Behav Ecol Sociobiol (1986) 19:417–424

Behavioral Ecology
and Sociobiology

The adaptive significance of reoriented migration of chaffinches *Fringilla coelebs* and bramblings *F. montifringilla* during autumn in southern Sweden

Åke Lindström and Thomas Alerstam
Department of Ecology, Animal Ecology, University of Lund, Ecology Building, S-223 65 Lund, Sweden

Received February 7, 1986 / Accepted June 7, 1986

Summary. Reoriented autumn migration of chaffinches and bramblings occurs regularly in southernmost Sweden. The reoriented birds fly in a northeasterly direction from the coast and inland, i.e. approximately opposite to the normal autumn migration direction. The daily peak of reoriented finch migration, as observed at inland sites 20–40 km from the coast, occurs on average 3.5 h later than the early morning departure in the normal migratory direction, and 1 h later than the peak of migration at the coast. According to trapping data the average weight of reoriented migrants and birds interrupting their migration at the coastline is significantly lower than the weight of migrants proceeding in the normal direction, and the proportion of yearlings seems to be larger in the former category. Censuses of flocks of resting finches showed that they mainly forage at stubble fields of summer rape *Brassica napus*, preferably fields surrounded by wooded vegetation offering shelter from predator attacks. Preferred food and habitats are mostly located inland, 20 km or more from the coast. These findings are consistent with the interpretation that reorientation constitutes an adaptive response by migrants with small fat reserves. When confronted with an ecological barrier, they return to suitable resting sites for restoring the fat reserves before crossing the barrier.

Introduction

Autumn migration of birds in a direction more or less opposite to what is normal for the season has repeatedly been reported in the literature (e.g. Haartman 1945; Haartman et al. 1946; Evans 1968; Richardson 1978). Such reoriented or reverse autumn migration is more difficult to explain than temporary retreat migration in spring, which is often clearly associated with cold or snow. Richardson (1982) reviewed many different explanations that have been proposed to account for reoriented autumn migration, including orientation errors, effects of wind drift and responses to weather. He concluded that no single explanation is applicable to all cases of reoriented migration reported, but different causes are involved under different environmental circumstances.

We have studied the autumn migration and resting ecology of chaffinches, *Fringilla coelebs*, and bramblings, *F. montifringilla*, to test a hypothesis put forward by Alerstam (1978a) and discussed by Richardson (1982). It is suggested that, in coastal or other regions where migrants are confronted with ecological barriers offering no or only poor resting opportunities, reoriented migrations represent flights to suitable resting grounds. We will present evidence to throw light on three main predictions from this hypothesis as applied to the autumn migration of finches in southern Sweden.

(1) Daily timing of reoriented flights

Chaffinches and bramblings from northern Europe pass southern Sweden in autumn on their way to wintering grounds in western and central Europe (Roos 1984). Their main passage at Falsterbo (see Fig. 1) is between 25 September and 17 October (Alerstam 1978b). In the study area chaffinches and bramblings are mainly diurnal migrants with a peak of migration normally occurring during the early morning hours. Reoriented migration in this area, towards N–NE, has been described by Roos (1974) and Alerstam and Ulfstrand (1975). If birds taking part in reoriented migration are individuals that have flown in the normal direction in the morning and, when reaching the coast, change to the opposite direction, reoriented migration will be expected to show a peak later in the day than that of normal migration.

(2) Fat levels (weights) and age composition of reoriented migrants

When migrating birds encounter the sea, individuals with small fat reserves will presumably interrupt their flight at the coastline. If conditions for resting and refueling are unfavourable at the coastline (see below) these birds are expected to take part in reoriented migration. Adults have made the migratory journey once before and may be able to adjust their flight schedule in such a way that they to a larger extent than juveniles can avoid the extra costs of landing/turning at the coastline. Thus, it is predicted that interrupted and reoriented birds are birds with smaller fat reserves than those crossing the sea in the normal direction and the proportion of juveniles may be higher among reoriented birds than among migrants travelling in the normal direction.

(3) Food, competition and predation risk at the coast and inland

During the nonbreeding period chaffinches and bramblings are flock living, mainly feeding on seeds on the ground. The food mostly preferred by these finches seems to be beech mast (Zisweiler 1965; Newton 1972). As the beech *Fagus silvatica* sets mast in more or less irregular intervals of 2 or more years (Newton 1972; Nøhr 1984), the birds will have to use other seeds most of the time. Flocks of foraging finches are targets of numerous attacks from predators, above all sparrowhawks *Accipiter nisus* (personal observation).

