Speeds of migrating waders Charadriidae

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(Med et dansk resume: Trækhastigheder af vadefugle Charadriidae)

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INTRODUCTION

In 1957, N. O. Preuss and others measured speeds of migrating waders at Blåvandshuk, the westernmost point of Denmark. In a paper (Preuss 1960), a possible relationship between speed and flock size was investigated. However, because of a limited material, the results were inconclusive.

In 1970 and 1971, new measurements of speeds were carried out at Blåvandshuk. The results of these are treated in this paper with two purposes: 1) to investigate the dependance of speed on flock size, and 2) to decide whether and to what extent the birds compensate for the influence of the wind.

In both years, the period of investigation was ultimo July and primo August. During this period, the autumn migration of most species of waders at the west coast of Jutland peaks (Meltofte et al. 1972). The main direction of the migratory movements is south, and the majority of the birds passing Blåvand use the coast as a guiding line. Moreover, the birds normally fly at low altitudes less than 200 m from the coast.

Three species dominate in numbers: The Oystercatcher *Haematopus ostralegus*, the Knot *Calidris canutus*, and the Dunlin *Calidris alpina*. The majority of the Oystercatchers have emigrated from south western Norway and follow the west coast of Jutland on their way to the Waddensea (Thelle, 1970), while parts of the Knots and Dunlins observed are supposed to be recruited more to the north east of Blåvand (Meltofte and Rabøl, 1977).

METHODS USED IN THE FIELD

The method of the measurements has been described in detail by Preuss (1960), and only

a short description shall be given here. From Blåvandshuk, the coastline runs towards the NNE in almost a straight line, and, as mentioned, the majority of the waders follow this rather strictly towards the SSW. A baseline of known length is marked out along the beach, parallel to the edge of the water. At each end, an aiming line is constructed at a right angle to the baseline, and an observation post is established. These posts communicate by means of walkie-talkies. The time a flock of birds uses to fly the distance between the two aiming lines is measured by means of a stopwatch. Given this time, the ground speed of the birds is easily calculated. In 1970, a baseline of 525 m was used, and in 1971 one of 500 m.

As the flight direction is known, we can calculate not only the speed of the birds, but the velocity (here understood as a vector) as well. This velocity (ground speed vector) is the sum of two components: the velocity (air speed vector) of the birds, and the velocity of the wind (Fig. 1). Therefore, to permit calculations of air speeds, measurements of the wind were taken as well. By means of a rotating anemometer and a stopwatch the speed of the wind was measured in m/sec, and the direction was measured to the nearest 5° by means of a weathercock and a compass.

Measurements of the wind were carried out every half hour in heights of 1 and 2.5 m. If changes in the wind were noticed, new measurements were carried out immediately. Other meteorological parameters such as cloudiness and precipitation were recorded as well.

For the birds, species, flock size, and estimates of height and distance from the coast were booked. Only on completely calm days (wind less than 0.3 m/sec) a few flocks migra-

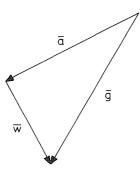


Fig. 1. The groundspeedvector g is the sum of the vectors a (the airspeedvector of the birds) and w (the windspeedvector).

Den hastighed, der måles, g (groundspeedvektoren), er summen af fuglenes egenhastighedsvektor a og vindhastighedsvektoren w.

ting higher than 4-5 m have been included, and flocks migrating more than about 100 m from the coast were always ignored. All flocks timed were watched while flying between the posts, and if any deviation from straight-lined flight (e.g. changes of height) was noticed, the timing was cancelled.

MATERIALS

In 1970, about 80% of the total number of passing flocks of Oystercatchers during the observation periods were timed. In 1971, this percentage was somewhat lower due to a larger number of migrating birds. For the other species, the percentage was in both years so-

