

Directions of visible Skylark *Alauda arvensis* migration in east central Sweden

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Flight directions of 3418 Skylarks were recorded in the field in the province of Uppland, Sweden. The main spring passage was towards NNE—ENE, with a broad dispersion of directions. At Uppsala the frequency of individuals whose orientation lay within the N—E sectors had two clear peaks, at NNE and ENE. The two-peaked distribution of flight directions could occur on the same day, but the movements in the two peak directions could also be separated in time (different days), in which case the distribution of directions differed highly significantly between the periods.

In SE Uppland SW-directed autumn migration was observed. This movement is probably concentrated over SE Uppland by the leading-line effect of the Finnish coastline. In central Uppland the dispersion of autumn directions was larger, with strong S and SW components. The greater dispersion is probably caused by the passage of north Scandinavian birds, which have more southern orientation than the birds arriving from Finland.

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Introduction

Spaepen & Cauteren (1968) have reviewed the migration of the Skylark *Alauda arvensis* in Europe, and ringing recoveries and phenological data from Sweden have been treated by Rendahl (1967). The results given in these reports indicate that migratory behaviour varies between Skylarks from different areas. To study such differences, careful field observations on the flight directions of migrating Skylarks were started at Uppsala in 1960. In 1960—78 field records of flight directions were collected in the flat landscape of east central Sweden. The present paper reports the flight directions recorded in spring and autumn, and discusses the information they provide about the origin and flyways of the Skylarks passing this area.

Material and methods

Field records of flight directions were made in the neighbourhoods of: A. Uppsala (59° 52'N, 17°38'E) on 35 days in spring and 25 in autumn, B. Vallentuna (59°39'N, 18°05'E) on 3 days in spring and 4 in autumn, and C. Ångskär (60°29'N, 18°04'E) on 4 days in spring (Fig. 1). The observation sites were selected in relatively uniform parts of the landscape to eliminate the influence of the local topography.

The spring passage culminates in late March — early April and the autumn passage in late September — first half of October. The visible migration is, as a rule, most intense in the morning hours, but on extremely good days it may continue during most of the day. The birds usually fly 10—200 m above the ground, individually or in small flocks. Calls are frequently heard. In spring fairly many individuals, probably males, sing more or less continuously while passing. A few skylarks have been heard at night, which indicates that nocturnal passage also occurs.

The directions were determined for 1209 flights of altogether 3418 individuals. The

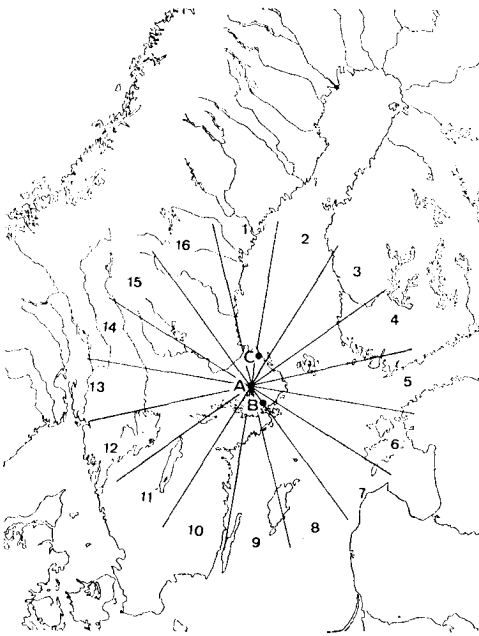


FIG. 1. Location of the observation places: A = Uppsala, B = Vallentuna and C = Ångskär. The 16 numbered sectors used for grouping the flight directions are superimposed on the map with origo at Uppsala and sector number 1 to the north.

following techniques were used. In 1960–66, Skylarks passing in directed flight above the observer were followed as far as possible using binoculars. When the bird flew out of sight the track direction was read to the nearest 10° on a 400° compass. In 1968–78 the directions were read from a plate on which was drawn a circle divided into 16 numbered sectors. The plate was placed on the ground beside the observer with sector number 1 to the north. Both techniques were used at Uppsala, which resulted in two samples of flight directions. Only the second technique was used at Vallentuna and Ångskär. Many of the observations were performed in fine weather with light winds and thus most of the directions recorded are little influenced by wind conditions.

Results

Autumn. At Uppsala the autumn orientation shows striking dispersion

(Fig. 2a), the Skylarks passing over the Uppsala plain in all directions. Movements towards S–SW are most common. Flights in the opposite directions occur with a dispersion around N and NE. The lowest frequencies are in the sectors around E and in W–NW. At Vallentuna distinct SW-directed movement was recorded (Fig. 2b).