Alerstam (1978a) suggested three reasons for a bird, grounded at the coast with depleted fat reserves, to return inland: low availability of food, high food competition and high predation risk at the coast as compared to inland. We expect to find evidence for at least one of these three factors, showing that reoriented migration has an adaptive value for the migrating finches.

Methods

Daily timing of migration

During the three autumns 1971–1973 migrating birds were counted between 0600 and 1400 h at different localities in the province of Scania, southernmost Sweden. These field observations have been analysed earlier in relation to simultaneous radar data (Alerstam and Ulfstrand 1975). For the present study we have used the field data from three sites in southwestern Scania: Sturup (site S) 17 September–10 October 1971 and 23 September–14 October 1973, Lund (site L) 17 September–8 October 1972, and Falsterbo (site F) 23 September–14 October 1973. These localities are shown in Fig. 1.

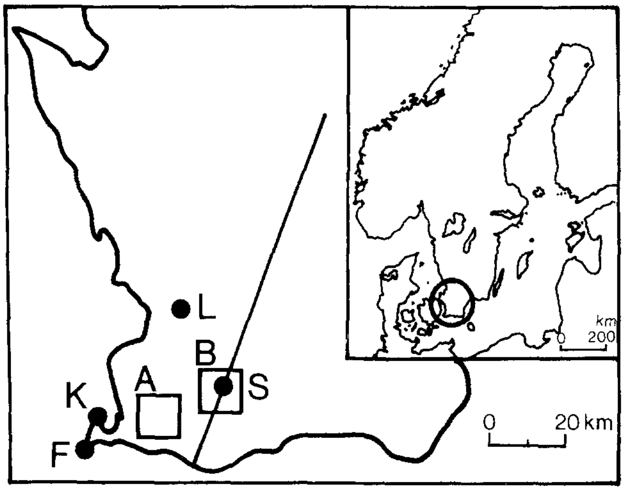

Fig. 1. Study sites in the province of Scania in South Sweden. The straight line shows the transect along which finch flocks were censused by car. A and B are the areas in which summer rape fields were studied. The four localities are Falsterbo (*F*), Knösen (*K*), Sturup (*S*) and Lund (*L*)

Chaffinches and bramblings very often fly in mixed flocks and counts of these two species are pooled. Birds flying towards directions between SE and W are considered to be on normal migration and are called "migrating birds". Those flying in directions between NW and E are called "reoriented birds". Numbers were summed over half-hour periods.

Weights and age composition

At Falsterbo Bird Station migrating birds are regularly trapped in mist nets during spring and autumn (Roos 1984) and birds are ringed, sexed and aged. During four autumns – 1980, 1981, 1984, 1985 – trapped chaffinches were weighed as well. We have separated these chaffinches into two categories. Those trapped on days with strong (>6 ms^{-1}) winds from directions between SW and NW are considered as "migrating birds" and those trapped during other wind conditions are considered as "interrupted" and "reoriented birds". In strong head winds chaffinches fly low over the ground and along the coastline to reduce energy expenditure (Alerstam 1978b). When passing the trees and bushes at the Falsterbo lighthouse under strong westerly winds, finches on migration in the normal direction repeatedly fly straight into the nets and get trapped. Birds trapped in other, more favourable winds, as the stream of normal migration proceeds at a higher altitude, ought to be individuals which for some reason have interrupted their journey, hesitating to cross the sea in front of them.

In two autumns, 1980–1981, chaffinches were also trapped, sexed and weighed at Knösen, a site 7 km NNE of Falsterbo (site K, Fig. 1). At this site almost all birds seen in autumn are flying NE (Roos 1974) so the finches from this site are considered reoriented birds. The number of bramblings trapped at Falsterbo and site K were too small to be analysed.

At site S, chaffinches and bramblings, feeding on fields with spill seeds of summer rape *Brassica napus*, were trapped, sexed and weighed in the autumns of 1984 and 1985. All birds in this study were weighed on a spring balance to the nearest 0.1 g, except at site K where they were weighed to the nearest 0.5 g.