Т	A	в	L	Ε	1

Year	Date	Time	Winddir.	Windspeed	0	D	К
1970	23.7. 24.7. 25.7. 26.7. 29.7. 30.7. 31.7. 1.8. 2.8. 2.8. 3.8.	$\begin{array}{c} 0430-0730\\ 0500-0730\\ 1500-1600\\ 0430-0730\\ 0445-0715\\ 0515-0715\\ 0515-0715\\ 050-0730\\ 0500-0800\\ 0615-0900\\ 1830-2030\\ 0445-0545 \end{array}$	245 170 175 135 280 330 255 185 090 185 090 120 090	$\begin{array}{c} 4 \cdot 2 - 5 \cdot 7 \\ 4 \cdot 9 - 8 \cdot 0 \\ 6 \cdot 6 - 7 \cdot 3 \\ 0 & - 0 \cdot 3 \\ 5 \cdot 3 - 6 \cdot 4 \\ 0 & - 3 \cdot 3 \\ 5 \cdot 9 - 7 \cdot 8 \\ 4 \cdot 2 - 5 \cdot 7 \\ 0 \cdot 3 - 2 \cdot 1 \\ 1 \cdot 2 - 2 \cdot 7 \\ 1 \cdot 3 - 5 \cdot 1 \\ 2 \cdot 0 - 2 \cdot 4 \end{array}$	24 2 22 28 17 15 10 9 31 17 7	0 6 1 1 8 5 5 1	0 5 0 1 0 1 1 7 0 0 0
1971	22.7. 25.7. 26.7. 27.7. 27.7. 28.7. 29.7. 1.8. 1.8. 1.8. 2.8. 3.8. 4.8. 6.6.	$\begin{array}{c} 0450-0550\\ 1800-2000\\ 0445-0745\\ 1900-2000\\ 0445-0545\\ 1815-1915\\ 0500-0700\\ 1845-2045\\ 0500-0730\\ 0500-0800\\ 0600-0845\\ 1830-1930\\ 0515-0745\\ 0445-0745\\ 0600-0700\\ 0500-0630\\ \end{array}$	230 180 235 180 - 040 - 300 205 220 120 180 185	$\begin{array}{c} 0.1 - 3.3 \\ 0 & -2.7 \\ 2.0 - 4.2 \\ 3.0 - 3.5 \\ 3.4 - 4.2 \\ 0 \\ 0 \\ -2.3 \\ 0 \\ 1.6 - 3.6 \\ 3.5 - 6.3 \\ 0 \\ -2.5 \\ 1.2 - 2.4 \\ 7.0 - 7.1 \\ 6.8 - 7.0 \\ 6.8 - 7.0 \end{array}$	2 3 10 1 4 1 17 22 24 23 2 22 38 9 4	0 3 5 6 0 20 10 17 17 11 10 4 3	0 3 2 0 1 1 0 6 0 1 4 1 2

mewhat lower. Yet in all cases, more than 50% of the number of passing flocks were timed.

Alltogether, 660 measurements were obtained, the majority of which were Oystercatchers, Knots, and Dunlins. A summary of the number of measurements for these three species is given in Table 1. Flocks containing individuals of other species are included. Therefore, in the following treatment, where only the pure flocks of each species have been included, the number of observations in any period may be smaller. A brief summary of the data for other species of waders is given below.

RESULTS

Flock size and speeds

To avoid any bias introduced by the calculations of air speeds, this part of the analysis concentrated on ground speeds. Plots of ground speed against flock size for some periods are given in Figs. 2-5. For the Oystercatcher, it is seen that while in one period (Fig. 2) a positive speed/flock size relationship is well defined, in the other it is far from being pronounced (Fig. 3). Periods similar to both of these as well as intermediate ones are found for this species. For the other species in question, the relationship between speed and flock size was generally better defined (Fig. 4 and 5).

Linear regression analyses were carried out

Table 1. All observation periods where measurements were obtained. Also showing the observation time, the winddirection (in degrees), the windspeed (in m/sec), and the number of measurements of the three species. O=Oystercatcher, D=Dunlin, and K=Knot.

Observationsperioderne. Foruden årstal og dato viser tabellen også observationstidspunkterne, vindretningen (i grader), vindstyrken (i m/sek), og antallet af målinger af de tre vigtigste arter. O=Strandskade, D=Almindelig ryle, og K=Islandsk ryle.

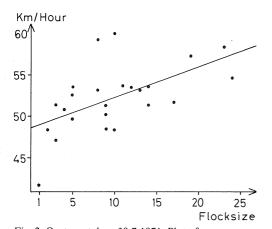


Fig. 2. Oystercatcher, 30.7.1971. Plot of groundspeeds against flocksize with the estimated regression line indicated.

Strandskade, 30.7.1971. Figuren viser trækhastigheden for forskellige flokstørrelser. Den beregnede regressionslinie er også vist.

for each period, and the problem of a possible relationship was solved by testing whether the slope of the regression line differed significantly from zero.

