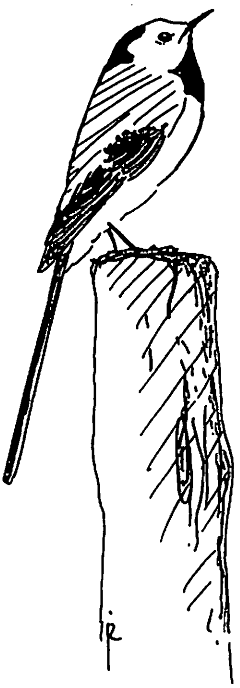
DO PASSERINE MIGRANTS CAPTURED AT AN INLAND SITE PERFORM TEMPORARY REVERSE MIGRATION IN AUTUMN?

SUSANNE ÅKESSON[1,2]



Åkesson S. 1999. Do passerine migrants captured at an inland site perform temporary reverse migration in autumn? Ardea 87: 129-137.

Ringing recoveries from 18 different passerine species captured at an inland ringing site in south Sweden (Kvismare Bird Observatory) were analysed with respect to direction and distance of migration in order to investigate the occurrence of temporary reverse movements opposite to the expected forward migratory direction towards south and south-west in autumn. The data demonstrate that movements in reverse or other directions were rare compared to forward movements among the different species and categories of migrants (short-distance or irruptive migrants, temperate and tropical migrants). Compared to birds captured on migration at a coastal ringing site in south-west Sweden (Falsterbo Bird Observatory), the proportion of birds performing reverse movements were significantly lower at the inland ringing site. The results from the inland site and previous results from the coastal site in south-west Sweden suggest that autumn reverse movements mainly occur in migrating passerines confronted with an ecological barrier, such as a sea. Presumably temporary reverse movements in coastal areas is an adaptive behaviour performed by migrants in order to locate suitable feeding grounds for refuelling before they are prepared to resume migration and cross the barrier.

Key words: orientation - reverse migration - ringing recoveries - autumn - ecological barrier - passerines

[1]Department of Zoology, Zürich University, Winterthurerstrasse 190, 8057 Zürich, Switzerland; [2]Present address: Department of Animal Ecology, Lund University, Ecology Building, 223 62 Lund, Sweden, E-mail: susanne.akesson@zooekol.lu.se

INTRODUCTION

Reverse bird migration has been reported repeatedly for passerines on migration in spring as well as in autumn (e.g. von Haartman 1945; von Haartman *et al.* 1946; Koskimies 1947; Evans 1968; Able 1977; Richardson 1978; Lindström & Alerstam 1986; Sandberg 1994; Sandberg *et al.* 1988; Åkesson *et al.* 1996). Birds may turn and temporarily migrate opposite to the seasonally appropriate direction. Such direction reversals may be due to bad weather, wind drift off the migration route or caused by orientation errors (for review, see Richardson 1982).

Recently, it was shown that different categories of passerine migrants regularly perform temporary reverse migration in autumn, when confronted with the sea at the Falsterbo peninsula in south-westernmost Sweden (Åkesson *et al.* 1996). The majority of the migrants have reached the Falsterbo area from north to north-east by flights mainly over land. When reaching Falsterbo during their migration the migrants are for the first time confronted with the sea. Within the first ten days after capture as many as 64% of the passerine migrants performed reverse movements (Åkesson *et al.* 1996), presumably to more suitable stopover sites further inland. These reverse movements are presumably performed in order to refuel before crossing the sea barrier (cf. Alerstam 1978; Lindström & Alerstam 1986). At this coastal site the proportion of reverse movements were higher in species which carried small fuel deposits compared to species with large fat reserves (Fig. 5 in Åkesson *et al.* 1996).

Why do passerine migrants captured at a coastal site at Falsterbo perform temporary reverse movements in autumn? Are coastal reverse movements adaptive, triggered by the confrontation with an ecological barrier such as the sea, and performed in order to reach more suitable stopover sites further inland? Do migrants making landfall at inland sites also perform reverse movements in order to reach stopover sites already known or located en route irrespective of contact with the sea? If migrants grounded on migration do search for stopover sites they have located during the previous migration flight, then we would expect migrants captured at inland sites to perform temporary reverse movements in autumn. To test this hypothesis autumn ringing recoveries were analysed of passerines captured at an inland ringing site, Kvismare Bird Observatory, in south central Sweden. Recoveries of 18 different species of passerine migrants were analysed with respect to direction and distance of autumn migration.