Distribution of resting finches

Finch flocks were censused four times by car along a 100 km transect extending inland from the coast, approximately parallel to the axis of normal/reoriented migration (Alerstam and Ulfstrand 1975; see Fig. 1). When a feeding finch flock was seen from the car, the car was stopped. All feeding finch flocks of more than 25 individuals were recorded. Flocks just flying over, or resting flocks that could not be connected with a certain field, were omitted. In one census, 8 October 1984, only flock size and position were noted. In three censuses, 25 September and 7 and 22 October 1985, food choices were recorded as well. All censuses were carried out by one person (ÅL).

Observations at site S indicate that foraging finches are strongly attracted to newly harvested summer rape fields (cf. below). Summer rape is sown in spring and harvested in September. In order to evaluate the importance of shelter for the habitat selection of feeding finches we surveyed 34 summer rape fields (in July 1985 when summer rape was in flower) in two different 100 km^2 squares (cf. Fig. 1).

Ten fields were located in an area with almost entirely open farmland (area A) and 24 fields in an area with scattered woodlands and groves, where forest covers about 10% of the total area (area B). Field sizes were estimated and the fields were classified into two categories, with none/poor shelter or with moderate/extensive shelter, depending on the number of trees, shrubberies and groves surrounding them.

These fields were visited again three times during the finch migration season and after the harvest (28 September, 8 and 24 October) when flocks of chaffinches and bramblings were censused. We kept a record whether the fields remained as stubble fields during the autumn finch migration or if they were ploughed and sown. After ploughing, seed availability is highly reduced.

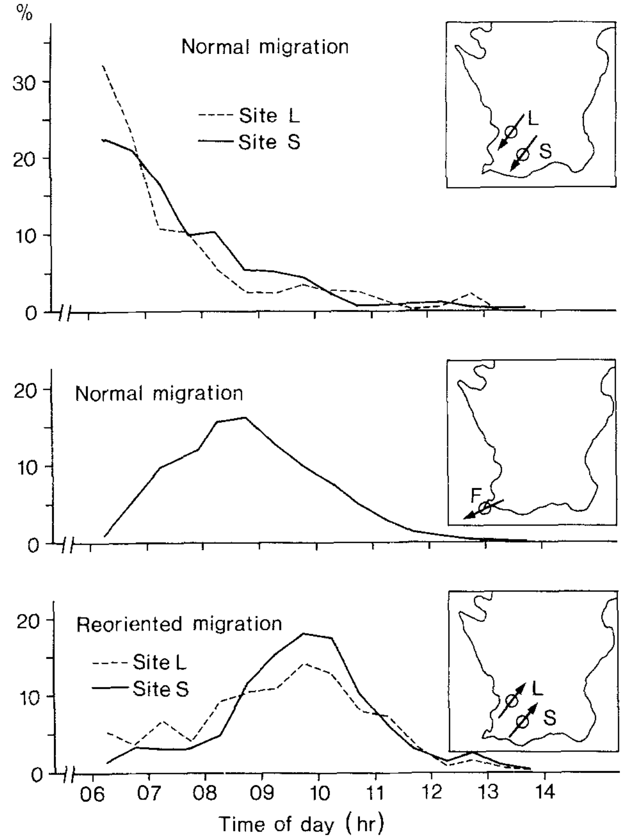

Fig. 2. Numbers of chaffinches and bramblings seen per half hour, as a percentage of the total number, on normal and reoriented migration in autumn at three sites in southwestern Scania. Field counts of migrating birds were carried out at site S in 1971 and 1973 (n=30,504 on normal and 27,114 on reoriented migration), at Falsterbo in 1973 (n=404,675), and at site L in 1972 (n=1,038 on normal and 9,728 on reoriented migration; cf. Alerstam and Ulfstrand 1975)

Results

Daily timing of migration

The migration of chaffinches and bramblings usually starts at dawn and ends about noon. The daily timing of migrating and reoriented chaffinches and bramblings at the three field observation sites is presented in Fig. 2. The migration peak at Falsterbo occurs later than at sites S and L, indicating a lack of suitable resting grounds in the close vicinity of Falsterbo. The reoriented migration at sites S and L occurs distinctly later in the day than the peak of migration in the normal direction. Note that some reoriented movements occur at sites S and L as early as dawn (local sunrise at approximately 06.10 h on 1 October).

Field observations at different sites on the Falsterbo Peninsula on 8 October 1967 demonstrated a heavy northeastward migration of chaffinches and bramblings (altogether 12,600 individuals) at site K. The peak of migration was between 08.30 and 09.30 h, which was one hour later than the peak of normal migration that day at Falsterbo, where 44,470 finches were recorded (Roos 1974).

