CRANE *GRUS GRUS* MIGRATION OVER SEA AND LAND

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During late March and early April tens of thousands of Cranes *Grus grus* migrate over the southern Baltic Sea and the province of Skåne in Sweden towards the north. The general pattern of migration has been summarized by Glutz von Blotzheim, Bauer & Bezzel (1973), and the process of the spring migration through the present study area has been described in an earlier report (Alerstam & Bauer 1973). During spring Cranes rest in large numbers along the southern coast of the Baltic, especially on the island of Rügen. Most depart over the Baltic Sea towards Skåne and the Swedish mainland via the northernmost promontory of this island. The distance of this sea crossing is about 80 km. Many Cranes, having passed Skåne, gather to rest at the lake of Hornborgasjön in southern Sweden (Swanberg 1970).

This report is concerned with the cruising technique and orientation ability of the migrating Cranes, over sea and land respectively. The data have been extracted from films of a surveillance radar station in Skåne during the spring migratory periods of 1972 and 1973.

METHODS

Films were obtained from an L-band radar station situated in southern Skåne as earlier described (Alerstam & Bauer 1973). The study area is shown in Figure 1.

The present report is based only on echoes from Crane flocks that were seen to depart from the island of Rügen. These, however, formed a great majority of all echoes of Crane flocks over the study area (Alerstam & Bauer 1973). Directions and speeds were measured over the Baltic Sea and over central and northern Skåne; no measurements could be made in southern Skåne, since the echoes from Crane flocks usually vanished from the radar screen in the area close to the radar site (cf. Fig. 1). Flight paths of individual echoes were plotted on maps and a daily mean track direction fitted by eye to these plots. The range was measured as the difference between the two most extreme track directions. Mean ground speeds on different days were calculated from *c.* 10 or more measurements. Values for directions and speeds used in the text below refer to such daily means. The behaviour of individual echoes was studied in close detail. Very small distances (1–2 km) could not, however, be measured accurately due to the restricted resolution of the radar, and the time-lapse filming technique (2·5 frames per min) entailed the risk that incidents of a very brief duration may have been overlooked.

Wind data were measured from ground synoptic maps, assuming wind direction to be parallel to the isobars and wind speed related to the distance between the isobars. Wind direction was measured to the nearest 10°. Such wind conditions prevail at about 500–1000 m altitude, which accords with radar measurements of the height of migrating Crane flocks in southern Skåne (Karlsson & Alerstam 1974).

CRUISING TECHNIQUE

Echoes from Crane flocks behaved in a strikingly different way over sea and land, respectively. Over the Baltic Sea the echoes moved with a constant rate of progress

