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Two Types of Orientation in Migrating Starlings, Sturnus vulgaris L., and Chaffinches, Fringilla coelebs L., as Revealed by Displacement Experiments

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ARDEA

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TWO TYPES OF ORIENTATION IN MIGRATING STARLINGS, *STURNUS VULGARIS* L., AND CHAFFINCHES, *FRINGILLA COELEBS* L., AS REVEALED BY DISPLACEMENT EXPERIMENTS

by

A. C. PERDECK

29th publication of the Foundation "Vogeltrekstation Texel"

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INTRODUCTION

The extensive marking of birds has revealed that many migrant species are divided in populations, each of which has its own restricted breeding range and winter quarters. In addition to this, field observations on such birds during their migration have shown that they tend to migrate in a fairly constant direction, provided the region flown over is more or less homogeneous ("preferred direction" or "standard direction", THOMSON 1953). Deviations from this direction occur mainly

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under the influence of topografical features, such as coastlines ("leading lines", THOMSON 1953). Since the preferred direction points more or less accurately to the aimed area of destination, a simple theory for the navigation of these broad front migrants may be set up. If the birds possess a method for steering in a fixed course (in the preferred direction), both in autumn and in spring, and if there are not too extensive barriers that deflect them from their route, they will reach their winter quarters from the breeding area and vice versa. In fact, this theory is, broadly spoken, able to explain what is known about the annual distribution of many migrants. The existence of a capacity to maintain a certain compass direction during migration, irrespective of the position of the breeding or wintering area ("one-direction orientation") is proved by the displacement of migrants sideways from their route (Starling: KRÄTZIG & SCHÜZ 1936, SCHÜZ 1950a; Hooded Crow: RÜPPELL 1944; American Crow: ROWAN 1946; White Stork: SCHÜZ 1949). The recent experiments of KRAMER and co-workers have provided a reasonable explanation of the mechanism involved in this type of orientation (KRAMER 1951, 1952, 1953; HOFFMANN 1954). But, even in the strict broad front migrants, this does not cover the whole ground. We know at present that individuals have in general a very restricted breeding area during their lifetime and a certain number of cases suggests that the same holds for individual winter quarters. Taken into consideration the effect of sideways transportation caused by weather and barriers, the exact location of these places, tiny as they are in relation to the covered area as a whole, must involve a more reliable method of orientation than merely steering in a certain direction. And further, certain observations suggest that the preferred direction of a certain population is different in various parts of the migration route. VAN DOBBEN (1944) and NIJHOFF (1958) found that Starlings and Chaffinches left Cap Gris-Nez in north-westerly directions, even if the opposite coast of England was invisible. The preferred directions of these species are between S.W. and W. in the Netherlands, and ringing results show clearly that these are birds from the same populations that reach Cap Gris-Nez. The same holds for the observations of the LACKS (1952) at Lands End[1]). Here Starlings and Chaffinches left in north-westerly directions, thus heading for Ireland which belongs to the wintering area of both species.

These observations suggest that the preferred direction is influenced by the relative position of the wintering area. Next to the one-direction

[1]) LACK made similar observations at Bull Point, N. Devon (Brit. Birds 50, pp. 10-19).

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orientation there seems to be involved another type of orientation, by which the birds during migration actually can determine (locate) the resting area. This faculty is probably present too in adult Sparrowhawks that were displaced during autumn migration from Heligoland to Silesia and after the displacement did not resume flight in the original course, but aimed more or less at their winter quarters (3 recoveries from the same season, DROST 1938a). The faculty of birds to orientate themselves not merely in a particular compass direction, but to a certain geographical position has been called "homing orientation", "complete navigation" or "true goal orientation". Its existence is doubtlessly proved by homing experiments in many species during the breeding

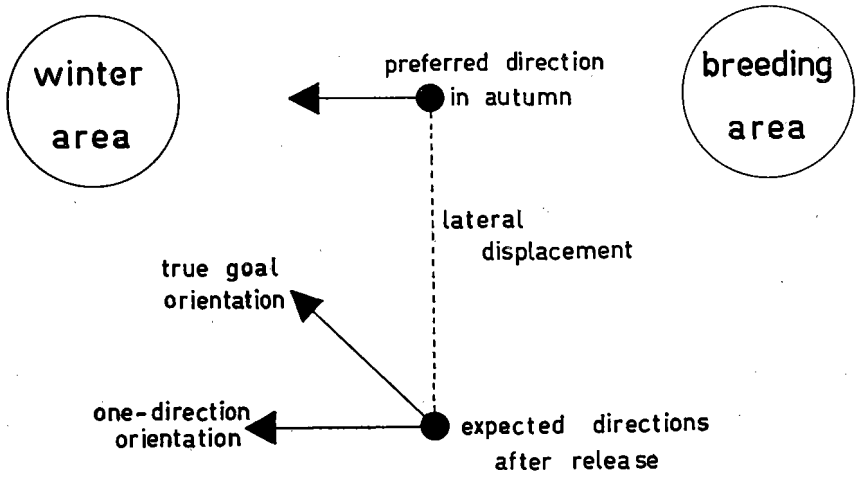


Fig. 1. Design of the experiment.

period (summary in MATTHEWS 1955). Therefore it seems unlikely that this highly developed mechanism of orientation is not used during migration where it has so many advantages as compared with one-direction orientation. Why then, has it not been found more emphasized in the undertaken displacement experiments? Both the mentioned experiment of DROST and the homing experiments suggest that this faculty is developed especially in older birds, which have been already one or more seasons in the area of destination. But adults formed a minority in the experiments hitherto undertaken, and this might be the answer to the question. However, taking all the evidence together, we have no certain base for the statement that true goal orientation is used by birds during migration.

This was the reason that the Board of the Vogeltrekstation planned a new experiment, in which due notice should be taken of adult birds.

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Obviously, the lateral displacement of migrants en route provides an ideal experimental set-up (compare fig. 1). If the birds use one-direction orientation they will fly parallel to their original course and do not reach the resting area which is normal to the population. If, on the other hand, they use a true goal orientation, they will go straight to the resting area in a direction different from the original course. As a preliminary to the experiments described in this paper VAN DOBBEN (1939) displaced in 1938 nearly 600 Starlings caught as autumn migrants near The Hague and Harderwijk to Ducey near Avranches (dep. Manche, France). The outbreak of the war made an end to this experiment before results were obtained.

Ten years later the project was resumed, and it was agreed that the displacement could be better directed to Switzerland, thus giving a higher chance of recoveries. Further, it was considered very important to make separate experiments with adults and first-year birds. In the light of the evidence given above a difference in the behaviour of adult and juvenile birds could be expected. In mixed groups they might influence each other, which would make the results less clear. After good results with these separate transports a number of displacements with mixed groups was undertaken in order to study the influence of the age-classes on each other. The main experiment was carried out on the Starling, but a displacement of Chaffinches on a smaller scale yielded also some interesting recoveries.

In 1948 and 1949 the displacements were carried out by KLOMP (1949, 1950), and from 1950 to the end (in 1957) by the author. Preliminary reports of the experiment have been given in the Annual Reports of the Vogeltrekstation (Jaarverslag Vogeltrekstation 1948-1956). The recoveries obtained from the Starling are published in the annual recovery lists of the Leiden Ringing Scheme (Limosa 24, 1951, p. 27 and subsequent reports). The few recoveries of the Chaffinch are given in this paper.

Acknowledgements

These experiments were planned by the Board of the Vogeltrekstation, but the main contribution to its framework was given by the late Prof. Dr. L. TINBERGEN. I owe to him many valuable discussions.

Without the help of our skilled bird-catcher, the late Mr. G. BERG, the project would have been scarcely practicable. He died shortly after the completion of the experiments. This paper may serve as a memorial for him. His constant aim to catch as many birds as possible, without regarding the labour involved, together with his thorough knowledge of the requirements of the birds, has saved me much trouble.

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During later years, his assistant, Mr. Q. J. VOORHAM, has lightened his heavy task with the same ability. I received much help with the working up of the catches from several students, but I will mention here especially Mrs. E. HENDRICHS and Mr. P. M. SCHENK, who aided me for several seasons. To Mr. A. HENDRICHS we owe generous financial aid and gifts in kind. Grants towards the high costs of the transport were provided by the "Pieter Langerhuizen Lambertuszoon Fonds" of the "Hollandse Maatschappij der Wetenschappen" and the "Netherlands Organisation for Pure Research (Z.W.O.)". For helping with the release of the birds in Switzerland Mr. L. HOFFMANN, Dr. E. SUTTER and Mr. H. WACKERNAGEL at Basle and Mr. P. GÉROUDET at Geneva deserve our sincere gratitude, together with the personnel of the airports, who undertook this in later years. The manuscript was read by Prof. Dr. H. KLOMP and Dr. H. N. KLUYVER. I thank them for their helpful criticism. The English text was considerably improved by Mrs. M. E. GELDERMAN.

EXPERIMENTS WITH STARLINGS

Methods

The Starling migrates in huge numbers each autumn along the west coast of the Netherlands. Refined catching methods (TER PELKWIJK 1941) are elaborated by the tenants of the formerly numerous fowling yards, one of which is still used by the Vogeltrekstation, situated near The Hague (in 1948-1954 at Loosduinen (52.03 N. 4.13 E.), in 1955-1957 at Wassenaar (52.08 N. 4.20 E.)). The experimental birds were caught and ringed during the months October and November. Essential was a good identification of age and sex of each bird. The distinction was made largely by about the same characteristics described by KESSEL (1951). Moreover it was found that the adults (both male and female) differ from the first-year birds (called in future juveniles) in the form of the white tips on the upper breast feathers. These tips tend to take the form of a V in the adults, but are more heart-shaped (with a shorter black central line) in the juveniles. The reliability of the characteristics was checked by the section of dead birds, sex by means of the gonads, age by the degree of ossification of the skull. Later we found that this latter very valuable criterion could be applied in living birds also. We made no cut in the skin as MILLER (1946) recommended, but found that it was possible to look through the skin. It is not even necessery to remove some of the feathers on the head, since near the ear a place is to be found without feather implants. We used this method frequently in difficult cases.

The release points were Basle, Zürich and Geneva, to which the birds were sent by aeroplane. Bamboo cages with a height of about 15 cm and of varying length and width were used for the transport. The available space

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for each bird was about 40-100 cm^2 of the bottom. These cages were wrapped in paper and, together with smaller holes a window was cut in the top-centre, ensuring a good aeration. The advantage of the central position of the window was that the birds, when disturbed, did not crowd into the corners.

As soon as possible after being caught the birds were transported after having being previously provided with food (mealworms and Sluis' Universeel food) and water. During the journey only food was given. As a rule the birds were released in Switzerland within 24 hours after being caught. Adult birds, however, often had to be kept for some days in the fowling yard, in order to get a workable quantity of them. The mortality was very low. Excluding the introductory transports in 1948 and the high mortality in one cage due to wrong treatment, only 30 of the total of 11.100 birds died or weakened considerably during the journey (0.27%).