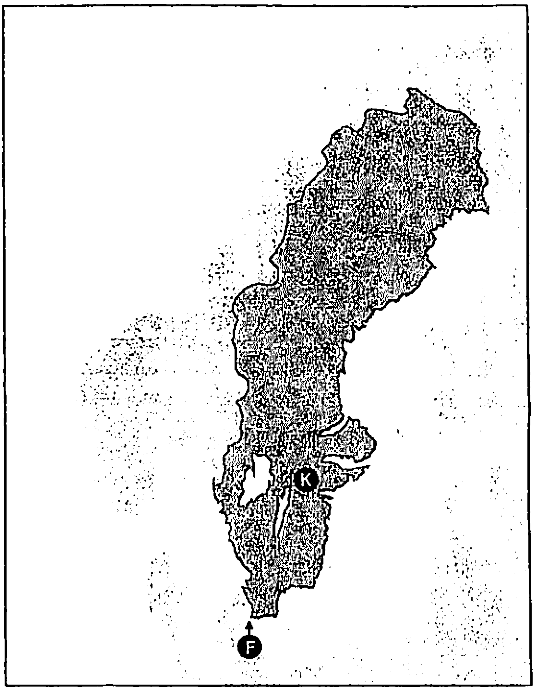


Fig. 1. The geographical position of the two study sites. Kvismare Bird Observatory (K) is located at Lake Kvismaren in south central Sweden and Falsterbo Bird Observatory (F) is located at the coast in the southwesternmost part of Sweden.

METHODS

Kvismare Bird Observatory (59°10'N, 15°25'E) is situated at Lake Kvismaren, in south central Sweden (Fig. 1). The area consists of several shallow euthrophic lakes located a few kilometres apart. Several of these smaller lakes have recently been restored. Regular autumn ringing activity of passerines making stopover on migration has been conducted in autumn (end of June to end of September) since 1961. The birds are captured in mist nets located in reed beds and deciduous shrub habitats at 2-4 sites located at maximum 15 km apart at the border of the lakes. Each autumn between 4000 and 7500 birds are ringed in this area.

I analysed all ringing recoveries of passerines ringed at Kvismare Bird Observatory and reported to the Swedish Ringing Office between the years 1961 and 1996. Only birds captured during the autumn migration period (from 7 July to October) and recovered within the same calendar year were included in the analyses. I selected only birds recovered at least 5 km from the ringing site, and used no restriction on the number of recoveries reported for each species to be included in further analyses. For comparative reasons, when possible I selected the same species that were ringed at Falsterbo Bird Observatory and reported on by Åkesson *et al.* (1996). For analyses of direction and distance of migration I divided the recoveries in two different groups. The first group contained birds recovered within 14 days after capture, while the second group represented birds recovered at least 15 days or later after capture. This time period of 14 days was selected because only a very limited number of birds were recovered within 10 days after capture (time period used in Åkesson *et al.* 1996) and this would have led to difficulties in performing such comparisons. I do not believe the differences in time period had great effects on the outcome of the comparisons. Only for the groups with tropical migrants, Sedge Warblers *Acrocephalus schoenobaenus* and Reed Warblers *A. scirpaceus*, respectively, was it possible to compare recoveries between the two time periods (≤14 days and > 15 days, respectively). The great majority (95.7%) of the birds were juveniles. Adult migrants were found in the following species: Redwing *Turdus iliacus* (n = 3), Sedge Warbler (1), Reed Warbler (7) and Reed bunting *Emberiza schoeniclus* (4).

The species included in further analyses were classified into different categories of migrants based on the distance of migration and the location of the wintering areas: (1) Short-distance and irruptive or partial migrants migrating relatively short distances (< 1000-1500 km): Coal Tit *Parus ater*, Blue Tit *P. caeruleus*, Great Tit *P. major* and Siskin *Carduelis spinus*; (2) Temperate migrants wintering mainly in south and south-western Europe: Dunnock *Prunella modularis*, Robin *Erithacus rubecula*, Song Thrush *Turdus philomelos*, Redwing and Reed Bunting; and (3) Tropical long-distance migrants wintering mainly in tropical Africa were: White Wagtail *Motacilla alba*, Yellow Wagtail *M. flava*, Sedge Warbler, Reed Warbler, Whitethroat *Sylvia communis*, Garden Warbler *S. borin*, Blackcap *S. atricapilla*, Willow Warbler *Phylloscopus trochilus* and Pied Flycatcher *Ficedula hypoleuca*. In some analyses the data from Sedge and Reed Warblers were treated separately from the group of other tropical migrants.