Spring. At Uppsala the spring passage shows a broad dispersion of directions around NE (Fig. 3a, 3b). The distribution of directions is double-peaked, with high frequencies of flights towards NNE and ENE but with lower frequencies of flights oriented exactly NE.

In 1960 and 1971 the run of most of the spring passage was followed in fine weather with only light winds, and it is possible to test whether the movements in the two main directions were separated in time.

In 1960 ENE passage dominated during the first part of the season 24–28 March and NNE passage during the latter part 29 March – 10 April (Fig. 5). The observed distributions of Skylarks passing in the directions from N to E differed highly significantly between the two periods ($\chi^2 = 61.8$, $P < 0.0005$).

In 1971 NNE passage dominated on 29 March. On 30 March, a day with very high migratory activity, there were peak numbers flying both NNE and ENE. On 2–3 April the dominant direction was ENE (Fig. 5). The distribution of passing Skylarks in the 5 sectors from N to E differed highly significantly between 29 March and 2–3 April ($\chi^2 = 101.4$, $P < 0.0005$).

Movements in the opposite directions occurred, but the numbers were usually low. Striking reversed migration

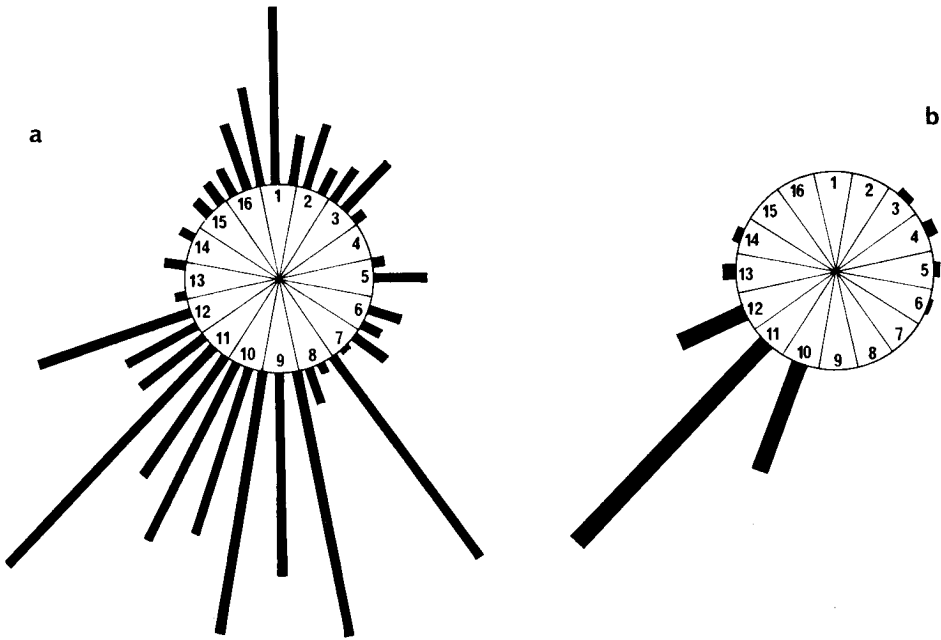


FIG. 2. a. Distribution of autumn flight directions at Uppsala in 1960—66 among 40 classes. For comparison, the 16 sectors later used for grouping directions are also shown, N = 620. b. Autumn directions at Vallentuna, N = 753.