Normal course of autumn migration

The birds used for the experiment were taken from the concentrated highway that follows the coast of the North Sea. From 1930 onwards extensive ringing of the Starlings migrating on this route near The Hague in the autumn has been carried out. If we combine all recoveries from the breeding season (April-August) a picture of the breeding area of the population can be gained, and in the same manner the recoveries from December-February enable us to locate their winter quarters. It appears that these Starlings breed in a large area covering South Finland, South Sweden, the Baltic area and adjoining Russian parts, North Poland, North Germany, Denmark and Holland. They winter in Holland, West Belgium, N. W. France, South England and Ireland (fig. 2). Thus a number of birds remain in Holland both during winter and summer. This, however, does not necessarily mean that these birds are all residents. As is shown by the piegraphs of fig. 2, the birds arriving at The Hague later in the season tend to breed more easterly than those caught earlier, and especially these later birds winter in the eastern part of the wintering area, including Holland. Thus the majority of birds found wintering in Holland seems to be migrants. In the same manner, the birds caught earlier breed mainly in the western part of the breeding area (including Holland). They, however, do not winter here, but do so preferably in the western parts of the winter quarters, and they must therefore be regarded as migrants too. It is, of course, likely that a restricted number of residents or birds that had finished their migration already have been caught among those that were used for the experiment. This shift of populations during the season causes a difficulty in the comparison with the displaced birds. For, if by chance,

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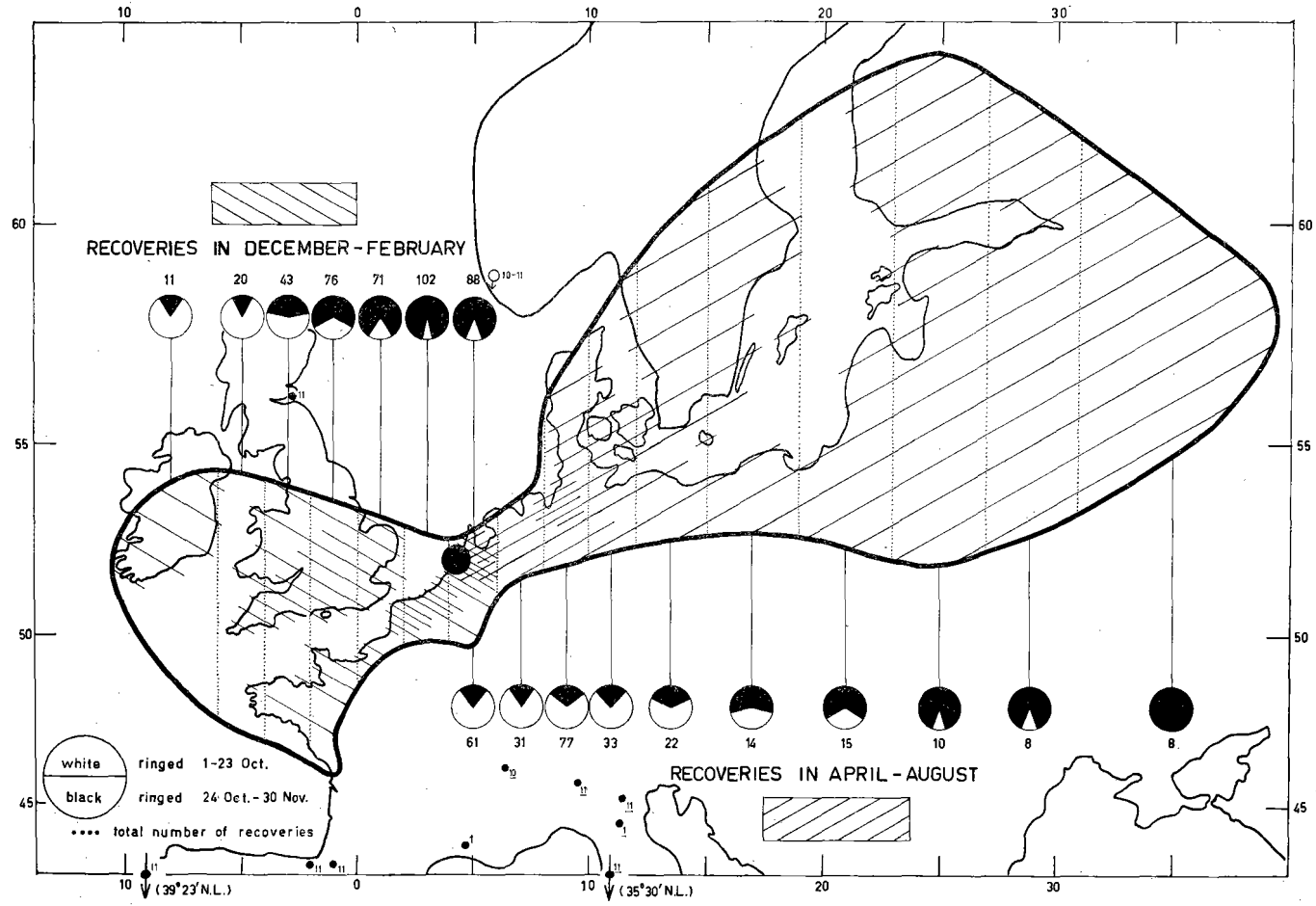


Fig. 2. Distribution of summer- and winterrecoveries of Starlings marked near The Hague in October and November. Small dots: recoveries outside the normal area (figures indicate month of recovery). Concentrations of recoveries shown by density of hatching. Each piegraph refers to the section it is connected with (for explanation see left bottom corner). The map is, as the others in this paper, drawn in the Mercator projection.

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mainly birds from the later part in the season are transported, the recoveries obtained from them are not quite comparable with the picture from fig. 2, in which recoveries from birds caught earlier in the season are also represented. In order to have a more reliable comparison a sample of the birds that were not displaced has been taken from the ringing lists. These birds were caught at the same catching station and within a few days at the same time and in equal numbers (within each year) as the experimentals. This could be done for the juveniles only, since nearly all adults caught were used for the experiments. The recoveries obtained from these control birds are shown in fig. 3 and 4.

Our principal interest in this chapter is, however, to determine the preferred autumn direction of these Starlings when they migrate over Holland. Reliable figures are not so easy to obtain. Something might be deduced from the relative position of breeding and wintering area. The overlap of these regions makes it, however, difficult to apply this to the case concerned. The directions of the separate recoveries shortly after ringing are also useless. They lie for the greater part along the coastline (West Belgium) and the directions involved are clearly influenced by this leading line (compare fig. 3).

There are, however, a number of field observations on the direction of the broad front migration, during which the birds are, by definition, flying in their preferred direction. From 1933 till 1939 VAN DOBBEN organised watches throughout the Netherlands. His conclusion is that in the northern parts W.-W.S.W. directions prevail, in the mid- and southern parts W.S.W.-S.W. directions (VAN DOBBEN 1935, 1936; VAN DOBBEN & MAKKINK 1934). TINBERGEN (1941 b) used these observations to make an estimate of the preferred directions of the Starlings migrating along the coast near The Hague, and he deduced that their mean direction lies between W. and W.S.W. (nearer to W. than to W.S.W.).In the same paper broad front observations are given of several places in the vicinity of The Hague, but so far inland that the birds were not yet influenced by the coast. In these observations (made in 1935, 1936 and 1938) too W. and W.S.W. directions dominate. In the autumns of 1941 and 1943 the same author made special watches in a barren polder near Leiden to obtain more exact figures about the preferred direction. Only the graph is published (TINBERGEN 1949, p. 46), but I had access to the original figures. The main directions of flight were W. (32.6%), W. by S. (20.9%) and W.S.W. (24.6%) (compare also fig. 9 A). It seems therefore fairly safe to conclude that in Holland the preferred direction of the Starlings used for the experiment lies between W. and W.S.W.

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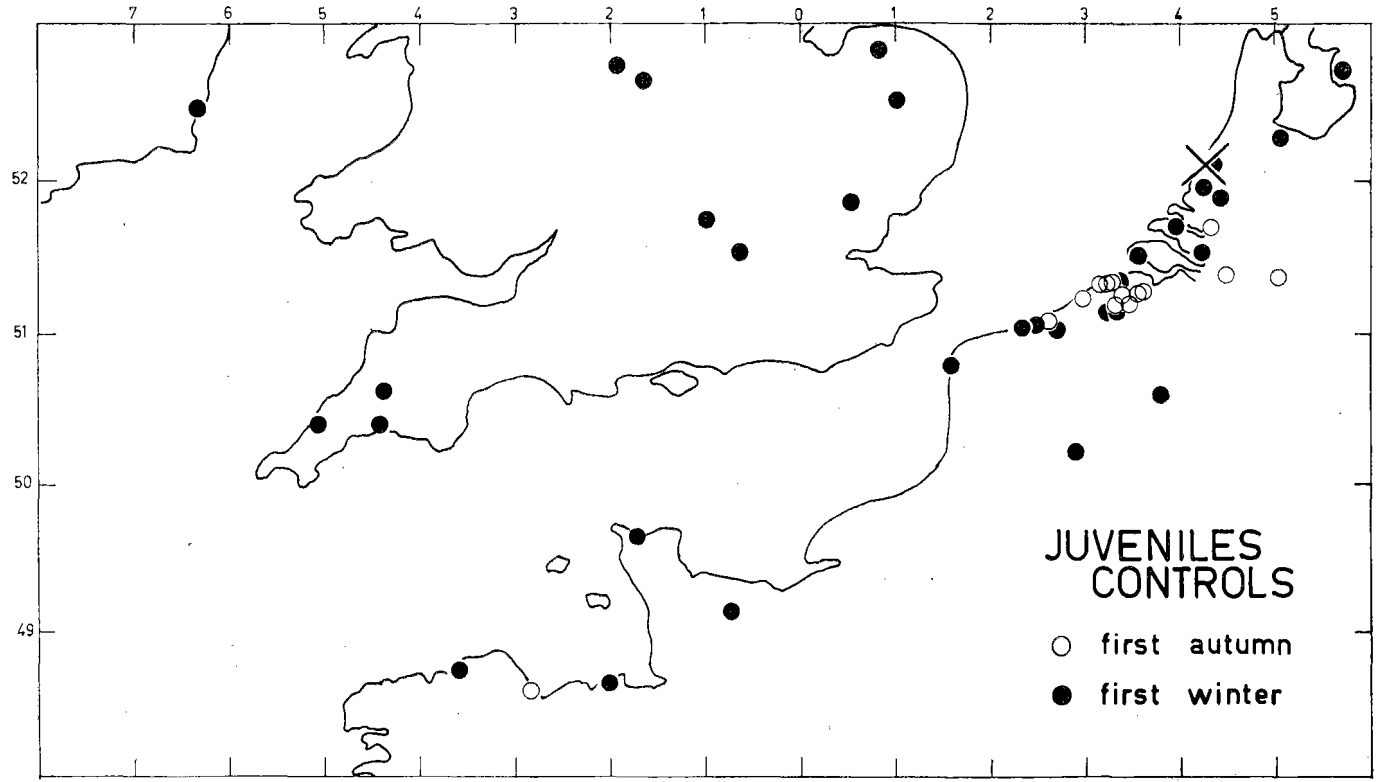


Fig. 3. Recoveries of non-displaced juvenile Starlings ringed at the same time and in the same numbers as the transported juveniles. Recoveries in the same season.