I used vector addition to calculate the mean angle of orientation based on individual directions of recoveries for each group of migrants (Batschelet 1981). The vector length, r, which ranges between 0 and 1, gives the measure of concentration of the circular distribution. The vector length is inversely related to the angular scatter of the circular distribution. The Rayleigh test was used to calculate the significance levels of circular distributions (Batschelet 1981). I analysed differences in concentration of mean headings (indicated by t) and mean orientation ($F_{1, df}$) between groups by using Mardia's test for homogeneity of concentration parameters and one-way classification test, respectively (Mardia 1972). For non-parametric statistical tests Siegel & Castellan (1988) was consulted.

RESULTS

Occurrence of reverse migration at the inland site

The analysis is based on a total of 351 recoveries of 18 different passerine species. In five of the species included only one recovery was reported within either of the two periods. The number of recoveries, direction and distance of movement for the different species are given in the Appendix. For short-distance and temperate migrants the majority of the recoveries were reported at least 15 days after capture (87.5% and 100%, respectively), while 24.9% of the tropical migrants were recovered within 14 days after capture. Reverse migratory movements towards north-west to east (315°-89°) were performed by 2.3% (8) of the total sample of birds, while 95.4% (335) of the birds moved in the expected forward direction towards south-east to west (135°-269°; cf. statistics for Falsterbo given in Åkesson *et al.* 1996). In total 2.3% (8) of the birds performed movements in other directions (90°-134°, 270°-314°). Date of capture, direction and distance of migration of recoveries reported in reverse and other direction north of a line 270°-89° are presented in Table 1.

The percent and sample size for different categories and species of migrants performing reverse or forward migration or movements in other directions are given in Figure 2. In the following analyses I compare the proportion of migrants performing forward movements towards south (90°-269°) with the proportion of migrants moving opposite to the expected migratory direction (reverse directions, 270°-89°) for different categories of migrants. Recoveries reported from 270°-314° and 90°-134° were pooled into the groups of reverse and forward recoveries, respectively, in order to increase the sample sizes of the

Table 1. Individual recoveries reported from reverse (R; 315°-89°) or other directions to the north (O; 270°-314°) for a number of bird species captured at Kvismare Bird Observatory in autumn. Date of capture, number of days passed between ringing and recovery, direction and distance between capture site and site of recovery according to a great circle route are given. Median and ranges of dates of capture are given for each species in the Appendix.

Species	Recoveries in reverse (R) or other directions (O)	Date of capture	Days	Direction (°)	Distance (km)
Blue Tit	R	16 Sep 1978	55	5°	20
	O	3 Sep 1987	39	275°	108
Reed Bunting	O	6 Aug 1996	29	291°	10
White Wagtail	O	13 Aug 1995	63	270°	9
Sedge Warbler	R	9 Aug 1991	16	12°	42
	R	21 Jul 1971	130	354°	9
Reed Warbler	R	22 Jul 1990	11	357°	20
	R	6 Aug 1979	14	317°	15
	R	8 Jul 1992	18	79°	80
	R	19 Jul 1981	18	317°	15
Garden Warbler	R	7 Aug 1996	11	358°	22
	O	16 Aug 1985	16	288°	917
Pied Flycatcher	O	29 Jul 1997	3	279°	12

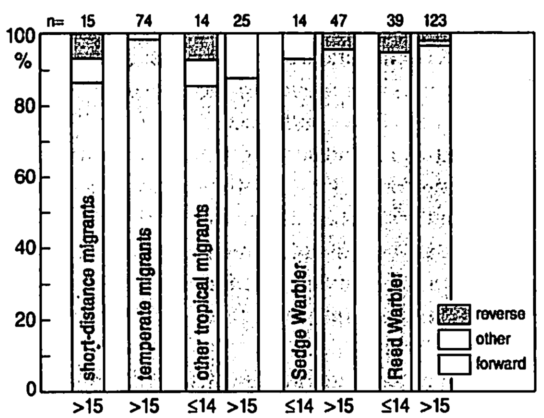


Fig. 2. The proportion of birds ringed at Kvismare Bird Observatory in autumn and recovered in reverse directions (315°-89°) or forward directions (135°-269°) or after movements in other directions (90°-134°, 270°-314°). Data from four different species are included in the category of short-distance/irruptive migrants, from five different species of temperate migrants and from seven species of tropical migrants.

