale forklaring i, at den vedligeholder f. eks. samme vinkel til vindens turbulente struktur eller fortsætter i samme vinkel i forhold til solens azimuth.

Denne argumentation fører os naturligt over i CHRISTENSEN og JACOBSENS (C. & J.) påstand: „– i II har RABØL fragået, at vektorkombinationer på instinkter eller adfærdsformer er den rette vej –". Denne påstand er ganske enkelt *ikke* rigtig. Det fremgår meget klart af II, at en trækbevægelse skal opfattes som værende retningsbestemt af *en eller flere* stimuli. At jeg har nævnt et special-tilfælde (træk langs en kystlinie der ikke forløber helt i overensstemmelse med mål- og/eller modvindsretningen), hvor simpel vektor-addition ikke kan forekomme, berettiger ikke C. & J. til at tale om inkonsekvenser i mine konklusioner.

En *trækbevægelse* (f. eks. træk mod vinden, mod en ø eller i en given kompasretning) kan opløses i et bestemt *bevægelsesmønster* og en *taxi* (reaktionen på de (den) retningsgivende stimuli). Bevægelsesmønstret er det *samme*, hvad enten det drejer sig om modvindstræk, måltræk eller træk mod en ø eller langs en ledelinie. Af denne grund er en slags stimulusvektor-summation ret så simpel at forestille sig – ihvertfald i princippet. Jeg opfatter derfor ikke de 3(4) trækkræfter som værende 3 forskellige „instinkter". Forekommer de i ren form viser de derimod tilbage til 3 forskellige taxier. Iøvrigt ville det være helt i overensstemmelse med de ethologiske håndbøger at kalde de forskellige trækkræfter (eller kombinationer af dem) for forskellig *instinktmæssig adfærd.*

Det fremgår klart nok af II, at udvælgelsen af de forskellige retningsgivende stimuli er „noget fuglen iboende". Her har C. & J. heller ikke læst mig omhyggeligt nok. I denne forbindelse skal jeg yderligere gøre opmærksom på, at selve bevægelsesmønstret er u-orienteret i rummet. Under orienteringsforsøg udviser fugle i „trækuro" isoleret fra ydre retningsgivende stimuli (f. eks. stjernehimlen) en u-orienteret adfærd.

Vedrørende determineringen af vindretningen: Jeg har *ikke* kategorisk hævdet, at trækfuglene *kun* kan opfatte vindens retning gennem iagttagelser af landskabets „bevægelser". Jeg har derimod nok lagt vægt på denne mulighed. Da II blev skrevet, var det efter litt. (med NISBET 1955 og DRUBY og NISBET 1964 som noget nær eneste undtagelser) den eneste mulighed. Herhjemme har jo bl. a. HESSELBJERG CHRISTENSEN med stor iver hævdet, at en trækkende fugl ikke kan *føle* vinden, så jeg betragter den forsigtige tilnærmelse i C & J til NISBET som et glædeligt tegn. I de senere år har især BELLROSE (1967) beskæftiget sig med vindens turbulente struktur som en vigtig retningsgivende stimulus for fugletrækket. Jeg vil *nu* anse det for sandsynligt, at (mod)vinden kan fastlægges *både* ad visuel og turbulent vej. Formentlig udnyttes begge muligheder ofte samtidigt, og under alle omstændigheder kan man ikke simpelt sætte lighedstegn mellem modvindstræk og topografisk tiltrækning.

Man vil ofte tale om en stor *trækdrift* (intensitet), hvis islættet af normaltræk i en populations træk er betydeligt og vedvarende til langt op på dagen. Det kan man se f. eks. efter en periode med dårligt vejr, der har holdt trækket tilbage. Populationens aktuelle *målområde* (se fig. 2) er under rasten rykket langt væk fra det sted, hvorfra trækket er udgået. Man kan tale om en betydelig uligevægt, der søges udlignet ved mål (normal) træk. Derfor er det forsvarligt at tale om en betydelig korrelation mellem måltræk (indvirkning af astronomiske retningsgivende stimuli) og stor trækdrift. Befinder en fugl sig i eller i nærheden af sit målområde, kan man enten ikke tale om en entydig måltrækkraft eller også vil dens nøjagtige retning være svær at determinere (i en koordinær form for orientering). Hvis trækdriften alligevel slår igennem vil trækbevægelserne være stærkt influeret af topografiske stimuli og modvinden. Man kan derfor forsvare at sige, at disse stimuli især indvirker, når trækdriften er lav. Iøvrigt har jeg i II udførligt diskuteret baggrunden for stimulus-udvælgelsen.