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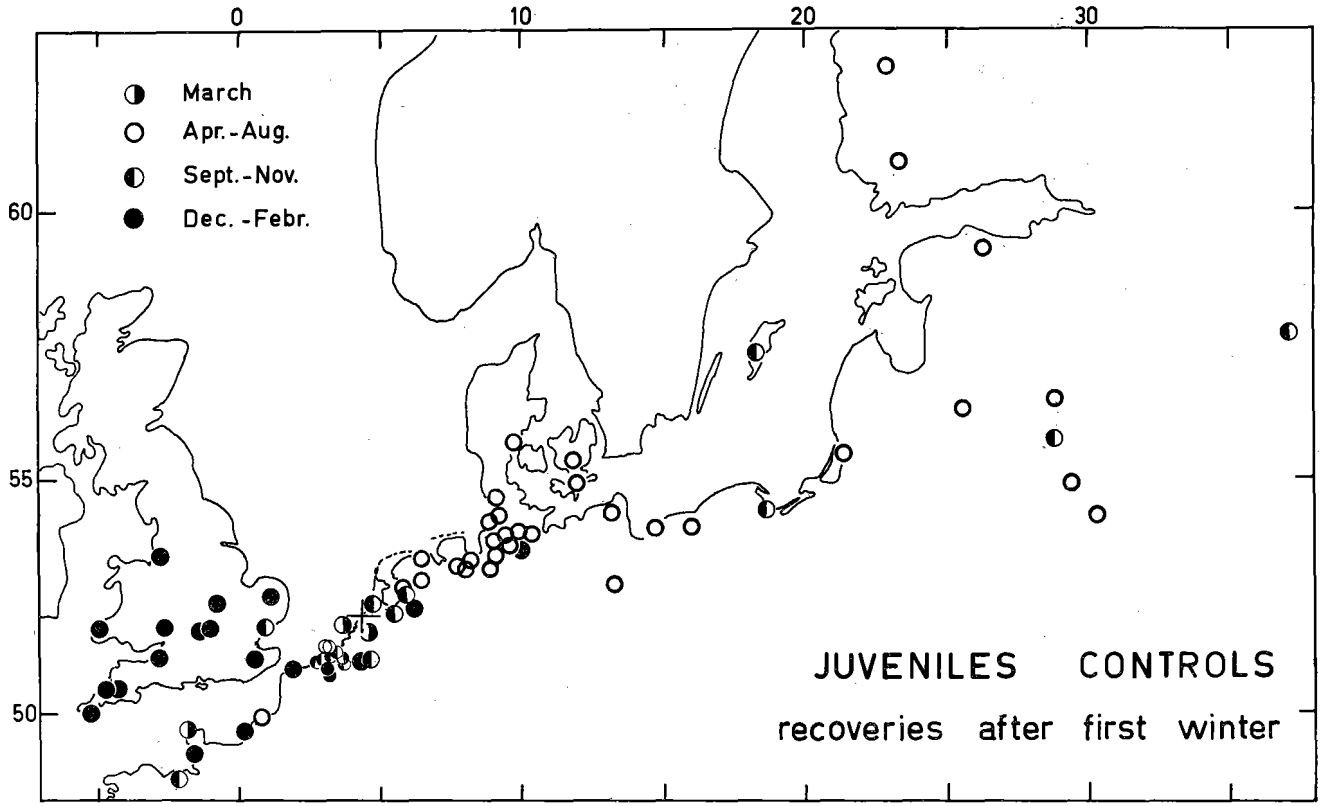


Fig. 4. Recoveries of non-displaced juvenile Starlings ringed at the same time and in the same numbers as the transported juveniles. Recoveries in later seasons.

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During the same years that the experiment was done, TINBERGEN organised watches in the northern part of the Veluwe (prov. Gelderland). Here the direction of wide front migration was definitely more southerly, the peak lying at W.S.W. Birds migrating from there in this direction will reach the coast at a point south to The Hague, and thus cannot contribute to the Starlings used for the experiment. For this reason these observations are omitted, although in a preliminary discussion of the results (PERDECK 1954) they were used. At the moment, however, I feel that this is not justified.

Numbers transported and recovered

Two types of transportation were made. In the first adult and juvenile birds were strictly separated by sending only one age-class in one year or by releasing them in the same year at different places. The other type consisted of mixed groups, each cage containing equal numbers of adults and juveniles. In the years of the experiments with mixed transports also a number of non-mixed young birds were displaced as controls to another place. Table 1 summarises the number of birds displaced in these different ways. In total 354 recoveries were obtained (3.1%). They will be divided in three groups:

(1) those from the same season, i.e. the same autumn and the following winter (up till Febr. inclusive) and recovered within 50 km of the release point;
(2) idem, but recovered at a distance of more than 50 km;
(3) the recoveries from later than the same season.

TABLE 1

Numbers of Starlings caught near The Hague in the autumn (Oct. and Nov.) and released in Switzerland

Year	Adults (separate)	Adults (released with juveniles)	Juveniles (separate)	Juveniles (released with adults)	Total
1948 (preliminary experiments)	—	15	—	162	177
1949-1953	2174	—	3212	—	5386
1954-1957	—	1598	2505	1581	5684
Total	3787 adults		7460 juveniles		11247

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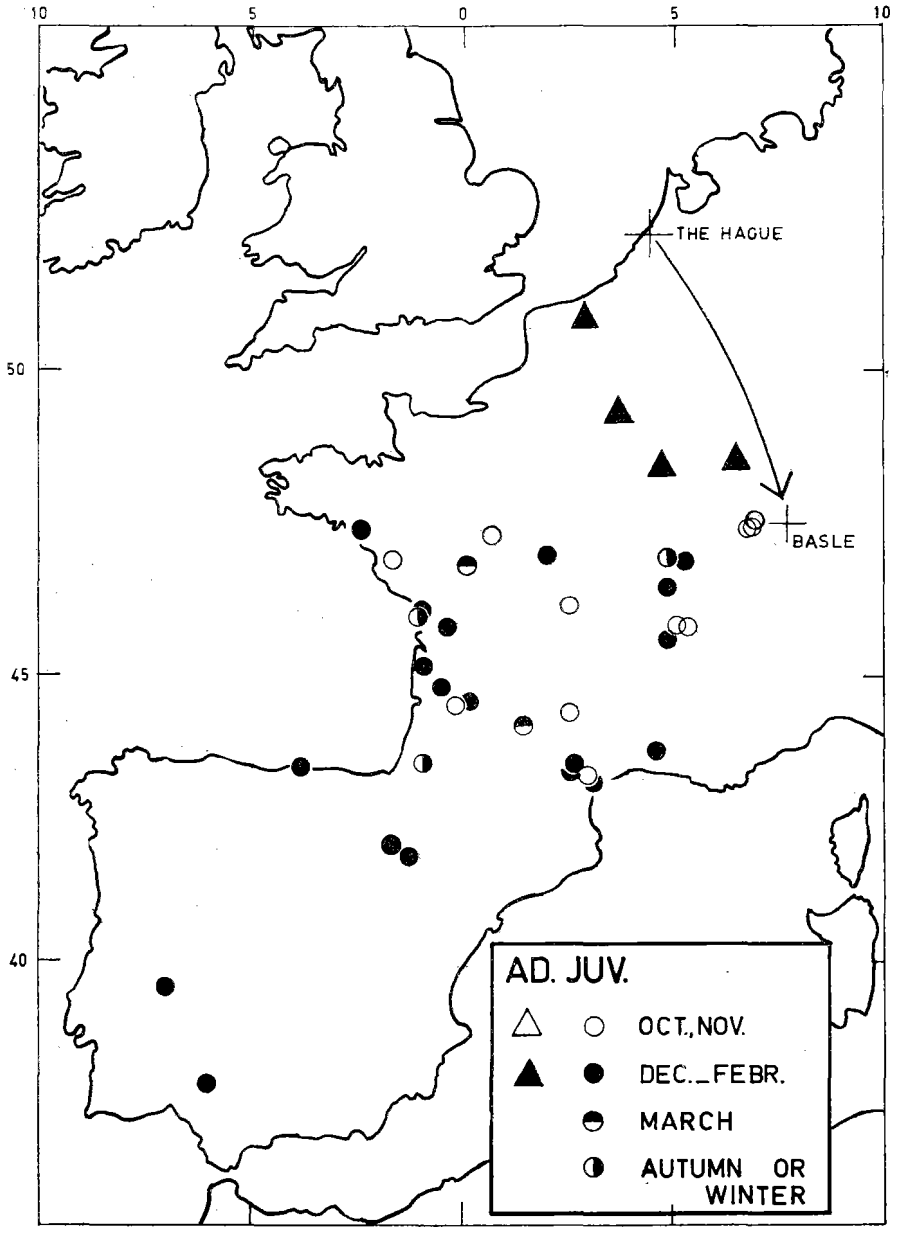


Fig. 5. Recoveries of Starlings in the same season, after displacement to Basle.

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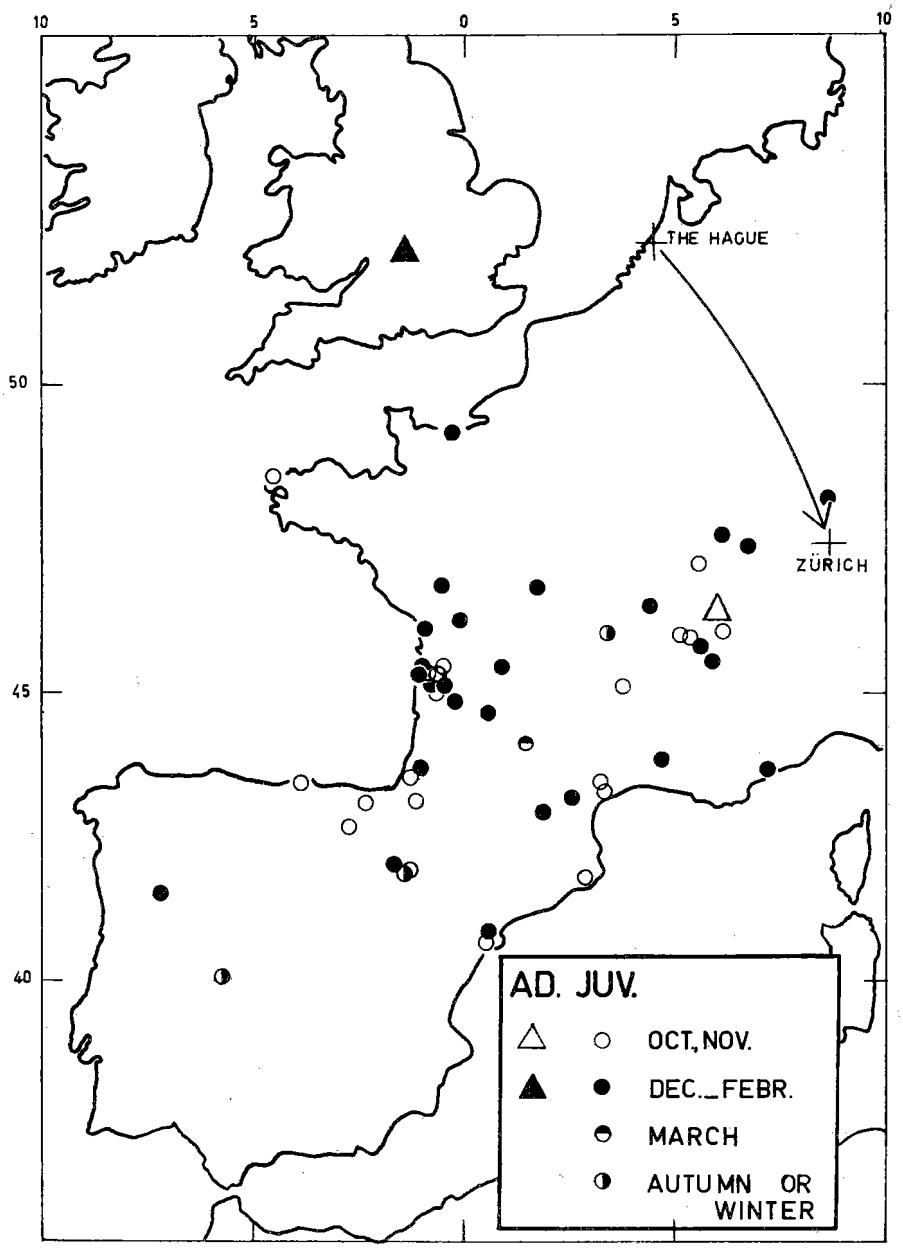


Fig. 6. Recoveries of Starlings in the same season, after displacement to Zürich.