groups. I found no significant difference in the proportion of birds performing reverse movements or forward migration between the two time periods in a number of comparisons (data on statistical tests presented in Table 2). However, the difference between short-distance and temperate migrants for the period > 15 days after capture was statistically significant ($\chi^2_1 = 5.98$, $P < 0.05$), such that short-distance migrants performed reverse migration more frequently than temperate migrants (Table 2). Mean angles of orientation for different categories of migrants are given in Figures 3 and 4.

For recoveries reported in reverse (315°-89°; n = 8) and other directions towards the north (270°-314°; n = 5) I compared the number of recoveries ringed before the median date of capture for each species with the number of recoveries ringed after this date (Table 1). There was no significant difference between the two groups; the birds recovered in reverse directions were not captured to a larger extent in the earlier part of the season ($\chi^2_1 = 0.077$, n.s.).

Table 2. Comparisons of proportion of recoveries reported from reverse and forward directions between different species and groups of species and with respect to capture period, respectively. Degrees of freedom (*df*) and significance levels (*P*) are given for each χ^2-test. For further information see text.

Comparison	species/group	χ^2	*df*	*P*
≤ 14 days vs. > 15 days	Sedge Warbler	0.62	1	n.s.
≤ 14 days vs. > 15 days	Reed Warbler	0.72	1	n.s.
≤ 14 days vs. > 15 days	other trop. migrants	0.70	1	n.s.
Sedge vs. Reed Warbler	≤ 14 days	0.75	1	n.s.
Sedge and Reed Warbler vs. other trop. migrants	≤ 14 days	2.82	1	n.s.
Sedge vs. Reed Warbler	> 15 days	0.39	1	n.s.
Sedge and Reed Warbler vs. other trop. migrants	> 15 days	1.03	1	n.s.
Short-d. vs. tropical warblers	> 15 days	0.44	1	n.s.
Short-d. vs. temperate warblers	> 15 days	5.98	1	< 0.05
Temperate vs. tropical warblers	> 15 days	2.66	1	n.s.

Occurrence of reverse migration at coastal and inland sites

In the following analyses the proportion of migrants performing movements in reverse or forward directions (given above) are compared for birds captured at Kvismare and Falsterbo Bird Observatories, respectively. To be able to compare statistically the distributions of recoveries of birds captured at the two sites, recoveries reported in directions between 270° and 314° for Falsterbo birds are included in the reverse group and recoveries reported between 90° and 134° in the forward group. Recoveries reported shortly after capture (Kvismaren: ≤ 14 days, Falsterbo: ≤ 10 days) are compared with recoveries reported later after capture (Kvismaren: > 15 days, Falsterbo: > 11 days). For Falsterbo Bird Observatory, data on number of birds recovered in different directions relative to the ringing site are given in Åkesson *et al.* (1996). Within the time period shortly after capture (≤ 14 days) there was a significant difference in the proportion of migrants performing reverse movements (270°-89°) compared with birds performing forward migration (90°-269°) between Kvismare and Falsterbo Bird Observatories, for Sedge and Reed Warblers combined (χ^2_1 = 11.0, $P < 0.001$) and for the group with other tropical migrants (χ^2_1 = 5.85, $P < 0.02$). During the second time period birds captured at Falsterbo

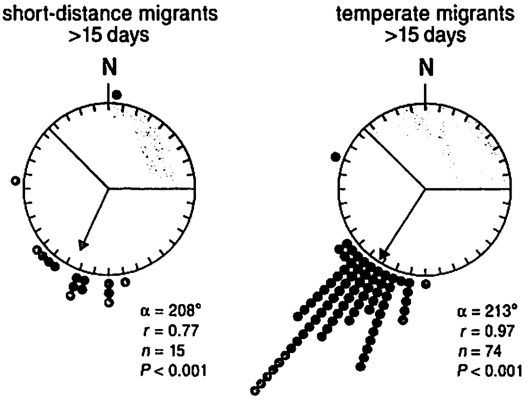


Fig. 3. The circular diagrams demonstrate the direction of migration for four short-distance migrants (Coal Tit, Blue Tit, Great Tit and Siskin) and four species of temperate migrants (Dunnock, Robin, Redwing Thrush, Song Thrush and Reed bunting), recovered 15 days or longer after capture. Details of circular statistics (mean angle of orientation: α, vector length: *r*, number of birds: *n*, and significance levels according to the Rayleigh test: *P*) are given for each circular diagram. The shaded areas in the circular diagrams represent the directions classified as reverse directions (315°-89°).