For the Oystercatcher, in fact, the slopes of the regression lines for the different periods only in a few cases differed significantly from zero, no doubt because the number of measurements often was too small for the relatively small slopes to be properly distinguished from zero. To solve the problem, it was necessary to obtain some sort of grouping of data from different periods. Therefore, the standard procedure for comparing a set of regression lines was applied. This procedure can be found in most textbooks of statistics, e.g. in

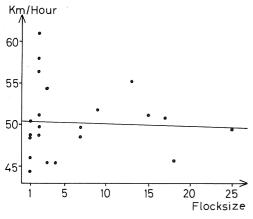


Fig. 3. As Fig. 2. Oystercatcher, 26.7.1970. Som fig. 2. Strandskade, 26.7.1970.

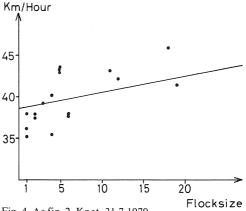


Fig. 4. As fig. 2. Knot, 31.7.1970. Som fig. 2. Islandsk ryle, 31.7.1970.

Hald (1971). First, in order to test the homogeneity of variances around the regression lines, Bartletts test was applied. Next, the hypothesis that the lines were parallel (i.e. had the same slope) was tested. If these two first steps were accepted, the third and conclusive step, to test whether the common slope differed significantly from zero, could be carried out.

Because Bartletts test is sensitive to too few degrees of freedom in the variance estimates, it was decided only to use periods with more than five measurements in this part of the analysis.

Oystercatcher

For 18 periods 6 or more measurements were obtained. The periods, numbers of measurements, estimated regression lines, and mean flock sizes are given in Table 2.

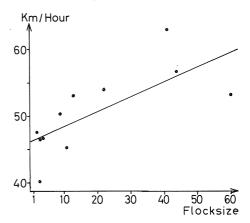


Fig. 5. As Fig. 2. Dunlin, 1.8.1971. Som fig. 2. Almindelig ryle, 1.8.1971.

The hypotheses of variance homogeneity and parallellity were both accepted. The estimate of the common slope was b = 0.0605. The estimate of the variance around this regression line is $s^2 = 14.4242$; b differed highly significantly from zero (p $\langle 0.0005 \rangle$).

Dunlin

For 10 periods six or more measurements were obtained. Table 3 gives the relevant data and the estimated regression lines for this species.

The hypotheses of variance homogeneity and parallellity were both accepted. The estimate of the common slope is b = 0.2333 and the corresponding estimate of variance $s^2 =$ 11.0120; b differed highly significantly from zero (p $\langle 0.0005 \rangle$).

Knot

For this species, only two periods of observation had six or more measurements. As the variances around those two regression lines did not differ significantly from each other, and as the hypothesis of homogeneity of variances had been accepted for both of the other species, it was decided to accept all periods with three or more measurements and to omit Bartletts test. In this way, the analysis covered six periods (Table 4).

The hypothesis of parallel lines was accepted. The estimate of the common slope was b = 0.2128, and the corresponding estimate of variance was $s^2 = 20.8513$; b differed highly significantly from zero (0.0005 $\langle p \rangle (0.0010)$).

The influence of the wind

Methods

2

In the analysis of the influence of the wind, a number of simplifications were carried out.

1) As shown in Fig. 1, the ground speed vector measured can be regarded the resultant of the air speed and wind speed vectors. This resultant (the ground speed vector) had, because the flocks measured followed the coastline strictly, always the same direction (abt. 210°).

Table 2. Oystercatcher. The estimated
regression lines for the periods used in
the groundspeed/flocksize analysis.
The lines have been calculated on the
form $Y=a+bX$, and columns a and b give
the estimates of a and b, respectively.
N is the number of observations, s ²
the estimated variance around the
regression line, and t the mean
flocksize.

Strandskade. De estimerede regressionslinier i de forskellige perioder, der blev brugt i hastighed/flokstørrelse analysen. Linierne er parametriseret på formen Y=a+bX, og søjlerne a og b giver de forskellige skøn over disse parametre. N er antallet af observationer, s² er variansskønnet omkring den enkelte regressionslinie, og t er den enkelte periodes gennemsnitsflokstørrelse.