Weights and age composition of migrants

Table 1 shows mean weights and age ratios of different categories of chaffinches. There were no significant differences in mean weight between adults and juveniles (young of the year). In all 4 years, mean weights of migrating birds at Falsterbo were higher than of interrupted/reoriented birds, though not significantly so in 1981 and 1985. Weight data from all years and both age classes are combined in Table 1. The difference in mean weight between migrating and interrupted/reoriented birds at Falsterbo is significant (both sexes, $P<0.001$, t-test), as is the difference between migrating birds at Fal-

Table 1. Autumn mean weights, range of yearly means, and age composition of chaffinches in different migratory categories. Weights were recorded at Falsterbo during 1980, 1981, 1984 and 1985, at site K during 1980 and 1981, and at site S during 1984 and 1985. For explanations of migrating and interrupted birds at Falsterbo, see Methods. Birds were not aged at site K

Category	Locality	Autumn mean weights (g) ± SD (*n*)		Range of yearly means	Adults (%)
Migrating birds	Falsterbo	Males	23.85 ± 1.60 (74)	23.1–24.5	54.1
		Females	21.54 ± 1.37 (77)	21.3–22.2	
Interrupted and reoriented birds	Falsterbo	Males	22.85 ± 1.76 (83)	21.9–23.2	38.8
		Females	20.79 ± 1.60 (135)	19.8–21.1	
	Site K	Males	23.08 ± 1.33 (22)	22.8–23.3	–
		Females	20.80 ± 0.80 (22)	20.6–20.9	
Feeding birds	Site S	Males	23.64 ± 1.25 (91)	23.6–23.7	27.0[a]
		Females	21.86 ± 1.36 (106)	21.8–21.9	

[a] Biased by a curtailed trapping effort (see text)

sterbo and reoriented birds at site K (males, $P < 0.05$; females, $P < 0.001$; *t*-test). The weights at site S are close to those of migrating birds at Falsterbo. At Falsterbo there was a significantly higher proportion of adults among migrating than among interrupted/reoriented birds ($P < 0.01$, χ^2-test). The even lower proportion of adults at site S is probably caused by a seasonally skewed trapping effort. At Falsterbo median trapping dates for migrating and interrupted/reoriented birds were 12 and 9 October, respectively (24% trapped in September), while at site S the median trapping date was 30 September (62% trapped in September). On average, juvenile chaffinches and bramblings commence their migration earlier than the adults (which are delayed by moulting), making juveniles overrepresented in September.

Distribution of resting finches

The three transect censuses in 1985 showed that chaffinches and bramblings are strongly attracted to summer rape fields. Of 15 recorded flocks, 9 were feeding on summer rape fields, in spite of the fact that only 1%–4% of the area of arable land along the transect were used for growing this crop. The dominating crops were cereals. The distribution of summer rape in Scania in 1984–1985 is presented in Fig. 3a. Notice the very sparse occurrence in the southwesternmost part, an almost entirely cultivated and highly exposed lowland area. Finch flocks observed during the transect censuses are also indicated on the maps. Table 2 shows that fields with stubble of summer rape are the most desirable, and the following analyses are restricted to these fields.

The importance of summer rape as food for the resting finches is also made clear by our studies

Table 2. Number of summer rape fields with (+) or without (−) finch flocks in relation to field status during three censuses in areas A and B (cf. Fig. 1). Stubble fields are newly harvested with all spill still available. Since many stubble fields are ploughed and sown during autumn, their number decreases throughout the migration period

Field status	Census I (28 Sept)		Census II (8 Oct)		Census III (24 Oct)		Total	
	+	−	+	−	+	−	+	−
Stubble	13	5	6	4	4	2	23	11
Ploughed/sown	2	13	4	19	1	27	7	59

at site S. There, in an area of 50 ha summer rape fields, normally 1,000 chaffinches and bramblings were present each day in the autumns of 1984–1985 and the spring of 1985. The highest numbers of resting finches during these seasons were recorded in 30 September 1984 (10,000), 14 April 1985 (10,000) and 4 October 1985 (25,000).

