On the influence of environmental factors on the autumn migration of chaffinch and starling
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Apart from these daily fluctuations in migration tendency long-term variations occur. In the first place there is of course the seasonal variation, which does not concern us here since our observations refer to a short period of the migration season only. Secondly, several days with bad weather may cause an increase of the migration tendency, which results in a “rush” when the external conditions slightly improve. Change in the threshold for the release of action patterns is a common phenomenon in all kinds of animals. Threshold lowering occurs in animals that are for a long time prevented – by absence of the releasing stimulus – to perform certain activities: isolated cocks may eventually perform courtship before their food-container; caged starlings that have no access to insects may perform the whole behaviour pattern of insect hunting, without any discernible external stimulus; very hungry birds may accept food that they reject under normal conditions (N. Tinbergen, 1951).

From the above it may be clear that migratory behaviour has to be explained by internal and external factors. By field methods, as employed in this study, much can be learned about the influence of external factors on migration. The analysis of the internal mechanisms asks for more detailed laboratory experiments, for example with birds in the Kramer-cage to investigate the relation between the migration system and other systems (feeding, aggression, comfort). In this respect much remains to be done. This shows again how field observations, started to test results from laboratory experiments, will raise questions that again have to be solved in the laboratory. Progress in our understanding of migration will only be made if these two kinds of research are in continuous interaction.

8 SUMMARY

This paper deals with the influence of environmental factors on the autumn migration of two common diurnal migrants in the Netherlands, the Chaffinch (Fringilla coelebs) and the Starling (Sturnus vulgaris). The study is based mainly on observations in the north-western part of the Veluwe; some additional observations from other points are used.

The chaffinches passing through the Netherlands are of Scandinavian origin and on their migration to England and Ireland, follow mainly the eastern coasts of the North Sea. They pass in a broad front over homogeneous country but are easily deterred by open landscapes and especially by the sea. The starlings observed at the NW.Veluwe originate from a large area in eastern and north-eastern Europe; they winter in England and the low countries.
The reactions of both species to the landscape are discussed in chapter 3. We distinguish four different landscape types in the area of observation: forest, wooded area, polders and sea. For chaffinches a classification into five migration patterns can be made according to their behaviour over these different landscapes. This classification is based on the occurrence of broad-front migration over the different landscapes. In this way we obtained a sequence of migration patterns running from broad-front migration over all landscapes (I), via broad-front migration over the less deterrent landscapes (forests, wooded area) and diversion at the edge of polders and/or sea (migration pattern II, III and IV), to no migration at all (V). A better quantitative basis could be given to the sequence by using the volume of seaward migration as an additional criterion. The sequence of migration patterns and volume of seaward migration proved to be correlated with volume of broad-front migration over the forests, dispersion of directions, percentage of reversed migration and flying-height.

The influence of landscape on flying-height has been treated separately. Generally chaffinches and starlings prove to fly higher the more deterrent the landscape is. Over the forests the mean flying-height of chaffinches is usually below 100 m, at the coast means up to 200 m were noted and seaward migration may proceed at altitudes up to 1500 m. However, under unfavourable weather circumstances, migration over the polders and along the coast may proceed at very low levels. Starlings usually fly lower than chaffinches, but also rise at the coast when flying out to sea.

To study the influence of the weather on the various characteristics of chaffinch migration a correlation analysis has been carried out, to analyse statistically the relations between weather and migration. The results of this analysis are summarized in Table XIV. Migration pattern and seaward migration are significantly influenced by wind direction (following winds being more favourable to migration than cross or head winds), temperature and rain (low temperature and no rain being favourable for migration). Volume of broad-front migration over the forests proved to be stronger with low temperatures and on days without rain than with high temperatures and rainy weather, but it was not significantly influenced by wind direction. Dispersion of directions and percentage of reversed migration were influenced by sun visibility, both increasing with decreasing visibility of the sun. Dispersion of directions was not significantly influenced by any other weather factor, but percentage of reversed migration increased significantly with high temperatures. Flying-height depends mainly on the wind direction and speed. The highest altitude of migration is found with following wind, an intermediate one with cross wind and with a head wind migration occurs at comparatively low level. Wind speed results in a lower flight height or darkness.

From these correlations it is clear that over the sea a following wind is preferable. The behaviour lies in the fact that under overcast conditions, winds are usually either low or head winds. A high flying height in strong following winds is advantageous, because following winds have their maximum velocity at the free upper air over the sea. The height of the sea meniscus is low, the aid of beacons in the landscape is helpful, but it is not clear enough. The volume of seaward migration proved to be highest with following and lowest with head winds.