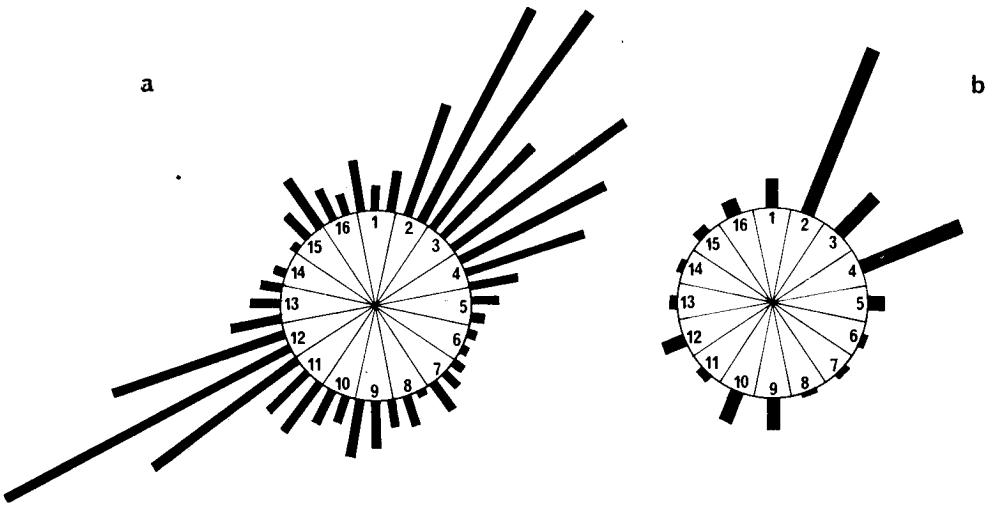


FIG. 3. Spring directions. a. Uppsala 1960—66, N = 590. b. Uppsala 1969—71, N = 881.

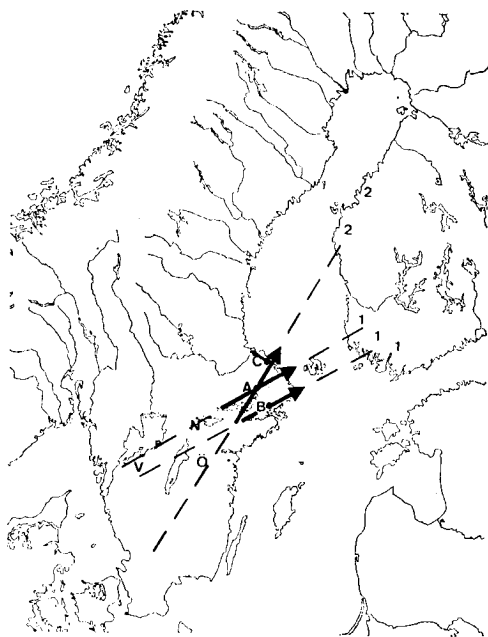


FIG. 4. Prolongations of the most commonly recorded directions of migration of Skylarks in spring superimposed on a map with the observation places (A, B and C), the two most densely populated breeding areas in Finland (1 and 2), and three areas with extensive resting habitats in Sweden (N, V and Ö).

was seen in connection with cold weather on 17 April, 1966. The flocks observed on this occasion caused high frequencies of SW—WSW flights (Fig. 3a).

At Vallentuna the most frequent spring direction observed was ENE. At Ängskär the observation point was situated in the forest about 1 km inland. A WNW-NW movement parallel to the coast was observed together with NE and SW movements. The spring samples from Vallentuna and Ängskär are too small to show whether the NE components are double-peaked or not.

Discussion

Why do Skylarks passing Uppsala in spring most frequently fly in the two directions NNE and ENE? According to Merikallio (1958), the most common breeding places of the Skylark in Finland are firstly in agricultural land in a southwestern region inland of the town of Turku, and secondly in agricultural land and seashore meadows in a region along the west coast around and northeast of Vaasa. The two main directions observed at Uppsala lead towards these two regions, which suggests that the destination of many of the Skylarks is Finland. Ringing recoveries also indicate that the Skylarks passing over south and central Sweden on migration originate from Finland (Spaepen & Cauteren 1968). Thus, many of the Skylarks seen on spring migration at Uppsala are presumably Finnish.

By extending the two main directions SSW and WSW we obtain the following two hypothetical spring routes through Sweden (Fig. 4):

1. Sjaelland — Scania — Östergötland plain — Uppsala plain — Western Finland.
2. Jutland — Västergötland plain — Närke plain — Uppland — South-west Finland.

Along these routes there are areas with extensive agricultural land, which should provide favourable resting habitats.

Why do the flight directions differ between central and southeast Uppland in autumn (Fig. 2)? On leaving Finland Skylarks that are oriented SW have to pass the Finnish coast. Coastlines are known to act as leading-lines for migrating Skylarks (cf. Evans 1966, Rabøl & Noer 1973). Birds that follow the Finnish west

coast to the Åland archipelago will reach the Swedish coast in east Uppland, and can be expected to continue their flight over the southeast part of that province. Consequently most of them will pass too far south to be observed at Uppsala. Organized field observations along the coast of Uppland have shown a larger number of Skylarks arriving on the east part of the coast than on the north and north-east parts, which indicates that autumn migration is concentrated over the Åland archipelago (S.-E. Swanqvist pers. comm.). Thus, a leading-line effect is probably the chief cause of the uniform SW movement observed at Vallentuna, which contrasts with the larger dispersion of flight directions, with strong S as well as SW components, observed at Uppsala.