Figure 3b shows the distribution of forest in Scania. The finches may be expected to prefer wooded regions, because feeding flocks use forests and groves surrounding the fields as protection when attacked by sparrowhawks (personal observation). The importance of woodlands close to the feeding sites may be evaluated by comparing the occurrence of resting finches on summer rape stubble fields in the region of exposed farmland (area A in Fig. 1) with mixed farmland/woodland (area B in Fig. 1), as in Table 3. There seems to be little difference between the presence of resting finches at summer rape stubble fields in these two regions, although flock sizes are significantly larger in the mixed farmland/woodland region than in the region of exposed farmland. However, considering the availability of local shelter at each summer rape

Table 3. Number of summer rape stubble fields with (+) or without (−) finch flocks and flock sizes, in areas A and B (cf. Fig. 1). As data from three censuses are treated together some fields are included more than once for this comparison. The data presented may still be regarded as independent observations, providing there is a complete turnover of resting finches between the censuses. This is highly probable in view of the relatively long intervals between the succeeding censuses, 10 and 16 days respectively. However, because of this uncertainty we have refrained from using statistical tests. In contrast, we have considered the flock sizes recorded as independent observations, and compared the data from the two areas with the two-tailed Mann-Whitney *U*-test

Area	Type of landscape	Censuses I–III		Flock size			
		+	−	Range	*n*	Median	
A	Open farmland	8	3	25–1,000	8	100	$P<0.05$
B	Mixed farmland/woodland	15	8	100–3,000	15	300	

Table 4. Number of summer rape stubble fields with (+) or without (−) finch flocks and flock sizes, in relation to the amount of shelter (cf. text) around these fields. Data recorded and tested as in Table 4

Shelter	Censuses I–III		Flock size			
	+	−	Range	*n*	Median	
None/poor	9	11	25–3,000	9	300	$P>0.1$
Moderate/extensive	14	0	100–1,000	14	275	

stubble field that was censused, there is a clear indication that finches prefer fields surrounded by shelter, though flock size does not seem to be affected (Table 4). When field size is taken into account, median flock size was significantly larger on large than on small fields (Table 5).

Discussion

Daily timing of migration

The field observations indicate that most finches in southernmost Sweden start from their inland resting grounds (like site S) at dawn and pass Falsterbo 1–2 h later. The peak of reoriented migration at sites S and L comes 1–1.5 h after the migration peak at Falsterbo. Thus, the results from these counts agree with the prediction that reoriented birds are individuals that have reversed their migratory direction at, or not very far off, the coast.

Weights and age composition of migrants

The prediction that interrupted/reoriented birds have smaller fat reserves than migrating birds is supported by weight data (Table 1). Resting birds at site S have approximately the same average weight as the migrating birds at Falsterbo. This is not surprising, because at site S there ought to be birds with both depleted and filled fat stores.

A contributary cause of the weight differences between the two categories of finches trapped at Falsterbo may be that mean weight is higher among birds migrating on days with strong headwinds than on days with more favourable winds. Hence, weights of finches trapped under favourable wind conditions, and by us considered as interrupted/reoriented birds, may reflect the normal weight composition of migrants under these conditions. However, as the Falsterbo trapping site is highly unsuitable for resting/feeding of finches, we regard it as unlikely that birds landing there, dropping out from the normally high-altitude migration stream on days with favourable winds, constitute a representative sample of the migratory category. Unfortunately, we have no way to obtain weight data from the high-altitude migrants in favourable winds.

As predicted, there are more first-year birds among reoriented than among migrating birds.

Food and shelter

The distribution of food, in the form of spill seeds on summer rape fields, seems to be of major importance for explaining the reoriented migration in chaffinches and bramblings (Fig. 3a; Table 2). Summer rape fields are more or less missing in the southwesternmost part of Scania. As a consequence, birds at Falsterbo have to make a reverse flight 20–40 km inland to reach regions with relatively many summer rape fields.

Why are summer rape seeds preferred as food by the resting finches? The fat and fatty acid content of summer rape and some other common grains (rye *Secale cereale*, wheat *Criticum aestivum*, barley *Hordeum vulgare* and oats *Avena sativa*) are shown in Table 6. Summer rape contains the high-