Table 3. Dunlin. As Table 2. *Almindelig ryle. Som tabel 2.*

Table 4. Knot. As Table 2. *Islandsk ryle. Som tabel 2.*

Year	Date	N	а	b	s ²	Ŧ
1970	23.7. 26.7. 27.7. 30.7. 31.7. 1.8. 2.8. 2.8. 3.8.	24 22 28 17 15 10 9 32 17 7	45.104 50.452 53.873 51.730 41.466 38.764 55.352 53.098 53.284 57.604	0.184 -0.032 -0.229 0.030 0.237 -0.495 -0.474 0.096 0.113 -0.138	19.036 19.395 18.146 8.563 16.207 10.909 8.885 13.709 16.053 13.126	8.0 6.4 10.2 17.9 5.4 3.3 5.8 7.2 10.1 13.1
1971	26.7.	10	41.161	-0.049	12.123	8.2
	28.7.	21	50.869	0.095	20.789	19.1
	29.7.	22	50.393	0.045	8.711	40.3
	30.7.	24	52.265	0.364	11.902	10.0
	1.8.	24	38.202	0.099	13.888	10.5
	2.8.	23	50.269	0.092	16.308	5.5
	3.8.	38	46.680	0.114	9.417	8.8
	4.8.	9	35.403	0.259	4.425	11.0
Year	Date	N	а	Ь	s ²	Ŧ
1970	24.7.	6	41.485	0.326	31.587	5.5
	31.7.	6	41.750	0.114	9.886	5.0
1971	26.7.	15	42.363	0.043	8.113	6.5
	27.7.	7	44.607	0.249	3.604	7.4
	28.7.	20	48.808	0.003	8.365	6.5
	29.7.	10	47.722	0.308	3.101	15.0
	30.7.	17	51.414	0.281	10.853	8.3
	1.8.	17	39.819	0.182	10.556	6.2
	2.8.	11	52.476	0.427	12.168	6.1
	3.8.	10	46.935	0.928	19.610	3.8
Year	Date	N	a	b	s ²	Ŧ
1970	24.7.	4	46.583	0.185	4.291	15.0
	31.7.	11	50.542	0.226	20.916	19.2
	1.8.	6	58.592	0.269	17.511	11.8
1971	26.7.	3	48.210	0.844	11.583	8.7
	26.7.	3	49.130	-0.060	37.437	15.0
	1.8.	5	40.968	2.373	15.661	2.0
			·····			

Therefore, both the air speed vector and the wind speed vector were split up into two components, one along the coastal axis, and one at a right angle hereto (Fig. 6). As their resultant is parallel to the coast, the air speed vectors and wind speed vectors components orthogonal to the coastline must be equally sized and oppositely directed. Hence, the correla-

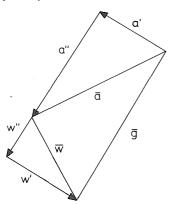


Fig. 6. The decomposition of the vectors a and w from fig. 1 into components orthogonal (') and parallel ('') to the coast. As the birds follow the coast, i.e. as g must have a constant direction, the components a' and w' must be equally sized and oppositely directed.

Vektorerne a og w fra fig. 1 opløst i deres komponenter hhv. vinkelret på (') og parallelt med ('') kysten. Da fuglene altid følger denne, skal vektoren g altid have samme retning. g er summen af a og w, så for at dette kan lade sig gøre, må komponenterne a' og w' være lige store og modsat rettede — altså ophæve hinanden.

tion between these components is trivial, and all the information in the data is contained in the relations between the winds and the air speeds components along the coast.

2) Since within all periods of observation the wind conditions had been sufficiently constant, it was decided to use a mean level for each period in the analysis, because such levels would vary less than the individual measurements.

3) From the ground speed/flock size analysis it is known that the speed depend on the flock size. Therefore, to compare different periods, it is neccessary for each period to refer to the expected speed for some given flock size. This was chosen as the mean flock size for all flocks included in the analysis.

4) All periods with two or more measurements were included in this part of the analysis. This, however, caused considerable variation in the estimates of slopes. As moreover some of these estimates were rather uncertain due to small numbers of measurements, it was assumed that the change of speed with flock size was the same for all periods. With the inclusion of periods not used in the speed/flock size analysis, the estimates of the common slopes changed a little. The new values were:

Oystercatcher:	b = 0.0638
Dunlin:	b = 0.2459
Knot:	b = 0.2228

In the end, the »level« of ground speeds for some period »i« was defined as $G_i = a_i - b(t_i - t_{..})$, where a_i is the mean of the observed ground speeds of the period, b is the estimate of the common slope, t_i is the mean flock size of all the period, and $t_{..}$ is the mean flock size of all the periods. This simply means that for any period it was estimated what speed a flock of e.g. 10 individuals would have had. This speed was then used in the analysis. This complication of the calculations was necessary because the speed vary with the flock size, and the mean flock size is not the same for different periods.