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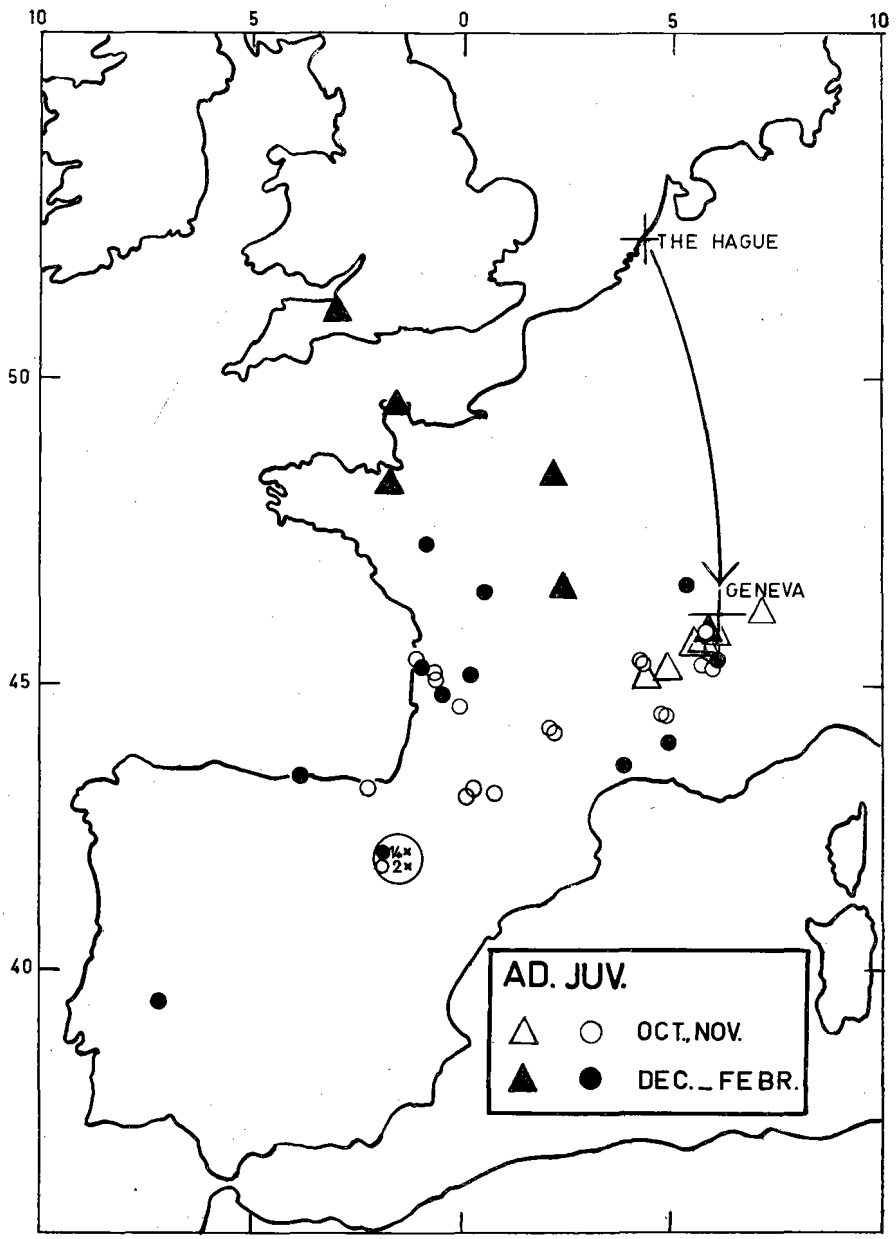


Fig. 7. Recoveries of Starlings in the same season, after displacement to Geneva.

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Since our interest is primarily in the directions, group (1) is not very useful and, unless otherwise stated, is omitted in the following argument. Table 2 gives the number of recoveries of each of these groups, separately for adult and juvenile birds, together with those from the controls. It appears that the recovery-rate is higher in the juveniles than in the adults. Comparison with the non-transported birds indicates that this is not due to age. This point will be discussed below (p. 20). The higher recovery-rate within 50 km of the displaced birds as compared with the controls, points to an effect of the experimental treatment. It is more evident in the adults, probably since they were in general held longer in captivity (see p. 6).

Recoveries in the same season from transports in which adults and juveniles were released separately

The recoveries of these transports (in which the age-classes were separated) are shown in figures 5, 6 and 7. Since they are plotted on maps in Mercator projection, the direction of each recovery can be measured. The

TABLE 2

Number of recoveries received up till 21-4-1958

	Totals released	Recovered in the same season (Oct.-Febr.)		Recovered later					Totals recovered
		within 50 km	more than 50 km	March	April-Aug.	Sept.-Nov.	Dec.-Febr.	Total	
Adults	3787	26 0.7%	32 0.8%	9	16	8	11	44 1.2%	102 2.7%
Juveniles	7460	27 0.4%	144 1.9%	5	19	30	27	81 1.1%	252 3.4%
Controls (juveniles not displaced)	7470	5 0.1%	41 0.5%	4	34	15	24	77 1.0%	123 1.6%

distance from the release point was taken from an atlas. In fig. 8 the recoveries are given for the three release points coincided and here they are placed in true compass-direction and distance. There is a striking difference in the directions taken by the adult and juvenile birds.

A few birds were recovered in the following winter just near the release point (2 adults and 2 juveniles). These birds may be considered as Dutch residents or as birds that were, when transported, already wintering (compare p. 6).

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a. Course of the adults.

At greater distance the adults held a north-westerly course (compare fig. 9:1) and 5 of them were recovered in the normal winter area. This means without doubt that they used a true goal orientation. It is the more convincing if one bears in mind that the general course of the normal starling migration through France is a very different one, namely about south-west (see p. 18). At shorter distances, however, a number of recoveries lie in south-westerly directions. But the fact that they all remain within 250 km from the release point indicates that such birds also turn to a north-west direction after some time. This is corroborated by the fact that these south-westerly recoveries are mainly from the autumn (6 out of 8), the north-westerly ones from winter (8 out of 10). Although we have no explanation of this behaviour of such adults, one is inclined to assume that such birds first used a similar method of orientation as the juveniles (see below) and then changed into the true goal orientation. Perhaps the shock of the treatment has something to do with it.

b. Course of the juveniles

The course of the juveniles shows a considerable variation. It is clear that the recoveries from the (same) migration period in general will give better information about the directions taken than those of the first winter. In fig. 9:3 therefore, the frequencies of the several directions are sepaparated accordingly. The main direction appears to be S.W. by W. This mean course did not alter at different distances (fig. 8) and it seems therefore that the birds used a mechanism of orientation providing them with a fixed direction during the journey. This direction is close to that of the broad front migration over the Netherlands, which was concluded to be between W. and W.S.W. (see p. 8). There is, however, a difference of some 20 degrees. This raises the question how close the similarity of the directions has to be to conclude safely that a one-direction orientation is involved. Obviously, the comparison is between two quite different sets of data. The direction of the broad front migration over the Netherlands is from field observations. These are limited in numbers as well as in localities in which they were observed. Moreover they have not been carried out in the same years as the experiment, although we have no reason to believe that the directions are very different in various years. The directions of the displaced birds had to be taken from recoveries, and they are likely to be biassed by the rate of recovery in different regions, the influence of authochthonous populations, the influence of certain leading lines, etc. Further, the experimental flocks differed from

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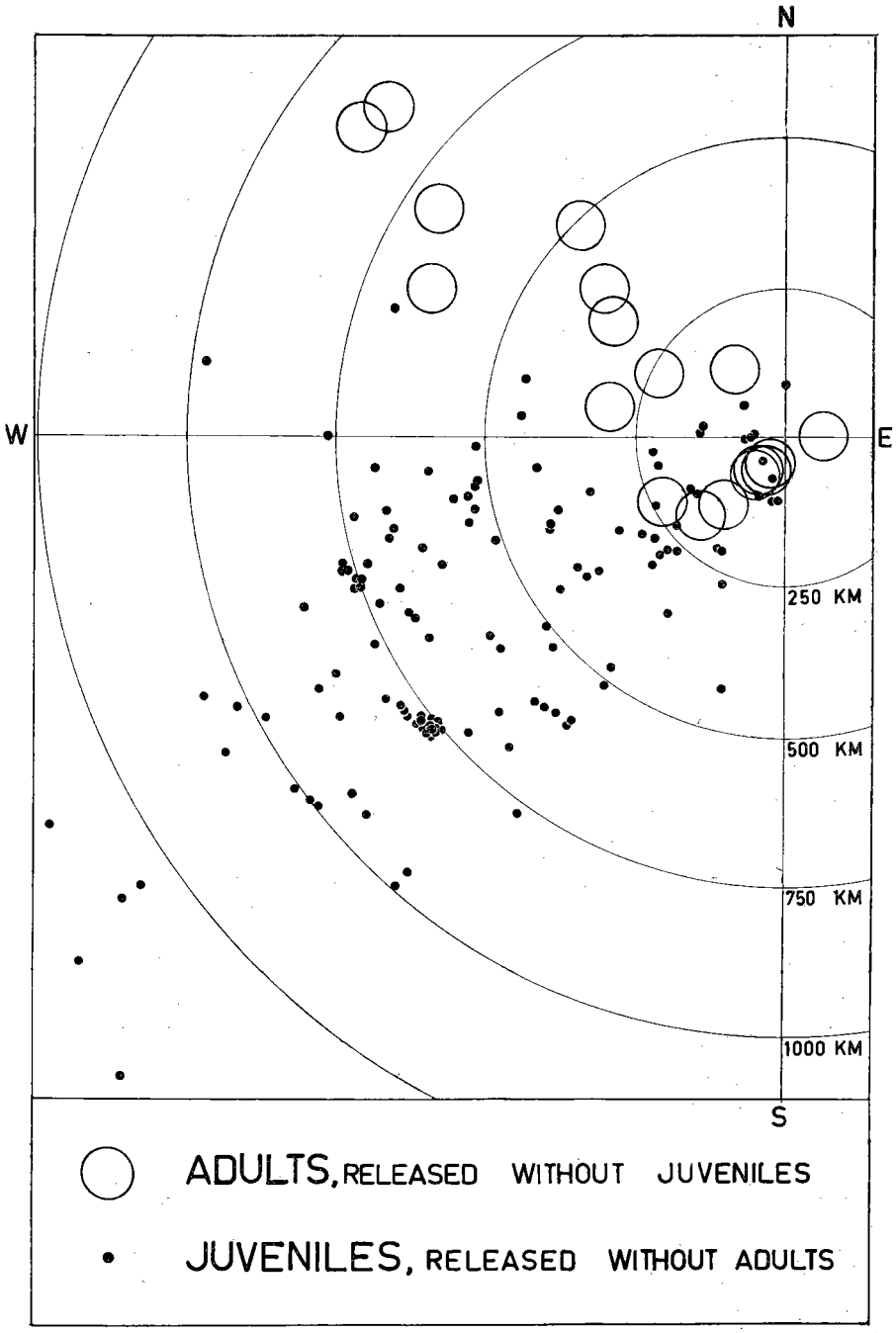


Fig. 8. Recoveries of fig. 5-7 coincided at one release point (recoveries in March excluded).

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those on which the field observations were done in the fact that in the first only one age-class was present, whereas in the latter normally both were present. So there are several factors that might cause a difference between the direction taken from the field observations and the direction taken from the recoveries of displaced juveniles, even if their preferred direction is exactly the same. In this light, it seems unnecessary to emphasize the observed difference, which, after all, is a small one. Our conclusion therefore is that the juveniles continued to migrate in the same direction as they did before their displacement and that their navigation mechanism is a one-direction orientation.

The latter part of this conclusion is, of course, never quite safe, even in the case when no difference was found between the directions of controls and experimentals. For instance, the method of orientation of the juveniles could be the same as that used by the adults (directed to N.W.), but, owing to a lesser degree of independency, drawn to S.W. by joining the autochthonous migrating flocks. Such an assumption, however, is rather strained. Our conclusion would gain in strength if we could explain the difference of 20 degrees mentioned above. If we assume that the field observations have given a correct idea of the preferred direction, the difference must be due to errors inherent to the experiment. The distribution of the recoveries (especially those of the same autumn) does not point to an influence of special leading lines, such as coasts and rivers. Excluding this source of error, there remain some important factors that will be discussed at some length.

1. The high sociability of migrating Starlings raises the question whether the birds did join the populations that normally migrate over the area in question. Reliable data about the preferred direction of these populations are lacking. In Switzerland, mainly in Sempach, Starlings have been ringed during autumn migration (October, fewer in September). I have measured the direction from the recoveries in the same season (the recoveries are to be found in the annual ringing reports of the Vogelwarte Sempach, published in the Orn. Beob. vol. 25-33). As is to be seen in fig. 9 B the prevailing direction is S.S.W., definitely more to the south than the direction of the displaced juveniles. If the latter are influenced by the Swiss migrants, this has only been so to a certain extent. As regards the populations migrating through France, ringing results have shown that they are mainly birds breeding in a zone of about 100-200 km wide, and extending about from Frankfurt a. Main to Minsk.