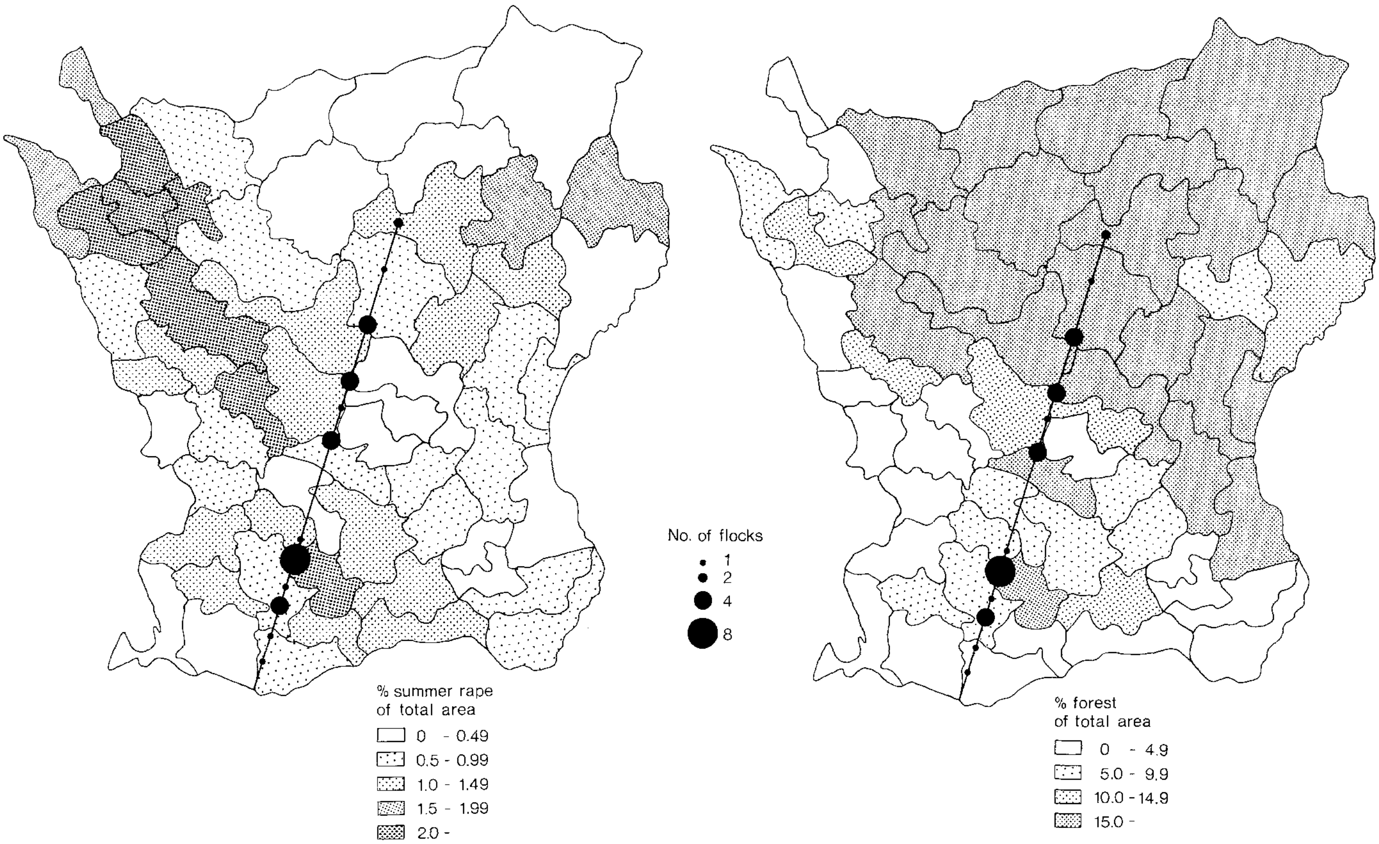

Fig. 3. **a** Distribution of summer rape in Scania in 1984 (in total 7,800 ha) and 1985 (7,700 ha), expressed as percentage of total land area in different official harvest areas. **b** Percentage of forest in 1984 in the same areas as in **a**. In both **a** and **b** the numbers and locations of finch flocks during four transect censuses in 1984 and 1985 are shown. Information on summer rape cultivation and distribution of forest in Scania was obtained from the Swedish Oilseed Association, Malmö, and Statistics Sweden, Stockholm

Table 5. The importance of shelter and field size on the presence (+) or absence (−) of finch flocks on summer rape stubble fields. Flock sizes on large (>4.5 ha) and small (<4.5 ha) fields are compared as well (range 0.5–45 ha). Data recorded and tested as in Table 4

Field size	Shelter				Flock size			
	None/poor		Moderate/extensive		Range	n	Median	
	+	−	+	−				
Small	5	8	3	0	25–500	8	100	$P<0.002$
Large	4	3	11	0	100–3,000	15	350	

Table 6. Fat and fatty acid contents of some common crops available to finches during the autumn migration season in Scania. Data from Simmonds and Campbell (1976) and Ackman (1983)