The level of air speeds of period $\ast i \ll$ was finally found by subtracting the mean wind speed vector for the period from G_{i} .

Results

Plots of air speed components along the coast against wind speed components along the coast are given in Figs. 7-9 for the three species in question. All of them showed a well defined linear dependance, the birds flying fastest against the wind. This was most pronounced in the two smaller species. Regression analyses on the form y = a + bx were carried out. In these analyses, the different daily »mean levels« have been weighted by their respective numbers of observations. Therefore, the regression lines found (and shown) are not the same as would have been the case if all points had been allowed the same weight.

For the Oystercatcher, the overall mean flock size was 11.56, and the results are plotted in Fig. 7. The estimated regression line was y = 51.223 - 0.364x. The slope differed significantly from zero (p $\langle 0.0005 \rangle$).

For the Knot, the overall mean flock size was 12.42. The results are plotted in Fig. 8. The estimated regression line was y = 56.960 - 0.408x. The slope differed significantly from zero (p $\langle 0.005 \rangle$).

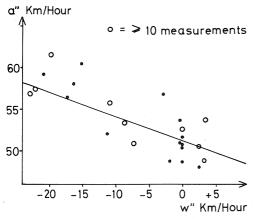
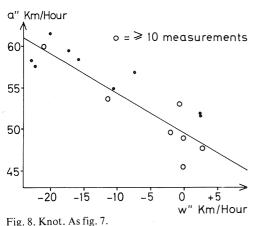


Fig. 7. Oystercatcher. Plot of airspeedvectors component along the coast against windspeedvectors component along the coast (with headwinds counted negative). Each dot represents a period of observation. The regression line estimated by weighting the points by their respective numbers of observations is shown. *Strandskade. Egenhastighedsvektorens komponent langs med kystlinien plottet mod vindhastighedsvektorens (med modvind regnet negativt). Hvert punkt repræsenterer en observationsperiode. Figuren viser også den regressionslinie, der fremkommer ved at vægte punkterne med de antal målinger, de repræsenterer.*

For the Dunlin, the overall mean flock size was 6.72. The estimated regression line was y = 49.612 - 0.484x. The slope differed significantly from zero (p $\langle 0.0005$). The results are plotted in Fig. 9.



Islandsk ryle. Som fig. 7.

Mixed flocks

The flocks of migrating waders at Blåvand are often mixed. For the Oystercatcher, Knot, and Dunlin, speeds of a number of flocks containing other species were measured.

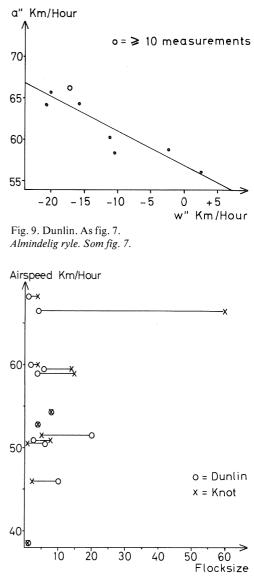


Fig. 10. Airspeeds of mixed flocks of Knots and Dunlins. Each horizontal line represents a flock, and the number of each species in the flock can be read on the abscissae.

Egenhastigheder af blandede flokke af Almindelig og Islandsk ryle. Hver af de vandrette linier repræsenterer een flok, og de to arters respektive antal kan aflæses på abscisseaksen. Fig. 10 gives the measurements of flocks consisting of Knots and Dunlins. The number of observations is certainly small, but, taking the difference in speeds into consideration (the Knot flying much faster than the Dunlin), there seems to be a tendency for the more numerous species in a flock to »decide« the speed of the flock.

Measurements of other species

The investigation was concentrated on Oystercatcher, Knot, and Dunlin. Therefore, rather few measurements of other species of waders were collected. Moreover, a large proportion of these measurements are of mixed flocks containing up to 5-6 species. Mixed flocks are largely omitted here.

Table 5 gives mean airspeed and range of air speeds observed for five species: Grey plover *Pluvialis squatarola*, Turnstone *Arenaria interpres*, Bar-tailed godwit *Limosa lapponica*, Redshank *Tringa totanus*, and Sanderling *Calidris alba*.