They constitute an intermediate population between the northern and the southern European Starling population (Schüz & Weigold 1931, Perdeck 1951b, Hilprecht 1954). These recoveries give a hint as to the direction of Starlings migrating normally through France. Judging from the published maps it is mainly about S.W., in each case more to the south than the direction of broad front migration over the Netherlands. For our comparison more exact figures are wanted. They cannot be taken from this material, however,

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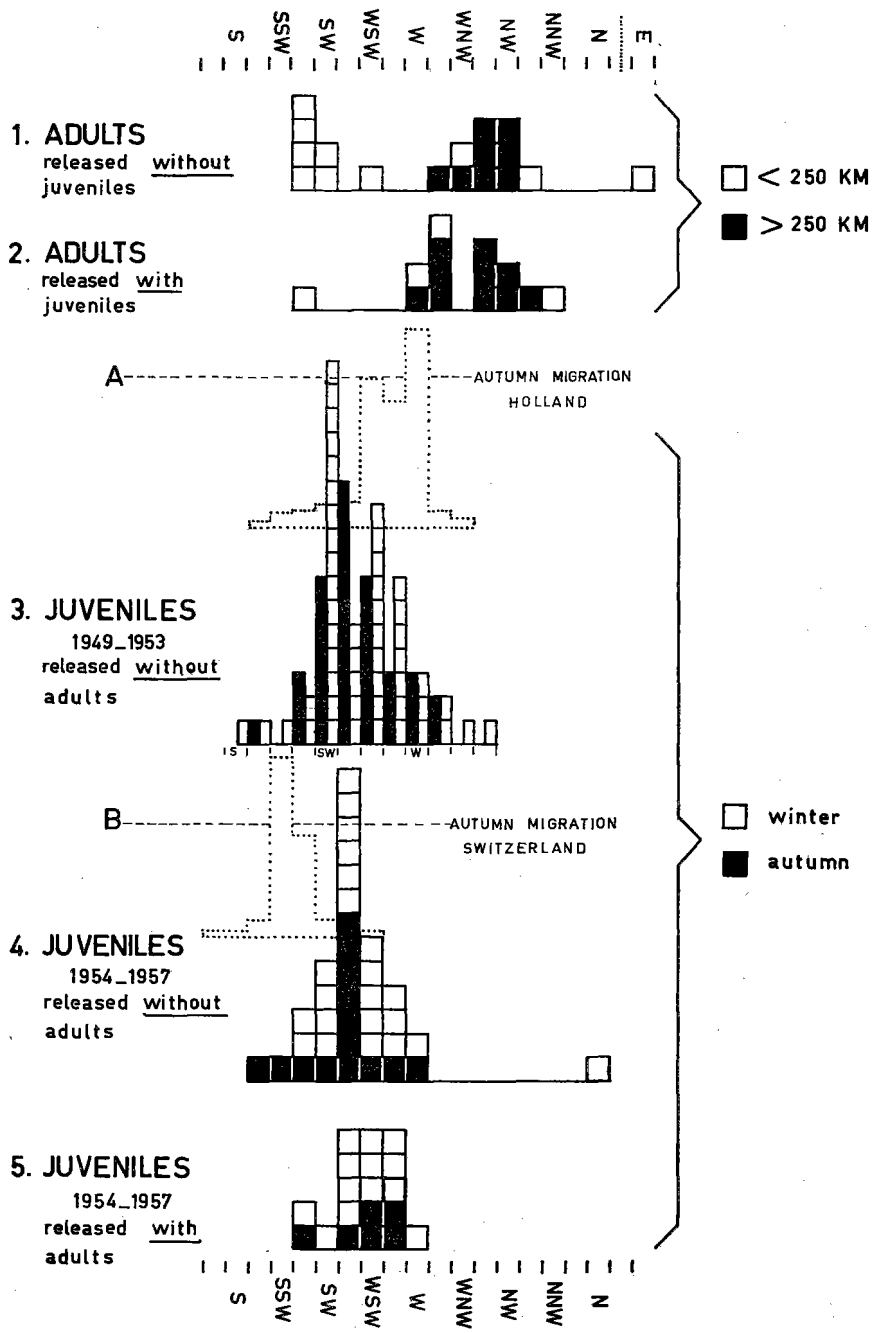


Fig. 9. Frequencies of directions of transported Starlings (1-5), broad front migration through Holland (A, after TINBERGEN 1949, based on 17285 individuals) and of Starling migration through Switzerland (B, based on 61 recoveries in the same season of Starlings ringed at Sempach in Sept. and Oct.).

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since in some parts of the area of origin ringing has been more intensive than in other parts. Thus populations from one part are represented by more recoveries than those from other parts. There is no way to make a correction for this, for we do not know how these populations are represented in the normal stream of migration through France. But, nevertheless, it remains safe to say that the transported birds encounter in Switzerland and France flocks of Starlings migrating in a more southerly direction than their own preferred direction. This might have caused the southerly deviation of the transported juveniles.

2. The mean direction of flight, as calculated from the recoveries is likely to be biassed by quite another factor, namely a difference in the rate of recovery from place to place. If, for example, the rate of recovery is higher in the southern part of the area through which the displaced birds migrate, the direction of flight, calculated from the recoveries is more to the south than the real direction taken by the birds. There is, in fact, an indication that this holds true. As is shown in table 2, the rate of recovery in the first autumn and winter of the displaced juveniles is higher than that of the adults and of the non-displaced juveniles. And since both the adults and the non-displaced juveniles did not reach southern France and Spain, this could be easily explained by a higher recovery-rate of these regions in comparison with the more northern parts. The juveniles flying from the release point in a more westerly direction will then yield lesser recoveries, and this will bring the mean direction of the recovered birds more to the south than the true mean flight direction. This alone gives a reasonable explanation of the difference in the directions between the field observations in Holland and the displaced juveniles. The higher rate of recovery in southern France and Spain is probably due to the more intensive hunting in these regions. This is corroborated by the ways of recovery of the displaced birds, as far as they are known. If we distinguish between recoveries made by intentional killing or catching ("shot", "killed", "caught") and those found by chance ("found", "found dead") recoveries from the latitudes 39 degree till 44 degree fall for 86% in the first category (out of 36 recoveries), those from 45 till 49 degree for 30% (out of 43 recoveries). The "intentional" recoveries are mainly from shooting or "killing", not from catching (40 against 4).

3. We have assumed that the preferred direction of the juveniles, when released without adults, has to be the same as the preferred direction in Holland. But this latter is based on field observations of flocks that normally contain both adults and juveniles. Now it is possible that the preferred direction of the juveniles is a more southerly one, but that they are influenced in their course by the adults, resulting in a more westerly direction of the mixed flocks. It would be worth while checking this assumption by releasing juveniles in a homogeneous area, e.g. at sea and observing their directions of departure.

It is noteworthy that the Baltic Starlings displaced by KRÄTZIG & SCHÜZ (1936) from Windenburg to Dresden and Breslau held exactly the same course as the juveniles in our experiment. They consisted for more than 90% of juveniles (SCHÜZ 1950a). I have measured the direction of flight from the recoveries in the same season. Out of 32 recoveries 2 were from S.W. by S.,

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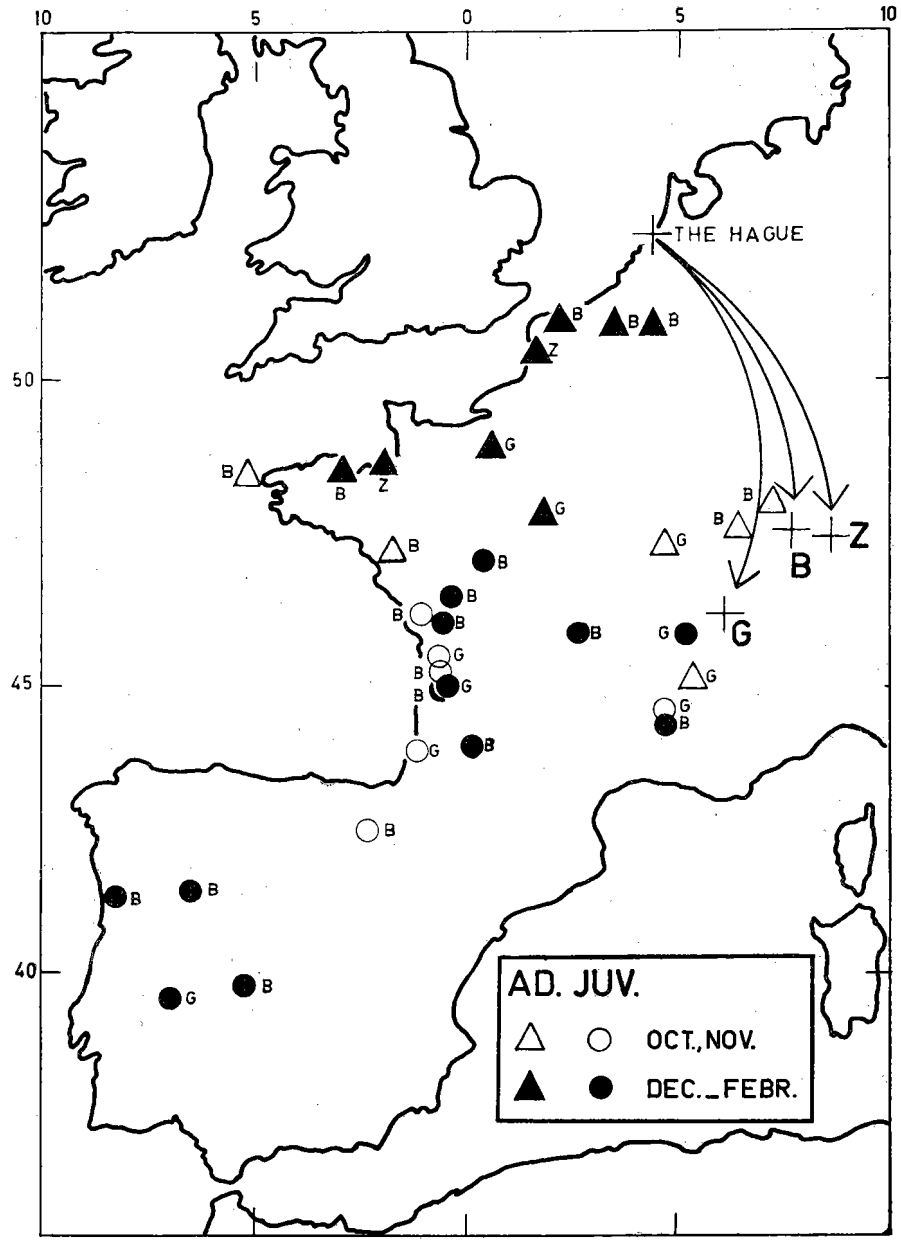


Fig. 10. Recoveries of Starlings in the same season, mixed transports.

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6 from S.W., 14 from S.W. by W., 3 from W.S.W., 2 from W. by S., 3 from W. and 2 from W. by N. The authors explained this shift to the south as compared with the normal direction by the influence of autochthonous Starlings, but explanations as given under the points 2 and 3 above might also be considered.

Recoveries in the same season from transports in which adults and juveniles were released together

We have seen that after their displacement, juveniles and adults took a quite different course when they were released separately. The question arises what would happen if both age-classes were released together. Would the groups influence each other? This question is of vital importance. For, in general the birds migrate in flocks containing both adults and juveniles. If, for instance, a flock, in avoiding the sea, has come south of the wintering area, the juveniles would not be able to reach it unless they followed the adults, that owing to their true goal orientation steer in the correct direction. In order to study this influence a number of displacements were made, in which each cage contained both juveniles and adults in equal numbers (for totals involved see table 1). As a control, in the same years of these experiments a number of juveniles were released without adults at a different place from the mixed transports. Such a control was not possible for the adults, since nearly all adults caught had to be used for the mixed sendings. The results of these experiments are shown in fig. 9:2, 9:4, 9:5, 10 and 11. The recoveries of the controls, given in fig. 11, are also included in fig. 5-8, but not in fig. 9:3.