Individuals flying in other directions than the primary ones were observed on several occasions. Attempts were made to obtain recordings only from individuals on migration by watching the behaviour of the birds as long as they were in sight. Only birds flying straight on were recorded. Despite this, the possibility remains that some movements of a more local character have been included. No clear case of wind drift or of reorientation was observed. However, two additional explanations can be given for the unexpected observations of NW flight directions in spring and S—SE directed movements in autumn:

1. Change of direction caused by the cloud cover. For example, on the morning of 30 March 1960 the sky was covered by heavy cloud, except in the north. During half an hour, 06.35—07.05, the distribution of light in the sky was similar to that at sunrise, but with the difference that the sky was lightest in the north instead of the east. Of the 13 Skylarks passing during this half hour, more than half were oriented NW, although the frequency of NW movements is usually much

lower. Later in the same morning, when the cloud front had moved south and the sky was clear, a further 16 Skylarks passed, all of them oriented NE!

2. S and SE migration of Skylarks from northern Scandinavia. There are some field observations of S—SE directed autumn movements in the area NW of Uppsala. At Torsåker, about 100 km NW of Uppsala, 295 Skylarks were seen moving S—SE on 5 days in

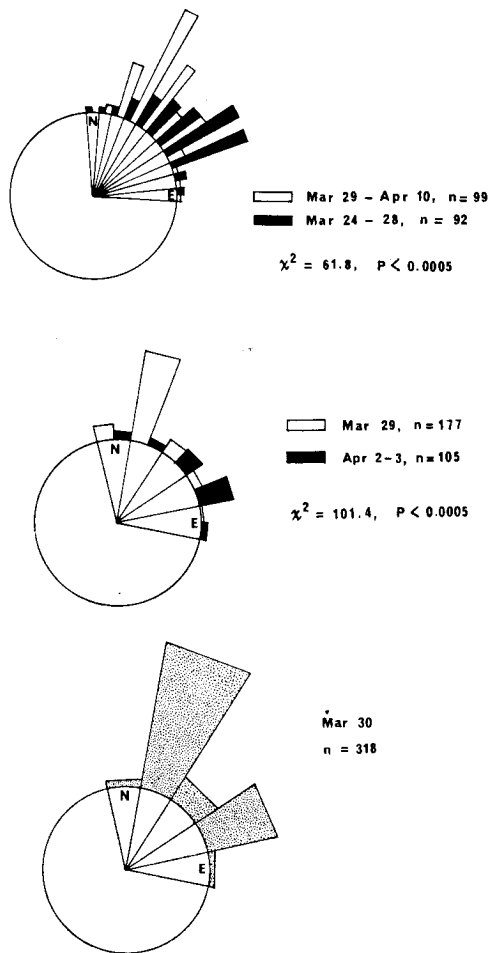


FIG. 5. Records of Skylarks *Alauda arvensis* on migration at Uppsala. Distribution of flight directions within the N—E sector on different days. Upper graph in 1960, middle and lower graphs in 1971.

September-October 1971 (L. Risberg in litt.). The S—SSE directed component of the autumn migration at Uppsala may thus be caused by the passage of birds of north Scandinavian origin.

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Selostus: Kiurun muuttosuunnat Itä-Ruotsissa

Kiurun päivämuuton suuntia tutkittiin kolmella paikkakunnalla Upplannissa, Itä-Ruotsissa, 1960- ja 1970-luvuilla (kuva 1). Aineisto käsitti 3418 yksilöä. Kevätmuuton pääsuunta oli NNE—ENE, mutta muuttoa tapahtui kaikkiin suuntiin, erityisen voimakkaana lounaaseen takatalvien yhteydessä (kuva 3). Pääsuunta oli kaksihuippuinen, NNE ja ENE, mikä oli todettavissa sekä samoina päivinä että muuton eri vaiheissa (kuva 5). Tämän otaksutaan johtuvan siitä, että tutkimusalueen ylittävät kiuurut ovat matkalla kahdelle pääalueelle, Lounais-Suomeen ja Pohjanmaalle (kuva 4).

Syysmuutto suuntautui Kaakkois-Upplannissa vallitsevasti lounaaseen (kuva 2b), Keski-Upplannissa taas lähes kaikkiin suuntiin, mutta etenkin SW—SE (kuva 2a). Selitys lienee se, että edellisen alueen linnut saapuvat pääasiassa Suomesta ja jatkavat länsirannikon—Ahvenanmaan johtolinjan määräämää lounaismuuttoa, kun taas jälkimmäisellä alueella on mukana paljon Pohjois-Ruotsin lintuja, joiden vakio-suunta on eteläisempi.

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