Crop	Crude fat (% dry matter)	Fatty acids (%)						
		16:0	18:0	18:1	18:2	18:3	20:1	Others
Summer rape	45	4.5	1.5	59	21	11	1	2
Rye	1.5	16.5	0.6	15.6	55.6	10.4	1.3	
Wheat	1.6	17.8	0.6	14.5	60.5	5.7	0.9	
Barley	1.7	22.5	1.0	13.9	54.8	6.8	1.0	
Oats	5.2	16.3	1.0	40.2	40.1	1.7	0.8	

est proportion of fat, which may be of great importance to a bird depositing migratory fat. Moreover, summer rape fat consists largely of fatty acid 18:1, which is the fatty acid most abundant in the depot fat of migratory birds (Blem 1976). However, the significance of the fat composition and the costs of fatty acid transformations are poorly known (Blem 1976). Of course, handling times and energy contents of the different grains are also important for their profitability but we lack data about these factors. It may be noted that summer rape was introduced in Sweden as late as the 1940s (Brusewitz and Emmelin 1985).

In none of the study years (1971–1973, 1980–1981, 1984–1985) were there any noticable beech mast crops in southern Sweden (Nøhr 1984; H. Källander, personal communication). But as the distribution of beech strongly correlates with the distribution of forest (Fig. 3b) the overall course of reoriented migration probably remains much the same in years with a large beech mast crop.

While feeding on summer rape fields the finches are exposed to numerous predator attacks. During 150 observation hours at site S in the autumns of 1984 and 1985, 170 attacks of sparrowhawks on feeding flocks were recorded. Metcalfe and Furness (1984) showed that birds feeding for pre-migratory fattening reduce their vigilance. This increases their vulnerability to predators and enhances the need for a safe feeding site. When attacked, the finches often take shelter in woods, groves and large shrubberies surrounding the fields. Furthermore, before a new feeding attempt, the finches use trees or bushes as gathering points (the flock often scatters when attacked). The importance of these factors is indicated by the censuses of finches at fields with different amounts of shelter (Table 4). Woods and groves ought to be of importance for roosting as well.

Moreover, flocks were larger in the mixed farmland/woodland region than at the few and scattered summer rape fields in the southwesternmost part of Scania (Table 3; Fig. 3b). Thus, besides food availability, the distribution of shelter may be a contributary cause of reoriented migration.

Finches feeding in flocks on summer rape fields hardly ever show any aggressiveness towards each other (personal observation). Furthermore, finch flocks were repeatedly seen feeding on the same spots of the fields throughout the autumn and even in the following spring. This implies that there is a rich surplus of food at the summer rape stubble fields and, consequently, weak food competition.

Hence, we have found evidence for two of the three suggested reasons for individuals with depleted fat reserves to return inland, i.e. the preferred food is more abundant, and there is better protection against predators.

Flight range capacity in migrating and reoriented birds

Dolnik and Gavrilov (1973) found that migrating chaffinches under calm conditions loose 0.5 g of their weight during a 50 km flight, corresponding to a mean weight loss of 0.01 g km^{-1}. According to Dolnik and Blyumental (1967) the average weights of lean chaffinches are 21.0 g for males and 19.1 g for females. However, it seems that birds on migration very seldom consume all of their fat reserves (Pettersson and Hasselquist 1985). At site S only 4 of 261 chaffinches had no visible fat. The mean weights of birds in the second lowest fat class were 22.1 g for males and 19.7 g for females. Assuming that these weights correspond to the normal minimum weights tolerated by finches before stopping to refuel, we can calculate the flight ranges, during calm conditions, for migrating and reoriented birds at Falsterbo (adopting the estimated weight loss of 0.01 g km^{-1} and using weight data from Table 1). The reoriented birds would be able to fly about 75 km (males) and 109 km (females). The corresponding estimates for the migrating birds are 175 and 184 km respectively. After the departure from Falsterbo, migrating finches fly across the Baltic Sea either to the Danish Islands (a sea crossing of 25–50 km) or to northern Germany (100–180 km).

It seems reasonable that birds with a flight range capacity of merely about 100 km, or even less if headwinds prevail, should return 20–40 km inland to suitable resting sites rather than crossing the sea. Once they have crossed the sea, they have to fly an additional uncertain distance to find new feeding sites.