The picture is basically the same as in the non-mixed transports. A slight difference is to be noted in the directions of the juveniles from the mixed groups. They lie a little more to the north. This difference is, however, not significant (Wilcoxon test : P is between 0.14 and 0.18). We have to conclude that this experiment did not show that the age-groups influence each other. But, as was realised before the experiment was started, this negative result does not prove that in natural flocks such an effect is lacking. We built up our „flocks" from birds of different natural flocks, and the coherence in a natural flock may be better than in our artificial ones. The observations of VAN DOBBEN (1944) and NIJHOFF (1958), quoted on p. 2, show that at Cap Gris-Nez Starlings leave for England in large numbers in a north-westerly direction. One cannot believe that only adult birds are involved here and therefore an influence of the adults on the direction of the juveniles seems very probable. It would be of importance to check this by catching and aging Starlings at that locality.

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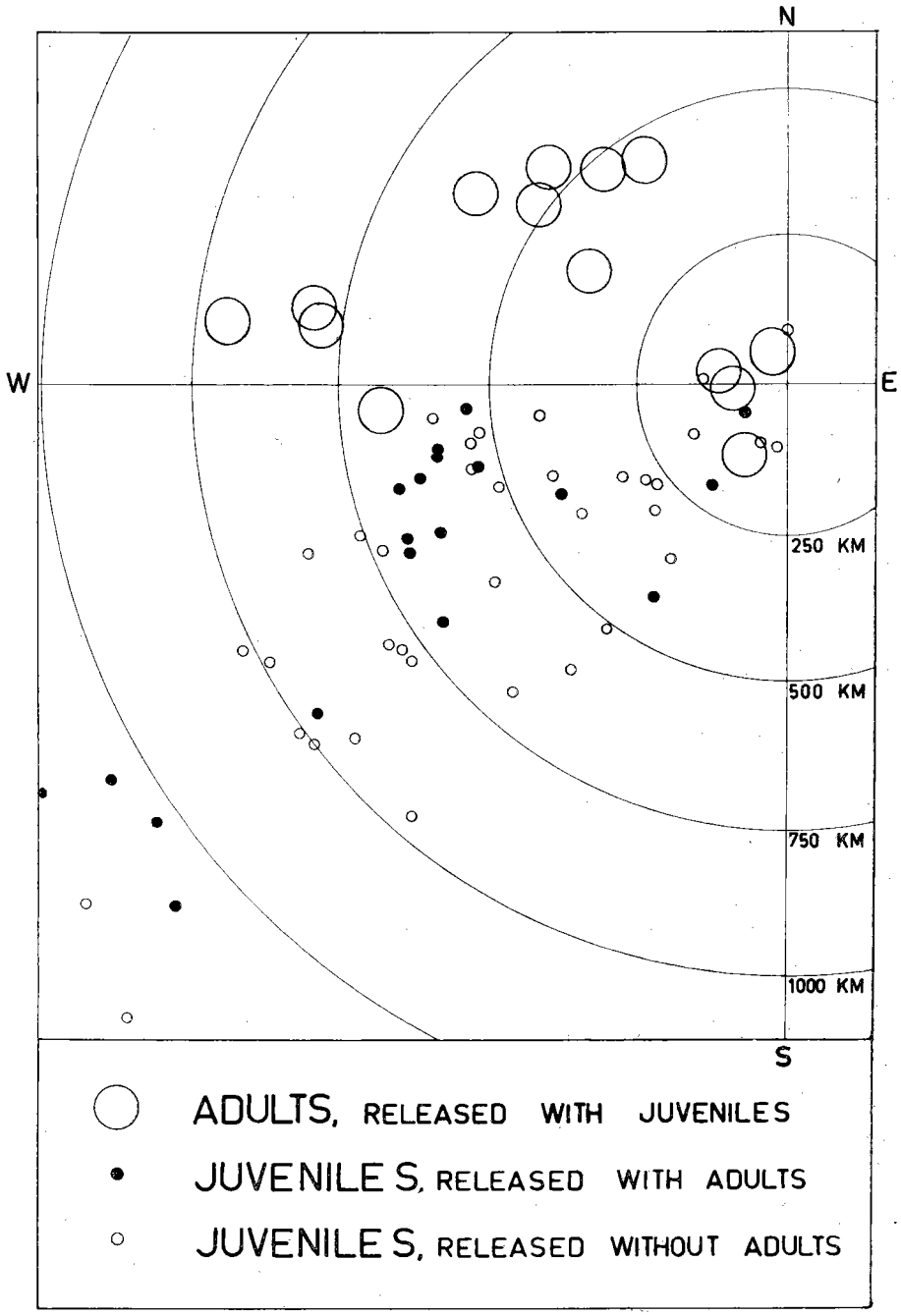


Fig. 11. Recoveries of fig. 10 coincided at one release point, together with recoveries of juveniles released without adults in the same years.

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Recoveries in later seasons

The main object of the experiment was to determine the course of the birds in the season immediately following the displacement. We got, however, quite a number (compare table 2) of recoveries in later seasons and they can give an idea of the finally adopted breeding and winter quarters. Recoveries from mixed and separate transports (as regards age-classes) are treated here together, since the first wintering area after the displacement did not show significant differences.

a. Adults.

Nearly all recoveries of the adults from later seasons fall within the normal area of distribution (fig. 12). This is in complete accordance with the conclusion made above that these birds after their displacement flew to their previous winter quarters. One bird was recovered in a later winter near the mouth of the Gironde, but this is not so exeptional since a few of the recoveries of non-displaced Starlings marked near The Hague have even been found more to the south (compare fig. 2). Another bird was recovered in the breeding season quite near the release point. This perhaps was a Dutch resident bird (compare p. 6).

b. Juveniles.

1. Breeding grounds. The breeding area of the birds that were displaced as juveniles is the same as that of the non-displaced birds. This is concluded from the recoveries from April till August (fig. 13). The distribution within this area, however, shows a difference with the non-displaced birds. In general the recoveries are shifted more to the eastern part of the area (compare fig. 4). One bird, probably a resident, remained near the release-point, another was found in July, following the displacement, in the first winter area.

2. Winter quarters. From fig. 13 it is clear that the juveniles in general did not winter in the regions that are normal for the population they were taken from. A large proportion is found in the same regions, where, owing to the displacement, they arrived in their first winter. This means that these birds did not use the same orientation in a fixed S.W.-W. direction as they showed in the autumn of their transport, but really „homed" to these new winter quarters. It is in fact the same result which was reached with the displacement of the adults. We may conclude therefore that many Starlings fix as their wintering place that region in which they wintered for the first time. And, in addition, that they are able to return to this place by means of a true goal orientation. This is, however, not a fixed rule, since a number of birds returned to the normal winter quarters of the population

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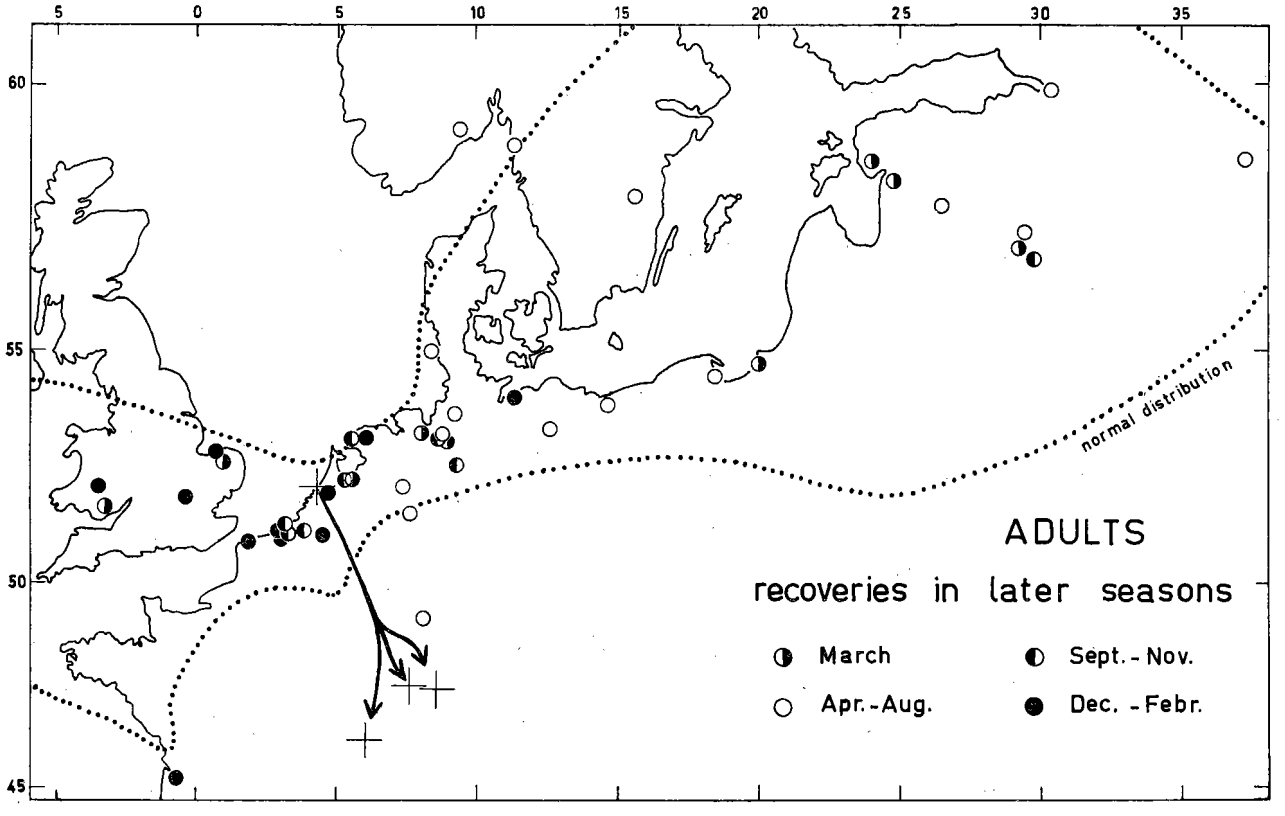


Fig. 12. Recoveries of displaced adult Starlings after Febr. subsequent to the displacement.

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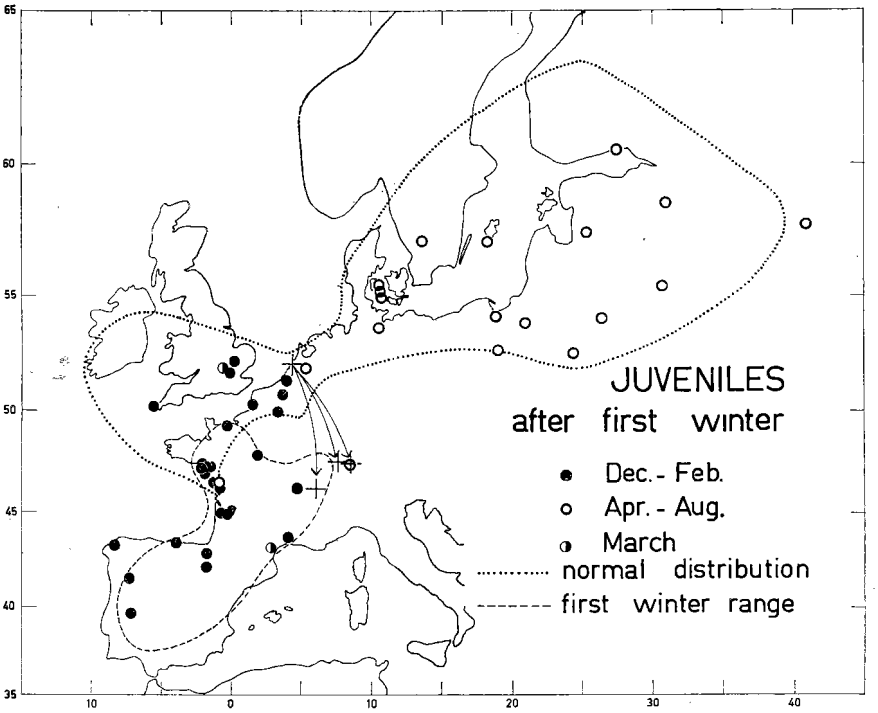


Fig. 13. Recoveries of displaced juvenile Starlings. The recoveries in March are not subsequent to the displacement. (These are shown in fig. 5 and 6.)

or at places intermediate between the normal and the experimental winter area. These birds were perhaps taken along by the normally westwards migrating flocks of the population inhabiting the same breeding territory.