Eleven measurements of flocks of Redshanks were within the same period of observation, but though the correlation between speed and flocksize was positive, it was not significant. Some of the flocks of Redshanks

Species	Ν	Mean	Range	
Grev Plover	6	52.0	39.7-59.3	
Bar-tailed Godwit	10	60.1	52.7-71.5	
Turnstone	8	54.6	47.2-65.6	
Redshank	15	56.3	47.0-64.8	
Sanderling	13	52.0	47.7-56.4	

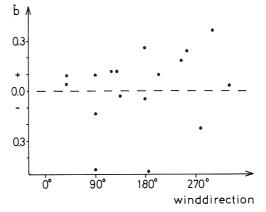


Fig. 11. Oystercatcher. Plot of estimates of slopes of groundspeed/flocksize regression lines against winddirection.

Strandskade. Plot af hældningerne af hastighed/flokstørrelse regressionslinierne mod vindretning.

some nonlinear curve might have been preferable. However, throughout the material there are few examples of this. Moreover, at Blåvand, more than 80% of the Oystercatchers migrate in flocks containing less than 40 individuals, and an even larger percentage of the other species. Within such limits, the use

Table 5. Data of other species of
waders. The table gives the species,
the number of observations, the
mean airspeed, and the range
(smallest and largest observations), the
two latter in km/hour.
Målinger af andre vadefuglearter
(Strandhjejle, lille Kobbersneppe,
Stenvender, Rødben og Sandløber).
Tabellen viser art, antal observationer,
den gennemsnitlige egenhastighed

(Mean), og de mindste og største observationer for hver art (Range). Alle hastighederne er opgivet i Km/time.

contained 1-2 individuals of Spotted Redshanks Tringa erythropus.

DISCUSSION AND CONCLUSION

The flock size analysis

It may be argued that the use of straight lines in the speed/flock size analysis could not possibly be correct. As the birds obviously cannot keep on increasing their ground speed indefinitely with increasing flock size, some function converging asymptotically to a constant level would have been more biologically correct. Fig. 4 is an example where the fitting of of straight lines gave the best fit which could be obtained — and no systematic deviations were observed.

The assumption of parallel lines may be discussed as well. It would be odd, if the change of speed with flock size would be the same no matter the circumstances. However, it has not till now been possible to demonstrate that the slopes depend on any other parameter. An obvious possibility would be the wind direction. A plot of slope estimates (Oystercatcher) against wind direction is given in Fig. 11, but there is no clear correlation between the two variables.

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It is rather difficult to give this increase of ground speed with flock size a reasonable interpretation at our present state of knowledge. Lissaman and Shollenberger (1970) show that for birds flying in »vee« formations - as do the Oystercatchers - a flock of 25 individuals may increase their range by as much as 70% compared to a single individual. This, however, is for the optimal speed which is some 20% below that for a single bird. These results are, however, derived in an attempt to maximize the distance covered by some given amount of energy. The situation at Blåvand is probably quite another since the birds observed here presumably are not covering a distance which would be likely to drain their energy reserves (the birds have never been significantly exhausted when observed at Blåvand, near the end of their flight across the North Sea). But viewed from the point of energy considerations, larger flocks may with the same consumption of energy be able to fly faster and thus to shorten the time spent on migration. This could be the reason. However, Lissaman and Shollenberger (1970) argue that the »vee« formation is optimal. Of the three species concerned here, only the Oystercatcher migrate in »vee« formations, while the Knot and the Dunlin fly in flocks of more complex structures. But the increase in ground speed with flock size is about four times as large for the two latter species, indicating that either do the energy considerations not hold true in practice, or some other agent may play a role.

Speed and wind

Figs. 7-9 and the statistical analysis indicate that the birds raise their levels of air speeds in headwinds. It is rather obvious to interpretate this as some sort of compensatory act.

In this connection it is remarkable that the three species analysed compensate for about the same amount of the influence of the headwind component (abt. 40%). Bellrose (1967) found for birds observed on radar (and flying downvind) values of 32-39%. Bruderer (1971) found for all species (radar) compensation for 15-32%. For Chaffinches *Fringilla coelebs*, he found 32%. Seemingly, values ranging from thirty to some forty per cent are the usual, even for widely different groups of birds.

It is also remarkable that the birds apparently always compensate for the same proportion of the wind. Of course it is to be expected that the birds cannot compensate fully for strong headwinds, but according to the measurements (Figs. 7-9), they should be more than able to do so for the weaker winds. Why then do the birds always compensate for the same proportion of the wind, instead of compensating fully for weak winds, as far as they can increase their air speeds, and then less? Could the calculation of air speed be wrong, and the results produced an artifact? The results may be explained in this way, and it must be emphasized that the demonstration of wind compensation rests on the validity of the air speed calculation.