C. & J. har ganske ret i, at træk mod vinden gennemgående går lavere end træk med vinden. Det registreres derfor ved bl. a. min obs.metode lettere (et helt lavt træk er dog let overset). Endvidere bliver den topografiske påvirkning større, hvad der vil føre til at flere fugle registreres på trækstederne – alt andet lige – i modvindssektoren. Hollandske undersøgelser af gennemsnittrækhøjderne for normaltrækket af Bogfinke gav dog ikke store forskelle mellem med- og modvind (mest 40–70 m i medvind og 20–50 m i modvind). Sådanne forskelle kan dog godt tænkes at blive af betydning gennem kumulation.

Jeg skal dog tillade mig at „mene“ følgende – som ihærdig iagttager af trækbevægelser: Træk rettet mere eller mindre strikt *mod* vinden bærer faktisk altid et umiskendeligt præg af *med-indflydelse* af (mod)vinden som retningsgivende stimulus. Modvindstrækket kan måske „blot“ være *startet* som en passiv ensretning mod vinden gennem topografisk tiltrækning (II Fig. 16). Det „SØ“- og „NV“-gående udtræk i II Fig. 7 kan imidlertid som nævnt ikke *forklares* ved inerti. I dette tilfælde vil det være mest sandsynligt, at udtrækket retningsgives i måske ene grad af (mod)vinden – enten det så sker „visuelt“ eller gennem vindens turbulens. Det samme vil utvivlsomt gælde mange andre reaktioner – bl. a. udtrækbevægelser på Knudshoved.

Som ofte og gerne fremhævet opfatter jeg modvinds-reaktioner som værende af selektions-værdi. De formindsker vind-driftens indflydelser, og der er jo noget der tyder på, at ihvertfald dagtrækkere i Sydskandinavien ikke kan udligne afdriften ved *kompensation* alene (Fig. 1c i C. & J.). Herpå tyder bl. a. det store forårstræk i Nivå-bugten med V-vinde og ved Gilleleje med Ø–SØ-vinde. Afdriften manifesterer sig trods stædige forsøg på at udligne den – bl. a. gennem en betydelig udnyttelse af (mod)-vinden som retningsgivende stimulus.

REFERENCES

BELLROSE, F., 1967: Radar in orientation research. – Proc. XIV Int. Ornith. Congr.: 281–309.

DRURY, W. H. and I. C. T. NISBET, 1964: Radar studies of orientation of songbird migrants in south-eastern New England. – Bird Banding **35**: 69–119.

EMLEN, S. T., 1967: Migratory orientation in the Indigo Bunting, Passerina cyanea. Part I: Evidence for use of celestial cues. – Auk **84**: 309–342.

EVANS, P. R., 1967: Migration and orientation of passerine night migrants in Northeast England. – J. of Zool. **150**: 319–369.

FRAENKEL, G. S. and D. L. GUNN, 1940: The orientation of animals. – Oxford.

GRUYS-CASIMIR, E., 1965: On the influence of enviromental factors on the autumn migration of Chaffinches and Starlings: a field study. – Arch. Neerl. Zool. **16**: 175–279.

KOEHLER, O., 1950: Die analyse der taxisanteile instinktartigen verhaltens. – Symp. Soc. Exp. Biol. Nr. IV, Animal Behaviour 1950.

LINDAUER, M., 1964: Allgemeine sinnesphysiologie. Orientierung im raum. – Fortschritte der Zool. **16**: 58–140.

NISBET, I. C. T., 1955: Atmospheric turbulence and bird flight. – Brit. Birds **48**: 557–559.

RABØL, J., 1964: Fugletrækket ved Knudshoved. – Dansk Ornith. Foren. Tidsskr. **58**: 49–97.

RABØL, J., 1967: Visual diurnal migratory movements. – Dansk Ornith. Foren. Tidsskr. **61**: 73–99.

SCHMIDT-KOENIG, K., 1965: Current problems in bird orientation. – Advan. Study Beh. **1**: 217–78.

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