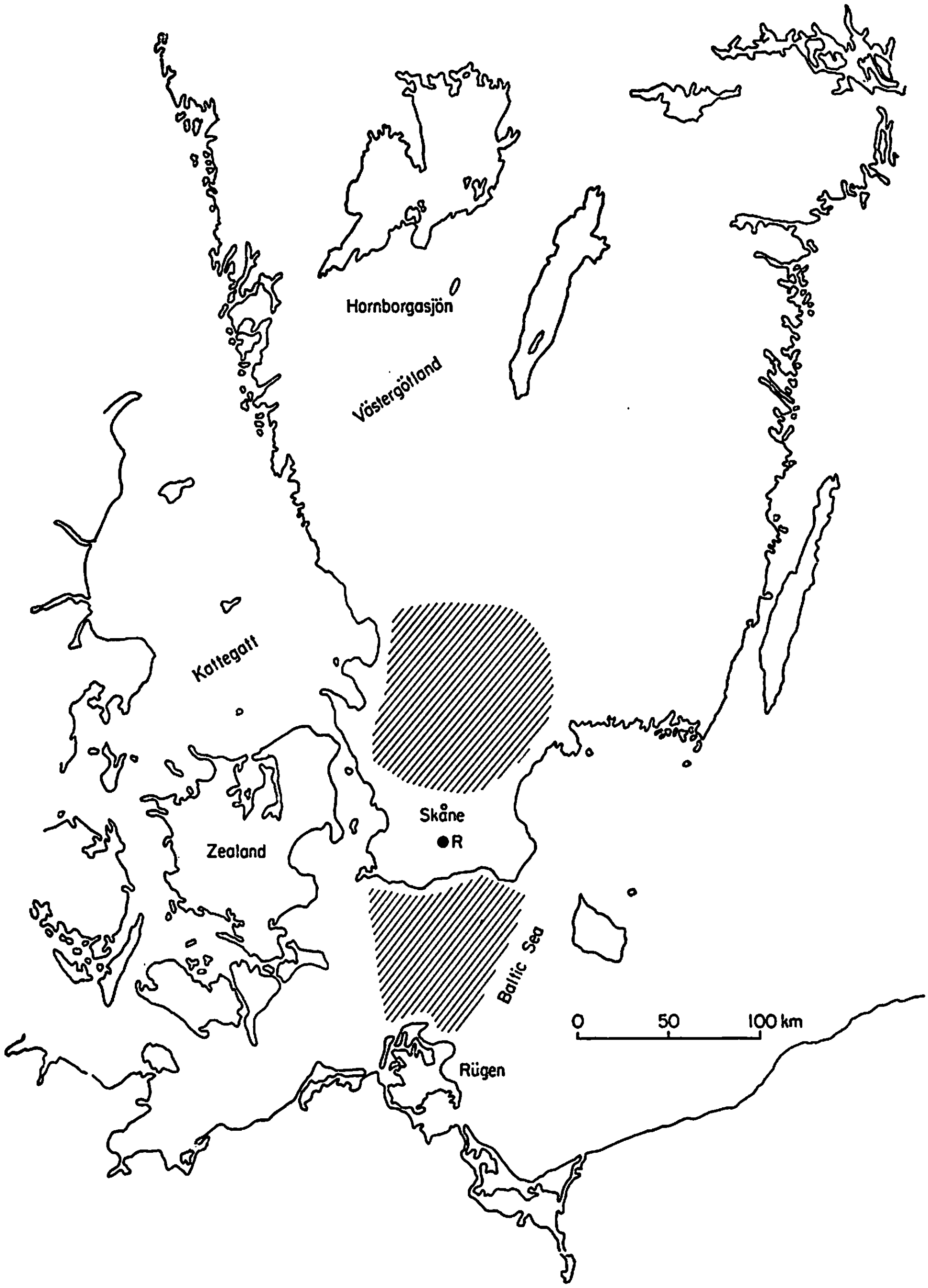

FIGURE 1. Study area. The radar site (R) is indicated as well as the zones in which measurements were made over land in Skåne and over the Baltic Sea (hatched areas).

indicating active flight. Over land, the echoes frequently halted and sometimes disappeared from the radar scope (due to the MTI-effect) for a brief period, moved for a short distance to make another halt, and so on, clearly indicating the technique of flight involving soaring in thermal air. Evidently the flocks of Cranes alternately soared to gain height in a thermal (climbing phase) and then glided off towards north, gradually losing height after having left the thermal (gliding phase, cf. Pennycuick 1972a). Over the sea no thermals develop, and evidence of soaring were not seen until the Crane flocks had crossed the south coast of Skåne and proceeded inland for 5–10 km.

On days with strong tailwinds the echo stops were difficult to demarcate since the flocks drifted towards the north while soaring, and in effect merely alternated between two flight speeds. On 6 days, however, the performance could be analysed: the distance between the echo stops varied between 4 and 33 km (mean $13{\cdot}3\pm$s.d. $6{\cdot}5$ km, $n = 79$). There were no significant differences between different days. The climbing phase lasted 2·8–10·4 min (mean $6{\cdot}3\pm2{\cdot}0$ min, $n = 65$), with no significant differences between days.

On 6 April 1972 most Crane flocks crossed Skåne without soaring. Not until late during this day were a few echoes noted to behave in the way that was typical for soaring. It might be relevant that on this day particularly strong southwesterly winds prevailed so that the soaring flocks had to change their heading direction into the wind by a larger angle than on any other day to be able to keep a northerly track (cf. below).