Schmidt-Koenig and Tucker (1971) argue that though the evidence for a raise of air speeds in opposing winds is strong, the results of e.g. Bellrose (1967) might be an artifact, due to overestimate of wind speeds. However, in this case, a 40% overestimate of the wind speed is far outside the uncertainty of the rotating anemometer used in this study. It can thus, at least in this case, be concluded that granted the validity of the air speed calculations the birds raise their air speeds with increasing headwind as earlier described.

Speeds of migrants

From the results given in this paper it can be seen that speeds of migrating birds — at least of the three species analyzed here, cannot be expressed as single numbers. Instead, speeds might be expressed by (and predicted from) the estimated regression lines.

As indicated earlier, this means that in completely calm weather a flock of 11.6 Oystercatchers would have a ground speed of 51.2 km/h, 6.7 Dunlins would migrate with 50.6 km/h, and 12.4 Knots with 56.9 km/h, these values of course being mean values. Dunlins may raise their speed, if flying in a bigger flock of Knots, which means that pure Dunlin flocks do not fly as fast as they can. Moreover, the Oystercatchers would increase their ground speed with 0.6 km/h for each additional 10 individuals in the flock, and for the Knot and the Dunlin these figures would be 2.2 km/h and 2.5 km/h, respectively. As the results obtained for these three species are rather similar, much the same would probably be found for the other species of waders. Therefore, the means and ranges given in Table 5 should only be taken as rough indications.

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DANSK RESUME

Trækhastigheder af vadefugle Charadriidae

I juli-august 1970 og 1971 måltes hastigheder af trækkende vadefugle ved Blåvand. Formålet var dels at nå frem til en konklusion m.h.t., om hastigheden afhænger af flokstørrelsen, dels at undersøge, om fuglene kompenserer for vindens indflydelse.

Metoden består i at udmåle en strækning langs kysten (i 1970 og 1971 undersøgelserne brugtes hhv. 525 og 500 m). For enderne af denne linie oprettes observationsposter, der står i forbindelse med hinanden v.hj.a. walkie-talkies. Når en flok fugle passerer den første post, startes et stopur, og når de passerer den anden, stoppes det. Man kender nu en afstand og den tid, der er brugt til at tilbagelægge denne, og kan derfor udregne trækhastigheden.

I alt foretoges 660 målinger, hvoraf de fleste var af arterne Strandskade, Islandsk ryle og Almindelig ryle. Tabel 1 giver de enkelte måleperioder, hvor mange flokke der måltes af de tre arter, og vindretning og vindstyrke.

Fig. 2-4 giver plot af hastighed mod flokstørrelse for forskellige perioder. Selv om sammenhængen i visse af perioderne var klar nok (f.eks. Fig. 2), var den langt fra tydelig i andre. Der blev derfor udført en række statistiske analyser af materialet. Der beregnedes først regressionslinier for de enkelte perioder. Resultaterne heraf er givet i Tabel 2-4. Disse linier blev derefter sammenlignet som beskrevet af Hald (1971).

For alle tre arter er konklusionen klar. Trækhastigheden stiger som funktion af flokstørrelsen. Med hele materialet inde i beregningerne findes for Strandskaden en stigning på 0.638 km/t for hver 10 individer, flokken øges med. For Islandsk ryle er stigningen på 2.228 km/t pr. 10 individer, og for Almindelig ryle 2.459 km/t pr. 10 individer — altså 3-4 gange større for de små arters vedkommende.

Når flokstørrelsen vokser, er det klart, at fuglene ikke kan blive ved at flyve hurtigere og hurtigere. De opgivne stigninger gælder således kun for mindre flokstørrelser (op til 30-40 individer).

Analyserne af trækhastighed og flokstørrelse udførtes direkte på de målte hastigheder. Den hastighed, der måles, er imidlertid en sum af to komponenter: fuglenes egenhastighed, og vinden. Dette forhold er skitseret i Fig. 1, der viser de tre hastigheder som vektorer. den målte trækhastighed er g. Men samtidig blev vinden w også målt, vindhastigheden med en ret nøjagtig vindmåler, og retningen v.hj.a. en vejrhane og et kompas (til nærmeste 5°).