In chapter 6 the influence of wind on the orientation of the migrant birds was investigated. The mean direction of migration of chaffinches and starlings measured in the early morning on clear days with no wind was found to be very close to the mean direction of the species. For chaffinches, we found a mean reverse of 2.8 degrees, which is due to the fact that on days of mean migration direction on different days, this influence was such that direction was reversed compared with the overall mean, particularly on days of high wind speed. It was noticed that overcompensation may increase with time. On days with low wind speed, the mean direction of migration was found to be about the same as on clear days with no wind. Generally, the birds flew in the direction of the mean wind direction. However, the maximum one. Generally gusts of varying speed, at least at distribution of speeds around day, larger gusts occur upwards than make it rather difficult for a bird to make it rather difficult for a bird to arrive at the mean wind direction. These observations were explicable for lateral drift due to gusts. If the heading to the mean wind overcompensation may increase with decreasing visibility of the sun. Dispersion of directions was not significantly influenced by any other weather factor, but percentage of reversed migration increased significantly with high temperatures. Flying-height depends mainly on the wind direction and speed. The highest altitude of migration is found with following wind, an intermediate one with cross wind and with a head wind migration.
occurs at comparatively low levels. With all wind directions, a high wind speed results in a lower flight than a low one.

From these correlations it is clear that chaffinches migrate preferably on clear days with low temperature, and, moreover, for a flight over the sea a following wind is preferred. The biological significance of this behaviour lies in the fact that in this way the risk of disorientation on fully overcast days is lessened, while the preference for a following wind on a sea crossing is advantageous in view of energy consumption. Flying high with a following wind has its significance in attaining a high ground speed since wind speed increases with altitude. The decrease of flying-height in strong following winds may lie in the increased turbulence under these conditions. A high flight may be assumed to be favourable for the navigation of migrants that presumably set out their course with the aid of beacons in the landscape.

The volume of seaward migration and the flying-height of starlings prove to be highest with following winds, intermediate with cross winds and lowest with head winds.

In chapter 6 the influence of weather on the direction of migration is investigated. The mean directions of chaffinches and starlings were assessed in the early morning on days without rain or fog in a homogeneous landscape (forest) to estimate the standard direction of these species. For chaffinches, we found significant differences between means of different days. This was due to an influence of wind direction on mean migration direction on days with wind speed over 4 m/sec. This influence was such that directions were somewhat into the wind compared with the overall mean, pointing to overcompensation of lateral drift at high wind speed. It was shown that in the course of a day this overcompensation may increase gradually, thus leading to a shift of directions. On days with low wind speeds (under 4 m/sec) the birds started in about standard direction and also show a gradual shift of directions in the course of the morning, due to increasing overcompensation. A similar phenomenon was observed in the Mid-European subspecies of the chaffinch (Fringilla coelebs hortensis) and in the starling.

These observations were explained by assuming that the birds in compensating for lateral drift do not react to the mean wind speed but to the maximum one. Generally, the wind is more or less turbulent with gusts of varying speed, at least at mean wind speeds of over 4 m/sec. The distribution of speeds around the mean is not symmetrical, usually larger gusts occur upwards than downwards from the mean. This might make it rather difficult for a bird to keep a constant track by adjusting its heading to the mean wind speed. The increase of the turbulence with higher wind speeds and with warming of the earth's surface by the sun in the course of the morning, may account for the increase of over-
compensation at high wind speeds and towards the end of the morning.

Finally, variations in volume of migration are dealt with in chapter 7. Characteristically, a peak of migration occurs in the first hour after sunrise, followed by a minimum; later in the morning several more peaks may follow. It is shown that weather changes cannot account for these variations in volume of migration. Therefore it is assumed that they are due to changes in the birds' migration tendency. Similar changes may account for the variability of the strength of migration between days with apparently the same external circumstances. A long term decrease of the migration tendency is assumed to result from a prolonged period of favourable weather, whereas the migration tendency should increase during a hold-up in bad weather.

In this appendix some details are given in chapter 5.

Simple correlation coefficients between migration pattern and volume of seaward migration.

<table>
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<tr>
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</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>+ 0.403</td>
<td>+ 0.642</td>
<td>+ 0.772</td>
<td>- 0.052</td>
</tr>
<tr>
<td>Rain</td>
<td>+ 0.629</td>
<td>+ 0.562</td>
<td>+ 0.988</td>
<td>+ 0.869</td>
</tr>
<tr>
<td>Wind speed</td>
<td>+ 0.235</td>
<td>+ 0.389</td>
<td>+ 0.541</td>
<td>- 0.192</td>
</tr>
<tr>
<td>Cloudiness</td>
<td>+ 0.237</td>
<td>+ 0.418</td>
<td>+ 0.507</td>
<td>+ 0.218</td>
</tr>
<tr>
<td>Barometric pressure</td>
<td>- 0.179</td>
<td>- 0.391</td>
<td>- 0.353</td>
<td>- 0.369</td>
</tr>
</tbody>
</table>

The coefficients between migration directions are - 0.791, - 0.727,