SPEED

The Cranes usually migrated with following winds (Alerstam & Bauer 1973), and mean ground speeds over the Baltic Sea varied between 56 and 102 km h^{-1} on different days (overall mean 77 ± 14 km h^{-1}, $n = 19$). Allowing for the effect of wind the mean true air speed was 67 ± 9 km h^{-1} ($n = 19$), a value according with expectation from calculations based on mechanics of bird flight (Pennycuick 1969). The true air speed was not correlated with the ground speed (Spearman rank corr. $= -0{\cdot}12$, $n = 19$, *N.S.*).

Over land, by contrast, the mean ground speed on different days ranged (with one exception, see below) from 40 to 66 km h^{-1} (overall mean 50 ± 9 km h^{-1}, $n = 10$), and the mean true air speed was 44 ± 9 km h^{-1} ($n = 10$). On all days with simultaneous migration over sea and land the ground speed was lower over land. This difference between speeds over land and sea is clearly attributable to the different cruising techniques adopted. Intervals of soaring will retard the progress of the birds. The height gained in the thermals has to be paid for in longer travelling time.

From data on all 10 days when ground speed over land could be measured, the calculated speed during the gliding phase under calm conditions was 67 km h^{-1} (using mean distance of gliding phase and mean duration of climbing phase for the calculations). Using data from only the 6 days when gliding distance and climbing time could be accurately measured, the corresponding mean air speed during the gliding phase was 71 ± 9 km h^{-1} ($n = 6$).

On 6 April 1972, as mentioned above, most Cranes did not soar over land, and the flocks travelled with a mean ground speed of 92 ± 7 km h^{-1} ($n = 18$ individual flocks), very similar to that over the sea on this day (95 ± 7 km h^{-1}, $n = 27$ flocks). After noon a few echoes were noted to use soaring technique, and the average ground speed for four such echoes was 57 ± 5 km h^{-1}.

DRIFT

The majority of Crane flocks adopted a course almost due north over the inland of Skåne. Only a small, clearly demarcated fraction (11%) migrated with tracks east of 05° over the northeasternmost part of the province. These few flocks were disregarded when analysing the track directions over land (cf. Discussion). In Figure 2 the mean track directions on different days over sea and land are plotted against the angle between the heading and track directions. This angle corresponds to (i) the amount of drift when the bird flies on a fixed heading or to (ii) the amount of compensation when keeping a fixed track direction. In case (i) the regression coefficient between track direction and the angle between heading and track directions as in Figure 2 would be 1 and in case (ii) would be equal to 0.

As seen from Figure 2a the track direction over the sea was clearly correlated with the angle between heading and track directions. The variation of track direction was,