performed reverse movements more frequently than birds captured at Kvismare Bird Observatory, for short-distance migrants (χ^2_1 = 4.46, $P < 0.05$), temperate migrants (χ^2_1 = 8.04, P <

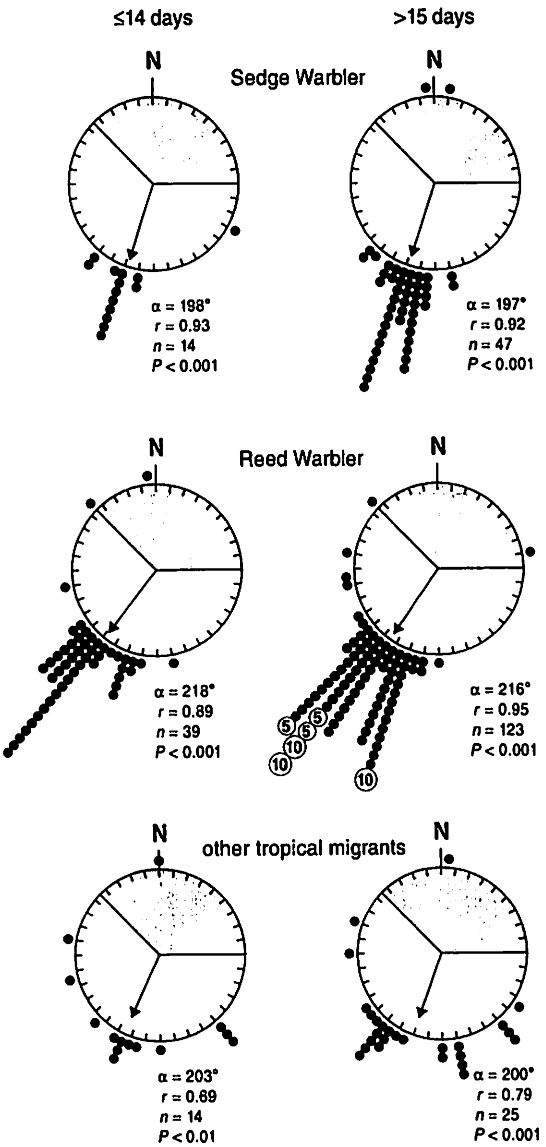


Fig. 4. Directions of recoveries for Sedge and Reed Warblers and a third group consisting of other tropical migrants (White Wagtail, Yellow Wagtail, White-throat, Garden Warbler, Blackcap, Willow Warbler and Pied Flycatcher) captured and recovered in autumn within 14 days after capture and 15 days or longer after capture, respectively. Numbers of recoveries are given within enlarged open circles for three directions with particular high numbers of recoveries reported for the Reed Warbler. For further information see Fig. 3.

0.005), Sedge and Reed Warblers ($\chi^2_1 = 7.39$, $P <$ 0.01), but not for other tropical migrants ($\chi^2_1 =$ 0.53, n.s.).

DISCUSSION

Occurrence of reverse migration

The results from this study show that reverse movements directed approximately opposite to the expected natural direction of migration (i.e. towards south-east to south-west) are rare among passerines captured at this inland locality in autumn. This was true for birds recovered shortly after capture (≤14 days) as well as later in autumn (> 15 days). A comparative analysis of ringing recoveries of mainly the same species of migrants captured at Falsterbo Bird Observatory in autumn (a coastal site), revealed that temporary reverse migration is widespread among different species of migrants at the coastal site. Reverse movements away from the coast most frequently occurred shortly after capture at Falsterbo (Åkesson *et al.* 1996). This indicates that preparedness for reverse migration is universal among different migrants and that reverse movements mainly occur after contact with an ecological barrier, such as the sea. The data do not support the hypothesis that reverse migration is performed by migrants making landfall on migration at inland sites and that migrants from such sites move in reverse directions in order to locate stopover sites encountered earlier en route. Instead, birds making landfall at inland sites mostly move in forward directions when locating resting sites since by applying this behaviour they will decrease the distance to the migratory goal (cf. optimal migration theory; Alerstam & Lindström 1990).