3. Spring migration. It would be of great interest to know what routes the birds that were displaced as juveniles follow in later years during their journeys between the breeding quarters and the new wintering area. As regards spring migration, recoveries from this season are scarce. There are only 5 recoveries from March, and these happen to lie within the wintering area (fig. 5, 6 and 13). Later recoveries are already within the breeding territory. At first sight one is inclined to use the return to the original breeding area as an argument that during spring migration true goal orientation is involved. The shift to the eastern part of the breeding area (see above) throws some doubt on this. The birds could have used a one-direction orientation in about the same direction as the spring migration of the non-displaced birds. If they halted after having travelled the same distance as the controls, they would have come, at least partly, south of the normal area. But it is quite possible that the birds migrated till reaching the latitude of their native places. In that

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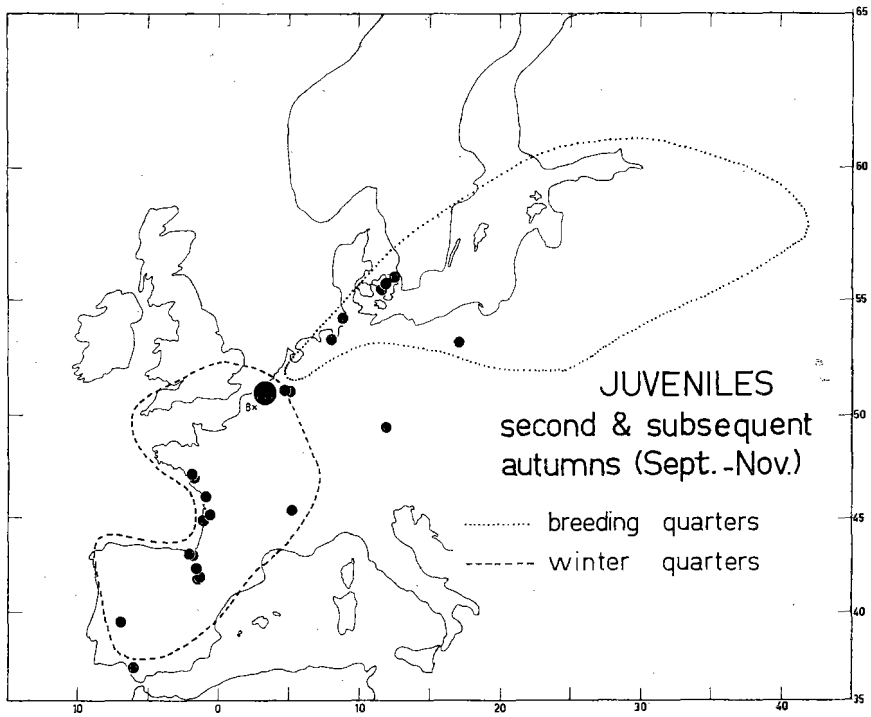


Fig. 14. Recoveries of displaced juvenile Starlings.

case there would be, indeed, a shift to the eastern part of the breeding area. Displacement experiments durig spring migration could elucidate this question. DROST (1938 b) displaced 90 Starlings migrating in March over Heligoland to Silesia. The recoveries of two birds (470 km N.W. and 600 km N.W.) suggested a true goal orientation. The age of the birds, however, was unknown.

4. Autumn migration. The displacement of the adult birds revealed that they used a true goal orientation during their autumn migration. The same could be concluded from the recoveries of the displaced juveniles in later winters. This makes it probable that the latter ones (now being adults) migrate in a straight course from their breeding area to the new winter quarters. To check this assumption quite a number of recoveries in later autumns (Sept., Oct. and Nov.) are available (fig. 14). Of special interest are those situated between the finally adopted winter and summer area. This is roughly the area enclosed by a triangle, of which the angular points are Calais, Minsk and Marseilles. The distribution of the 12 recoveries from this area is surprising. Instead of being about equally distributed they show a strong

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concentration in the extreme north-western part. Actually 10 are from western Belgium, 1 from southern Germany and 1 from south-west France. In a preliminary discussion about the results I suggested that this distribution could be explained by assuming that the birds did fly by an angled route (PERDECK 1957). At the moment, however, I feel that the number of recoveries are too scarce to warrant this conclusion. The most reasonable explanation is that the chance of recovery in Belgium, famous as this country is for its sport of bird-catching, is much higher than in the other parts of the region concerned. Although no data on this point are availabe (European ringing schemes have neglected to make the numbers ringed at various places and dates easily accessible) this is confirmed in general by the published maps of Starling recoveries (e.g. HILPRECHT 1954).

EXPERIMENTS WITH CHAFFINCHES

At our fowling yard near The Hague a second species is caught each autumn in large numbers, viz. the Chaffinch. This species has been the main subject of studies on migration in Holland and it is perhaps the bird of which the migrating behaviour is the best known. Therefore it was

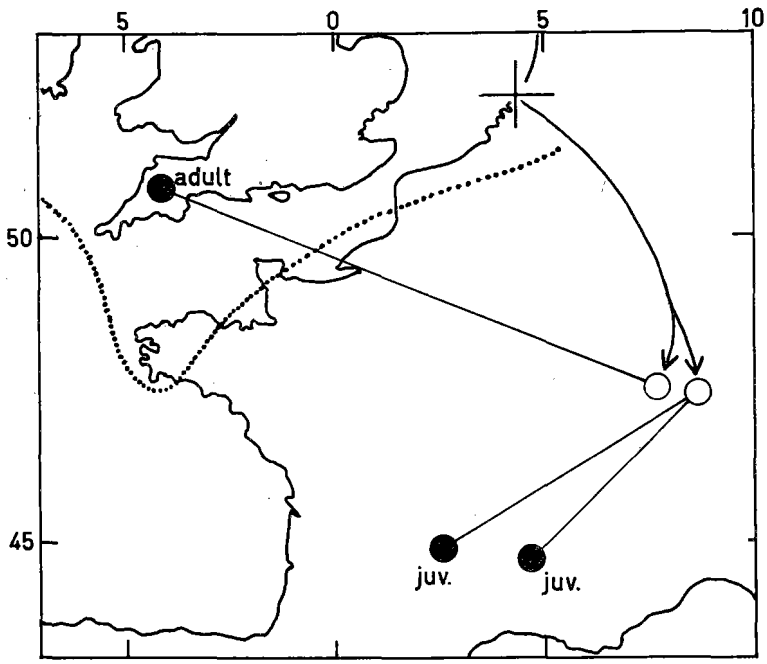


Fig. 15. Recoveries of displaced Chaffinches. Dotted line: southern limit of normal winter quarters.

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very promising to carry out similar experiments with this species. From ringing results we know that the Chaffinches migrating along the leading line of the coast of the North Sea belong to a population breeding in Scandinavia and wintering in England and Ireland (TINBERGEN 1941 a, PERDECK 1955). The preferred direction of the broad front migration in the Netherlands is about W.S.W. (TINBERGEN 1941b, 1949, p. 46, to quote some of the best observations). In 1955, 1956 and 1957 345 juveniles and 911 adults caught in October and November were displaced to Switzerland (Basle and Zürich). The age was determined by the criteria given by DROST (1931), which were controlled by the inspection of the ossification of the skull, both in dead and living birds (compare p. 5). The birds were transported by airplane in similar types of cages as the Starlings (p. 5). Juveniles and adults were released in the same year at different places. Owing to the small rate of recovery of this species only three recoveries were obtained. The details are given in table 3 and they are plotted on the map in fig. 15. Scanty as this result is, it shows, however, the same trend as was found in the Starling. The juveniles migrated in a south-westerly direction, the adult in a north-westerly one. Bearing in mind the results obtained with the Starling, they lead to the conclusion that, with the Chaffinch also, adult birds use a true goal orientation, juveniles a one-direction orientation.

TABLE 3

Recoveries of displaced Chaffinches

Ring number	Sex, age	Caught	Released	Recovered	Direction	Distance
H 16102	♂ juv.	11-10-55 Wassenaar (52.08 N. 4.20 E.)	12-10-55 Zürich, Kloten (47.27 N. 8.35 E.)	(16-2-56) (date of letter) Giou de Mamou (44.56 N. 2.30 E.) Cantal, France (found dead in snow)	S.W. by W.	535 km
H 16140 (ring received)	♀ juv.	12-10-55 Wassenaar (52.08 N. 4.20 E.)	13-10-55 Zürich, Kloten (47.27 N. 8.35 E.)	25-12-55 Vesseaux (44.39 N. 4.25 E.) Ardèche, France (shot)	S.W.	440 km
H 90004	♂ ad.	2-10-57 Wassenaar (52.08 N. 4.20 E.)	3-10-57 Basle, Blotzheim (47.36 N. 7.30 E.)	24-1-58 Northlew (50.46 N. 4.07 W.) Devon, England (found dead in snowstorm)	W.N.W.	915 km

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Discussion

The main result of this study is the proof that adult Starlings, when displaced sideways during autumn migration, are able to correct this displacement by steering to their winter quarters in a course quite different from the preferred direction. The conclusion is that these birds used a true goal orientation, a method of orientation hitherto only positively known in birds that were in the act of „homing" to their nest sites. It seems safe to extend this conclusion in the sense that the birds use this faculty during normal migration as well and it is not a „deus ex machina" provoked by the experiment only. Field observations confirm this in showing a relation between preferred direction and position of the wintering area (see p. 2). In sharp contrast with the adults, the juvenile Starlings after their displacement followed a course about the same as the preferred direction held in the region from where they were taken. Their method of orientation during autumn migration is therefore concluded to be a one-direction orientation. This has two important implications.

(1) The results support the evidence that the ability to find a certain place with true goal orientation has to be learned. Although the mechanism itself is likely to be innate, the bird can only direct itself with true goal orientation to those places where it has been at least once. Recoveries of starlings, displaced as juveniles, in later winters gave a good confirmation of this. Among these birds, there was a strong tendency to return to the region in which they had wintered in their first year. This area is strange to the population and it was only by the experiment that the birds reached it. To put it in a different way we can say that in adult Starlings the migration route is determined, among other factors, by the position of the wintering area, whereas in the juveniles it is rather the opposite, the path of migration determining the position of the goal.

In this light some differences in winter quarters between adjacent Starling populations may be considered. Starlings breeding in Northern Europe have their main winter quarters in the British Isles. But as ringing has taught us, they fall into two groups (Perdeck 1951b). Those breeding in Norway and Jutland winter chiefly in North England and Scotland. Only few recoveries are found along the continental coast of the North Sea, which indicates that they cross the North Sea over its whole width. On the other hand, those Starlings breeding in the Danish Isles, South Norway and the Baltic mostly winter in South England and they have yielded many recoveries from the Belgian coast in autumn. This means that a large part follows the leading line of the North Sea coast before crossing the sea to England. Obviously, this difference is induced by the form of the coastlines. The Starlings of Norway and Jutland would, if they followed the coast, have to migrate in a south or

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even southeast direction; a very different one from their presumably westerly preferred direction, and one which would necessitate them in leaving the coast soon. When the other populations meet the sea, they find a coast that runs in a more southwesterly direction, not differing so much from their preferred direction. They are therefore willing to follow it until they reach Cap Gris-Nez, where the coast turns abruptly to the south. As we know, they leave the continent here in great numbers. It is clear then, that the "natural displacement experiment" by the coast has induced a more southerly position of their winterquarters, as compared with those populations that are not "displaced". The same effect is even to be seen on a smaller scale within the Starlings breeding in Holland. The Starlings breeding on the isles of Ameland and Schiermonnikoog winter more northerly in England then those breeding in the adjoining continental area. The latter ones give frequent recoveries from Belgium, contrary to the first group. The island birds move off in autumn without deflection by coastlines, the continental birds follow the leading line of the coast (PERDECK 1951a).