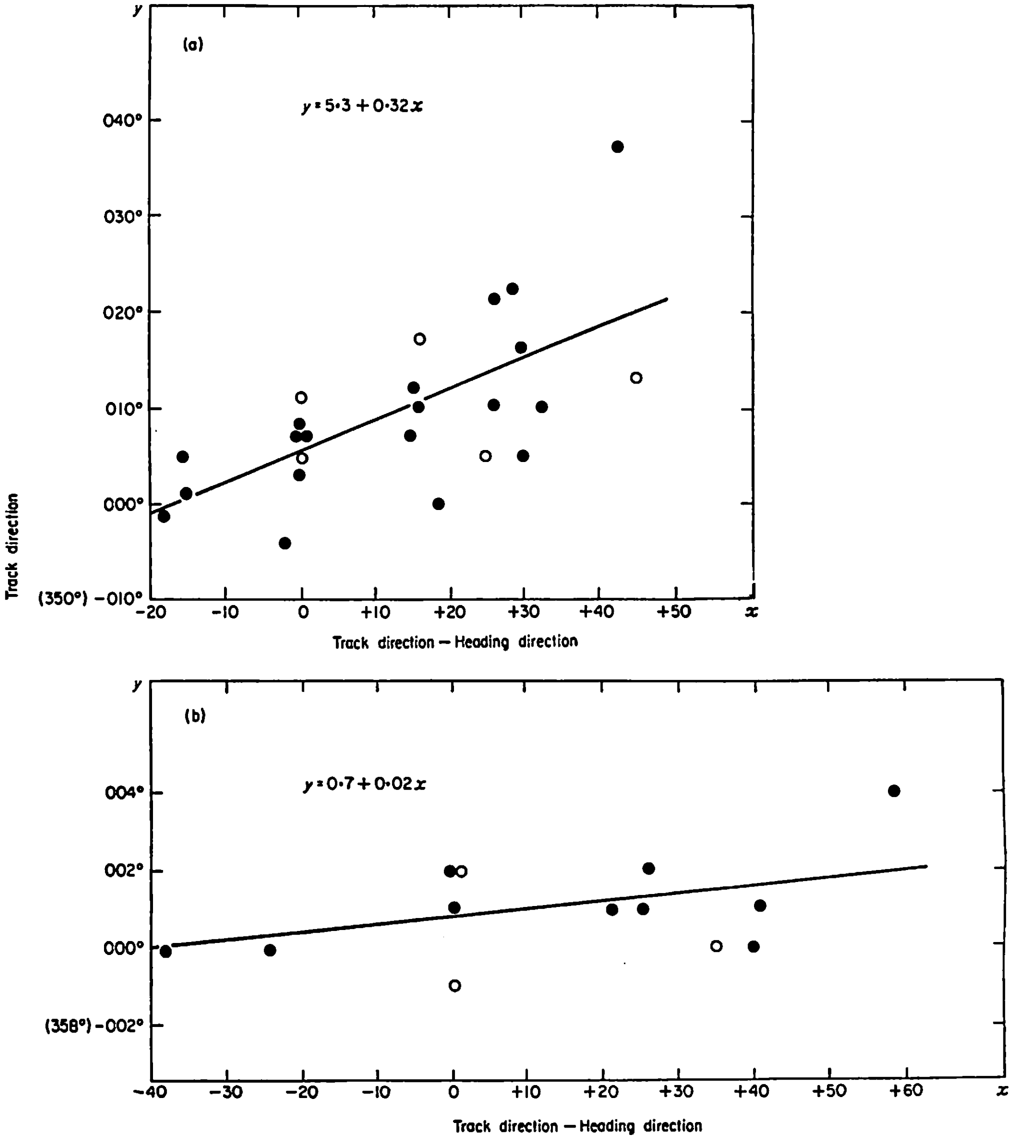

FIGURE 2. Track direction in relation to the angle between track and heading directions (a) over sea (b) over land. Bearings west of 000° are treated as negative. x = track direction minus heading direction. Thus x will be negative when heading direction is to the right of track direction and positive when heading direction is to the left. On days with open circles ground speed data were not available and the x value was calculated assuming an air speed of 67 km h^{-1} over the sea and 44 km h^{-1} over the land (cf. text). For (a): Spearman rank correlation coefficient = 0·65 (highly significant, $P < 0{\cdot}001$). For (b) Spearman rank correlation coefficient = 0·31 (*NS*, $P = 0{\cdot}15$).

however, considerably less than would be expected if the birds flew on a constant heading. The regression coefficient (0·32) could be interpreted as if the angle between the heading and track directions was composed of 68% compensation and 32% drift. This drift could be due not only to wind drift but also to 'pseudodrift', i.e., the result of Crane populations with different primary directions taking part in the movements in different proportions under different wind directions (Evans 1966, Nisbet & Drury 1967). Evidence is presented below, however, to rule out pseudodrift as a factor of significant effect.

In contrast to the situation over the Baltic Sea, no statistically significant variation of track direction in relation to the wind could be demonstrated over inland Skåne (Fig. 2b), indicating that here the Cranes compensated completely for wind drift.