Hence, reoriented migration of finches in southern Sweden seems to be an integral part of their migration strategy, constituting an adaptive response by which individuals confronted with an ecological barrier and having small fat reserves, can rapidly find suitable resting grounds for refueling before crossing the barrier. However, this explanation cannot be applied to all types of reoriented migration that have been documented (cf. Richardson 1982).

Acknowledgements. We are very grateful to Göran Högstedt for stimulating discussions and advice, for letting us use his trapping data from Knösen, and for contributing financial support of the field work in 1984. Furthermore, we are greatly indebted to Lennart Karlsson, Karin Persson and Göran Walinder for weighing finches at Falsterbo Bird Station. Göte Lindvall kindly permitted us to work on his fields at Sturup. Lars-Åke Johansson, Folke Sjöberg and Bo Thysell assisted with information on summer rape. We also thank W. John Richardson and Mats Grahn for comments on the manuscript, Gösta Lindström for improving the English, and Steffi Douwes for drawing the figures. This study was supported by grants from the Swedish Natural Science Research Council. This is Report No. 114 from Falsterbo Bird Station.

References

Ackman RG (1983) Chemical composition of rapeseed oil. In: Kramer JKG, Sauer FD, Pigden WJ (eds) High and low erucic acid rapeseed oils. Production, usage, chemistry and toxicological evaluation. Academic, New York, pp 85–129

Alerstam T (1978 a) Reoriented bird migration in coastal areas: dispersal to suitable resting grounds? Oikos 30:405–408

Alerstam T (1978 b) Analysis and a theory of visible bird migration. Oikos 30:273–349

Alerstam T, Ulfstrand S (1975) Diurnal migration of passerine birds over South Sweden in relation to wind direction and topography. Ornis Scand 6:135–149

Blem CR (1976) Patterns of lipid storage and utilization in birds. Am Zool 16:671–684

Brusewitz G, Emmelin L (1985) Det föränderliga landskapet. LTs förlag, Stockholm

Dolnik VR, Blyumental TI (1967) Autumnal premigratory and migratory periods in the chaffinch (*Fringilla coelebs coelebs*) and some other temperate-zone passerine birds. Condor 69:435–468

Dolnik VR, Gavrilov VM (1973) Energy metabolism during flight of some passerines. In: Bykhovski BE (ed) Bird migrations. Ecological and physiological factors. Wiley, New York, pp 288–296

Evans PR (1968) Reorientation of passerine night migrants after displacement by the wind. Br Birds 61:281–303

Haartman L v (1945) Umschlagende Zugrichtung beim Buchfinken *Fringilla c. coelebs* L., im Herbst. Ornis Fenn 22:10–16

Haartman L v, Bergman G, Koskimies J (1946) Beobachtungen über umschlagende Zugrichtungen der Bachstelze, *Motacilla a. alba* L., im Herbst. Ornis Fenn 23:50–62

Metcalfe NB, Furness RW (1984) Changing priorities: the effect of pre-migratory fattening on the trade-off between foraging and vigilance. Behav Ecol Sociobiol 15:203–206

Newton I (1972) Finches. Collins, London

Nøhr H (1984) The winter occurrence of bramblings and wood pigeons in south Sweden and Denmark in relation to the beech mast crop as measured in Denmark. Vår Fågelvärld 43:241–243 (English summary)

Pettersson J, Hasselquist D (1985) Fat deposition and migration capacity of robins *Erithacus rubecula* and goldcrests *Regulus regulus* at Ottenby, Sweden. Ring & Migr 6:66–76

Richardson WJ (1978) Timing and amount of bird migration in relation to weather: a review. Oikos 30:224–272

Richardson WJ (1982) Northeastward reverse migration of birds over Nova Scotia, Canada, in autumn. Behav Ecol Sociobiol 10:193–206

Roos G (1974) Simultaneous observations of visible autumn migration at different sites near Falsterbo – a pilot study. Anser 13:137–148 (English summary)

Roos G (1984) Migration, wintering and longevity of birds ringed at Falsterbo (1947–1980). Anser [Suppl 13], Lund (English summary)

Simmonds DH, Campbell WT (1976) Morphology and chemistry of the rye grain. In: Bushuk W (ed) Rye: production, chemistry and technology. American Association of Cereal Chemists, Inc, St. Paul, pp 63–110

Zisweiler V (1965) Zur Kenntnis des Samenöffnens und der Struktur des Gaumens bei körnerfressenden Oscines. J Ornithol 106:1–48