(2) If adult and juvenile Starlings migrate together in one flock, the direction of the flock is the outcome of two different mechanisms, the one-direction orientation of the juveniles, and the true goal orientation of the adults. If this flock is deflected sideways by certain influences from the shortest route between winter and breeding area, adults will strive in a different direction from the juveniles. There are then three possibilities as regards the direction of the flock: 1. it is that of the adults; 2. it is that of the juveniles; 3. it is an intermediate one between these directions. In our mixed transports we have tried to study this influence of both age-groups on each other, without success, however. But it seems quite safe that even if one age-group has a stronger influence on the other, there must often be conditions under which the direction of the flock is a compromise. This impels us to make some comments on the concept of the „preferred direction". This concept was created by GEYR VON SCHWEPPENBURG (1933) under the name „Normalrichting". By this he meant the direction held by migrants when not influenced by coastlines and other leading lines. Since he saw that this direction differed according to species, he suggested that it had an innate base and considered this as a further characteristic. Later he realised that this definition had some ambiguity. There were reasons to assume that the direction of the inexperienced juveniles migrating without adults (and thus presumably innate) was sometimes quite different from the directions of these birds when migrating in flocks together with adults. Therefore he coined a new term, the „Primärrichtung", for the (innate) direction flown by young birds without contact with adults (GEYR VON SCHWEPPENBURG 1949). He omitted, however, to give a name to the direction as observed in the field (concerning often

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mixed flocks). Other authors (SCHÜZ 1950 b; THOMSON 1953) did not realise this distinction and continued to use the original term „Normalrichtung" (translated as standard direction or preferred direction) in the original ambiguous sense and used the „Primärrichtung" or primary direction as a synonym.
As has been shown above the direction, as it occurs from field observations when disturbing features from the landscape are absent, may have both a learned and innate base. I propose therefore to use the term „preferred direction" in future without any reference to the probable learned or innate base.

The considerations given above apply to the Starling during autumn migration. Is there evidence that the same holds for other species too? Most probably this is true for the Chaffinch (p. 29) and the Sparrowhawk (DROST 1938 a), although the dichotomy between adults and juveniles was less clear in the latter species. The other displacement experiments during autumn concerned only juveniles and are consistent with the theory that these used one-direction orientation (American Crow: ROWAN 1946; White Stork: SCHÜZ 1949). The results of the experiments with Hooded Crows, displaced during autumn migration (RÜPPELL & SCHÜZ 1948) cannot be quoted as evidence since the displacement was not sideways from the route, but to the winter quarters. The experiment with Starlings by KRÄTZIG & SCHÜZ (1936) is also unconvincing since (a) the displacement was carried out with birds not yet really migrating („Zwischenzug") and (b) the distance of the displacement was a relatively short one (see also p. 20). One would further like to know what is the orientation during spring migration. From the homing experiments one is inclined to believe that both adult and juvenile birds use true goal orientation. The recoveries from our Starlings, displaced as juveniles and recovered in the breeding time were not conclusive on this point (see p. 26). The small experiment of DROST (1938b) with Starlings displaced during spring migration points to true goal orientation, but the age of the birds was, unfortunately, unknown (see p. 27). The only experiment during spring migration that yielded definite results was that of RÜPPELL (1944) with Hooded Crows. Surprisingly enough, it was established that both adult and juvenile birds used one-direction orientation during spring migration. Recoveries from later seasons revealed that the whole area of distribution of these birds was shifted parallel to the original one and this, moreover means that in this species neither juveniles nor adults use true goal orientation during autumn migration. The Hooded Crow therefore

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behaves differently from the Starling and this may be a warning to us not to apply too easily to one species the results found in another. New displacement experiments carried out by other appropriate species and both during spring and autumn migration are still necessary. MATTHEWS (1955) seems not quite correct in suggesting that such field experiments have reached their useful end, although we admit that they will not teach us much about the underlying mechanisms of discussed types of orientation. But for a good understanding of bird navigation we need to know not only the mechanisms but also how the different types of orientation (which are, of course, not exhausted by one-direction and true goal orientation) work together during migration in each species. The addition of true goal orientation to the array of faculties available to the bird for its navigation will make several phenomena of bird migration more conceivable, e.g. exact return to restricted wintering and breeding areas; relation of preferred direction to the geographical position of these areas; and perhaps even angles in routes that cannot be explained by tradition or barriers.

SUMMARY

1. From 1948-1957 more than 11000 marked Starlings (one-third adults, two-thirds juveniles), caught during autumn migration near The Hague, were (by airplane) displaced to Switzerland (Basle, Zürich and Geneva). They yielded 354 recoveries.

2. Ringing has shown that these Starlings belong to populations breeding in South Finland, South Sweden, the Baltic area and adjoining Russian parts, North Poland, North Germany, Denmark and Holland. They winter in Holland, West Belgium, N.W. France, South England and Ireland. The birds breeding in Holland are not the same as those wintering there. The preferred direction of autumn migration in Holland is about W.S.W. -W. (field observations).

3. After the displacement juveniles and adults held a different course. The adults aimed at the original wintering area in a N.W. direction (S.W. courses only at shorter distances). The juveniles flew in a direction quite similar to the preferred direction normal in Holland (a small shift to the south is discussed). They wintered in Southern France and the Iberian Peninsula. The conclusion drawn is that during autumn migration, adult Starlings use a true goal orientation (homing orientation), the juveniles a one-direction orientation.

4. No significant differences were found in the directions of the birds when juveniles and adults were released together or separately (at diffe-

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rent places). As is pointed out, this does not imply that an influence of the age-groups on each other is lacking in natural flocks.
5. Recoveries from later seasons showed that the adults had come back in the original area of distribution; the juveniles, however, had a clear tendency to remain wintering in the area reached after their displacement. The breeding area of the juveniles was within the normal range, with a shift to the east. It is concluded that Starlings are able to fix their winter quarters in their first year, with an ability to reach it in later years by means of true goal orientation.
6. A similar experiment was carried out with Chaffinches (migrants through Holland belonging to the Scandinavian population, wintering in the British Isles). 1250 Chaffinches (900 adults, 350 juveniles) caught in autumn near The Hague were transported to Switzerland. In the same season they yielded 2 recoveries of juveniles (from Southern France: 535 km S.W. by W., 440 km S.W.) and 1 recovery of an adult (from England: 915 km W.N.W.). The same phenomenon as found in the Starling is suggested by these recoveries: juveniles fly parallel to original course (one-direction orientation) adults direct themselves to the original wintering area (true goal orientation).
7. The implications of these results are discussed, especially with reference to the influence of leading lines (natural displacement!) and the concept of the „preferred direction".

SAMENVATTING

1. Van 1948-1957 werden meer dan 11000 geringde Spreeuwen (waarvan één derde overjarigen en twee derden eerstejaars) per vliegtuig verplaatst naar Zwitserland (Bazel, Zürich en Genève). De vogels waren op de vinkenbaan van het Vogeltrekstation bij Den Haag gevangen gedurende de herfsttrek. Hiervan werden 354 terugmeldingen verkregen.
2. Uit ringgegevens wordt afgeleid dat deze Spreeuwen behoren tot populaties die broeden in Zuid-Finland, Zuid-Zweden, het Baltische gebied en aangrenzend Rusland, Noord-Polen, Noord-Duitsland, Denemarken en Holland. Zij overwinteren in Holland, West-België, NW-Frankrijk, Zuid-Engeland en Ierland. De vogels die in Holland broeden zijn niet dezelfde als die hier overwinteren (fig. 2, 3 en 4). De voorkeursrichting van de herfsttrek is W-WZW (ontleend aan veldwaarnemingen).
3. Na de verplaatsing hielden oude en jonge vogels een verschillende richting aan. De ouden trokken in NW-richting terug naar het oorspronkelijke winterkwartier (ZW-richtingen kwamen wel voor op kortere afstanden van de plaats van loslaten). De jonge vogels vervolgden hun trek

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in een richting, die weinig afweek van de oorspronkelijke voorkeursrichting (een kleine verschuiving naar het Z wordt besproken). Zij overwinterden in Zuid-Frankrijk en het Iberische schiereiland (fig. 5-9). Hieruit wordt de conclusie getrokken, dat gedurende de herfsttrek overjarige vogels gebruik maken van plaatsgerichte orientatie (als bij „homing"), eerstejaars daarentegen van kompasgerichte orientatie (vermogen om slechts één bepaalde koers in te slaan). Vergelijk fig. 1.

4. Er werd geen steekhoudend verschil gevonden in de richtingen van de vogels wanneer ouden en jongen tezamen of gescheiden werden losgelaten (op verschillende plaatsen) (vgl. fig. 8 en 11). Dit betekent echter niet, dat een beïnvloeding van jonge en oude vogels op elkaar ook in natuurlijke troepen ontbreekt.

5. Terugmeldingen uit latere seizoenen tonen aan, dat de oude vogels terugkeerden naar hun oorspronkelijke verspreidingsgebied (fig. 12). De als jong verplaatste vogels vertoonden echter een duidelijke neiging in latere jaren terug te keren naar het winterkwartier dat zij na hun verplaatsing hadden aangehouden (fig. 13). Hieruit blijkt, dat Spreeuwen hun winterkwartier in hun eerste levensjaar kunnen vastleggen en wel zodanig, dat zij het later met plaatsgerichte orientatie kunnen terugvinden. Het broedgebied der als jong verplaatste vogels lag wel binnen het normale gebied, maar hierbinnen was een verschuiving naar het oosten zichtbaar (vgl. fig. 4 en 13).

6. Een dergelijke proef is genomen met Vinken, die hier in de herfst doortrekken. Zij behoren tot de Scandinaafse populatie die overwintert in Groot-Britannië en Ierland. 1250 Vinken (900 overjarig, 350 eerstejaars) werden in de herfst op de vinkenbaan bij Den Haag gevangen en losgelaten in Zwitserland. Hiervan werden 3 terugmeldingen ontvangen (fig. 15), alle in hetzelfde seizoen: 2 van eerstejaars (uit Zuid-Frankrijk 535 km ZW ten W en 440 km ZW) en één van een oude vogel uit Engeland (915 km WNW). Deze terugmeldingen geven een sterke aanwijzing, dat voor de Vink hetzelfde geldt als bij de Spreeuw: jonge vogels vliegen evenwijdig aan oorspronkelijke richting verder (kompasgerichte oriëntatie), oude vogels vliegen doelgericht terug naar hun oorspronkelijke winterkwartier (plaatsgerichte oriëntatie).

7. De consequenties van deze resultaten worden besproken, speciaal in verband met de invloed van stuwlijnen (natuurlijke verplaatsing!) en het begrip voorkeursrichting.

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FIELD OBSERVATIONS ON THE BIRDS OF THE ISLAS LAS AVES IN THE SOUTHERN CARIBBEAN SEA[1])

by

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Introduction

Many uninhabited cays and islets in the Caribbean Sea could bear the name "islas las aves", which means "bird islands". However, the name "Islote Aves" (also Isla de Aves) has been given officially to a very small and remote island in the northeastern Caribbean south of Saba on the geographical breadth of the northern point of Dominica,

[1]) Publication of the Caribbean Marine Biological Institute, Curaçao, Netherlands Antilles.

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