Although soaring birds over land under strong crosswinds were susceptible to considerable drift during the climb, the track during the gliding phase did not differ conspicuously from the resulting track measured over a larger distance. On a few occasions when the expected differences between gliding and resulting track directions were 10–20°, measured difference was of the order of 2–4°. Likewise, when in a few instances the drift during 6·3 min climb was expected to be 3–4 km, the distances measured on the radar scope were only 1–2 km. Although drift from crosswinds definitely took place during the climbing phase, it seems that the Cranes behaved in some way to eliminate a considerable part of the deflection. Although impossible to analyse in detail, because of the limited resolution on the indicator screen, some echoes at least gave the impression of heading into the wind immediately before stopping and entering the climbing phase and again heading into the wind before setting out on their gliding track. Possibly the Crane flocks also moved horizontally during the climb within the thermal (which can extend over 2 km) to counteract the effect of wind drift.

The scatter of track directions was much larger over the sea than over the land. Crane flocks often departed over the sea in a fan-shaped pattern with the mean angular divergence of track directions $24 \pm 7°$ ($n = 20$). Over Skåne, the mean angular divergence of track directions for the different days was $7 \pm 3°$ ($n = 12$).

DISCUSSION

The weather during the days of Crane migration over land was characterized by 2/8 to 5/8 cumulus cloud cover with the cloud base at 500–1000 m altitude. Some cumulonimbus clouds sometimes developed later in the day. According to the experience of glider pilots average vertical wind speed in a thermal below such cumulus clouds should be about 4 m s^{-1} (ranging from 1 to 6 m s^{-1}) and still faster under cumulonimbus clouds (cf. Pennycuick 1972b). Assuming the sinking speed of the birds to be in the order of 1 m s^{-1} (Pennycuick 1972b) one may provisionally count on a rate of climb in the order of 3 m s^{-1} for the Cranes. During 6·3 min the Cranes thus would climb 1100 m and with a gliding distance of 13·3 km the glide ratio is 12:1.

In southernmost Skåne the altitudes of Crane flocks were measured on 7 days in 1973 with a mobile X-band radar (Karlsson & Alerstam 1974). Only a few flocks were noted above 1000 m altitude, and practically all flocks were cruising below the cloud base. The difference between highest and lowest altitude of flocks on different days was 250–500 m, presumably reflecting to some extent the climbing distance. These data thus indicate that the Cranes did not climb over 1000 m in the thermals, as calculated above, but at most half of this instance. There are, however, grounds to conclude that the measurements in southern Skåne may not be representative of the situation in the northern part of the province. First, the area surveyed by the X-band radar was close to the coast and the flocks had perhaps not yet been able to benefit fully from the thermals. Second, the Cranes passed this area 1·5–2 h before they passed northern Skåne, and thermals are comparatively poorly developed early in the day. Furthermore, cloud base regularly rose during the day and the altitude of the Crane flocks showed a tendency, although not statistically significant, to increase with rising cloud base (Karlsson & Alerstam 1974). These circumstances make it likely that the Cranes would climb higher in the thermals over northern Skåne than observed with the X-band radar in southern Skåne. Whether they climbed as much as 1100 m, however, remains an open question although, if they climbed on average considerably less, the Cranes could not have glided for 13 km, but must have used active flight during part of the intervals between the soaring interludes.

The figures of total and gliding speeds during overland migration flights of the Crane are well in accordance with those found for cross-country soaring of Rüppel's Griffon Vulture *Gyps rueppelli*, White-backed Vulture *Gyps africanus* and White Stork *Ciconia ciconia* by Pennycuick (1972b). The glide ratio of 12:1 is also according to expectation (Pennycuick 1972b).

The larger scatter of track directions over the sea than over land could be an effect of the lack of landmarks over the sea, suggesting different abilities of the individual flocks to orientate under such conditions. It might be a rewarding task to try to correlate the flocks' deviations from mean track direction to the flock sizes.