Det var på forhånd klart, at fuglene i hvert fald kompenserer for en del af vindens påvirkning. De flyver nemlig altid parallelt med kysten — uanset om de har modvind eller f.eks. sidevind. Man kan tænke sig vinden som bestående af to komponenter: een vinkelret på kystlinien og een parallelt med denne. Da fuglene følger kysten, må de kompensere fuldstændigt for vindens komponent vinkelret på denne. Tænker man sig altså, at også fuglenes egenhastighedsvektor deles op i komponenter hhv. vinkelret på og parallelt med kystlinien, må de to »vinkelrette« komponenter (fuglenes og vindens) være præcis lige store og modsat rettede - ellers ville fuglene ikke følge kysten. Dette er illustreret i Fig. 6. I den del af undersøgelsen, der beskæftiger sig med kompensation for vinden, blev alle disse komponenter udregnet. Undersøgelsen beskæftigede sig derefter kun med vindens og fuglenes hastighedskomponenter langs med kysten.

Den første del af undersøgelsen havde vist, at trækhastigheden stiger med flokstørrelsen. Dette giver problemer, når forskellige perioder skal sammenlignes med henblik på en analyse af vindens indflydelse, idet flokstørrelserne ikke har været de samme fra periode til periode. Dette problem blev omgået ved at definere »niveauet« for hastigheder i en bestemt periode som den hastighed, en bestemt flokstørrelse ville have haft.

Figurerne 7-9 viser »niveauernes« komponenter langs kysten for de enkelte perioder plottet mod vindens komponent langs kysten. For alle tre arter er der en tydelig (og statistisk set meget signifikant) tendens til kompensation, idet fuglene øger deres egenhastigheder, når de har mere modvind. Det er påfaldende, at de tre arter alle kompenserer for ca. 40% af vindens indflydelse (Strandskade 36%, Islandsk ryle 41%, og Almindelig ryle 48%). Tilsvarende værdier er fundet ved andre undersøgelser. Det er også påfaldende, at fuglene altid kompenserer for den samme procentdel af vindens indflydelse, idet man vel måtte forvente, at de skulle kompensere 100%, sålænge vinden ikke var for stærk, og derefter mindre. Forklaringen på alt dette kunne være, at den simple geometriske formel, man regner egenhastighederne ud efter, ikke er rigtig (f.eks. tager den ikke hensyn til turbulens). Man må altså holde sig for øje, at påvisningen af kompensation for modvind hviler på, at formlen for udregning af egenhastighed er korrekt.

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En del af de flokke, hvis hastigheder måltes, var blandede, d.v.s. bestod af flere arter. Fig. 10 viser målinger af blandede flokke af Islandsk og Almindelig ryle. Det fremgår, at der er en tendens til, at den talmæssigt dominerende art »bestemmer« hastigheden.

Tabel 5 giver resultater af målinger af fem andre vadefuglearter: Strandhjejle, Stenvender, Lille kobbersneppe, Rødben og Sandløber. Efter at det for de andre arter har vist sig, at en floks trækhastighed afhænger både af antallet af individer og af vindretning og vindstyrke, er det imidlertid problematisk at komme med udsagn om de andre arters trækhastigheder, idet materialet er for lille til at udføre detaljerede analyser. Når der alligevel for disse arter er givet simple gennemsnitshastigheder, er det fordi det skønnes, at de opgivne tal, når de tages med de nævnte forbehold, er bedre end intet.

Som det fremgår af det foregående, vil en flok på 11.6 Strandskader i helt stille vejr have en forventet trækhastighed (ground speed) på 51.2 km/t. For hvert individ, flokken vokser eller aftager med, vil dens hastighed øges eller sænkes med 0.06 km/t. I modvind vil flokken yderligere kompensere for noget af vindens indflydelse, således at for hver gang modvindskomponenten stiger med 1 km/t, vil flokkens trækhastighed (ground speed) falde - ikke med 1 km/t, men med 0.64 km/t. Ligeledes vil en flok på 6.7 Almindelige ryler i stille vejr trække med 50.6 km/t, og for ændringer i flokstørrelsen ville flokkens hastighed stige eller falde med 0.25 km/t pr. individ. Modvind ville, for hver gang komponenten steg med 1 km/t, sænke flokkens hastighed med 0.52 km/t. For Islandsk ryle siger disse tal, at en flok på 12.4 individer i vindstille trækker med en hastighed på 56.9 km/t og ændrer denne hastighed med 0.22 km/t pr. individ. Modvind ville sænke denne hastighed med 0.59 km/t pr. km modvind. Alle disse tal er naturligvis gennemsnitsværdier.

Alm. ryler. Fotograferet af Niels Nyholm.

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