Mean track directions over the sea were clearly influenced by wind conditions, whereas this was not so over the land. This drift cannot be attributed to pseudodrift. Over land, 89% of all flocks followed virtually the same primary direction (Schüz 1971). If the remaining 11% is considered when calculating the total weighted mean track directions over land in relation to wind conditions (as in Fig. 2b) the results ($y = 1{\cdot}9 + 0{\cdot}02x$, Spearman rank correlation coefficient 0·30, *NS*) are not significantly different. Thus this small percentage can reasonably be assumed not to have influenced the mean track direction over the sea on different days to any important degree. Furthermore the hypothesis of pseudodrift predicts a negative correlation between total range of tracks and the crosswind component of the wind (Nisbet & Drury 1967), whereas the correlation coefficient was in fact positive (Spearman rank correlation coefficient = 0·29), though not significantly so ($P = 0{\cdot}20$).

Hence one must conclude that the variation of track directions over the sea was due to incomplete compensation for wind drift. Over land, however, no wind drift took place. This strongly indicates that landmarks are important for exact orientation. Under very heavy WSW winds a few flocks crossed the Baltic on 1 April 1973. The mean track was about 10° within 20 km off Rügen, but further north the mean track was about 37° over the open sea. The echoes again moved more towards the north when 10–20 km off the south coast of Skåne. This indicates that the Cranes to some extent could use landmarks close to the coast, but over the open sea or when land is visible only at the far horizon they were subject to considerable wind drift.

The angle between the Cranes' track and heading directions over the sea, as explained above, was attributable to 32% wind drift and 68% compensation. By comparison, for the Wood Pigeon *Columba palumbus*, which also compensates incompletely over the sea (Alerstam & Ulfstrand 1974), drift amounted to 36% over the Baltic Sea and 26% over the Kattegatt; a minor part of this drift over at least the Baltic Sea was due to pseudodrift. During overland travel the complete compensation for displacement by the Cranes is in marked contrast to the considerable deflections due to wind drift during thermal soaring experienced by raptors, especially *Buteo* and *Pernis*, as described by Rudebeck (1950).

Many Cranes (though probably not the majority) departing from Rügen stop to rest at Hornborgasjön in southern Sweden (Swanberg 1970). This lake is situated 400 km north of Rügen, the exact bearing from the northernmost peninsula of Rügen being 01·4°. The mean track directions under no influence of the wind (as read from the equations in Figure 2) were 05° over the Baltic Sea and 01° over the inland of Skåne (disregarding a few flocks heading distinctly to the NNE). Both directions agree well with the bearing towards Hornborgasjön and it must be concluded that most Scandinavian Cranes pass the province of Västergötland via or close to Hornborgasjön. Under calm weather the Cranes would require 8·5 h to reach Hornborgasjön from Rügen. Usually they migrated with following winds, so the median expected travelling time was 7·8 h. Observations at Hornborgasjön reveal that a large part of the Cranes reach this lake at sunset on the same day as they left Rügen. Many Cranes however, do not, arrive until the following day (Swanberg *in litt.*). This is exactly what should be expected from the diel distribution of departures from Rügen (Alerstam & Bauer 1973) and the duration of the journey as calculated above. Sunset is about 19.00 hrs, and Cranes departing from Rügen before 10.00 or 11.00 hrs can reach Hornborgasjön on the same day. Still many flocks depart after 11.00 hrs, and they cannot arrive at Hornborgasjön before darkness.

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SUMMARY

The detailed process of Crane *Grus grus* migration over sea and land, respectively, was studied from films of a radar station in Skåne, southernmost Sweden, during the spring migratory periods in 1972 and 1973.

The true air speed for travelling over the sea was 67 km h^{-1}, whereas over land the Cranes made use of thermal air to soar and gain height and the true air speed was 44 km h^{-1}. Soaring lasted on the average 6·3 min and the distance travelled between the soaring interludes was 13·3 km. True air speed during the flights between thermals was about 70 km h^{-1}.

The Cranes compensated completely for wind drift over land, but only incomplete compensation took place over the sea. The angle between the Cranes' heading and track directions over the sea was composed of 68% compensation and 32% drift.

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