Distance of migration

The very few recoveries reported from reverse or other directions (W-SE) were of short distances compared to recoveries found in forward directions reported within the same time period. The reverse recoveries seem to be represented mainly by more or less local movements within the Kvismare area or between nearby lakes. These reverse recoveries could either be migrants arriving to Lake Kvismaren from further north in order to make stopover there or local birds performing post-breeding movements before migration is initiated. Baker (1983) suggested that migrants prior to autumn migration move around in the vicinity of where they were hatched in order to gain local experience from their natal area to facilitate return next spring (i.e. this could be achieved by memorising local landmarks, local geomagnetic cues or perhaps local odours; e.g. Wallraff 1991). In this way they will become familiar with a larger goal area which will increase the probability that they will be able to find the area on returning next spring. An alternative explanation for post-breeding movements suggests that migrants may visit future potential breeding sites already in autumn prior to migration (Oring & Lank 1992; Ketterson & Nolan 1979). The few recoveries reported from directions north of a line 270°-89° were not captured more frequently before the median date of capture for each species, suggesting that the reverse movements can occur at any time of the autumn migration period. Pre-migratory movements should be expected to mainly occur during the first part of the migration period. However, reverse recoveries reported for Reed Warblers were all from before the median date of capture, and hence, local pre-migratory movements can not be excluded in this species. Therefore, the reverse movements of relatively short distances observed at Lake Kvismaren in autumn could be birds searching for suitable stopover sites, or might in some species be caused by local exploratory movements.

For short-distance and temperate zone migrants some recoveries were reported from late in the autumn, and for these species some of these recoveries may be movements within the wintering range. It should be noted that such movements could have an effect on the direction and distance of recoveries reported on in the Appendix. However, these movements do not have a major effect on the main point of this paper: the proportion of reverse migration at the inland site.

Is temporary reverse migration in autumn a coastal phenomenon?

Temporary reverse bird migration in autumn has been demonstrated for a number of species, and all studies reporting on reverse migration in diurnal or nocturnal migrants have been performed in coastal areas (e.g. von Haartman 1945; von Haartman *et al.* 1946; Koskimies 1947; Alerstam 1978; Able 1977; Richardson 1978; Lindström & Alerstam 1986; Sandberg *et al.* 1988; Åkesson *et al.* 1996; Bruderer & Liechti 1998). Therefore it is of great interest to test whether reverse migration in autumn is a coastal phenomenon or whether birds making landfall at inland sites also perform temporary reverse migration. Based on the data presented here and extensive data from a coastal ringing site in south-west Sweden (Åkesson *et al.* 1996), I conclude that reverse migration in autumn is much more common in the coastal area than at my inland study site. Alternative explanations for reverse migration, for example orientation errors (cf. Alerstam 1990), can most probably be ruled out since such errors can be expected to cause approximately the same degree of reverse movements at different types of capture sites. Since few birds captured at the inland ringing site at Lake Kvismaren perform reverse migration in autumn compared with birds at the coast at Falsterbo, the most likely explanation for their reverse migration is an adaptive temporary retreat from coastal areas in order to find safe and more suitable stopover sites in inland areas. To further understand the selective factors involved it would be of great interest to compare habitat quality in relation to safety and food availability (cf. Lindström 1990; Moore & Young 1991), between coastal and inland stopover sites.

ACKNOWLEDGEMENTS

I am grateful to Bo Sällström at the Swedish Ringing Office and Bo Nielsen at Kvismare Bird Observatory for providing me with ringing recoveries and to Jan Sondell for permission to analyse the recoveries from Kvismare Bird Observatory. I am grateful to Anders Hedenström, Lucas Jenni, Lennart Karlsson and an anonymous referee for valuable comments on the manuscript. The study was financed by a grant from The Swedish Natural Science Research Council. This is report 99 from Kvismare Bird Observatory and 191 from Falsterbo Bird Observatory.

REFERENCES

Able K.P. 1977. The orientation of passerine nocturnal migrants following offshore drift. Auk 94: 320-330.

Åkesson S., Karlsson L., Walinder G. & Alerstam T. 1996. Bimodal orientation and the occurrence of temporary reverse bird migration during autumn in south Scandinavia. Behav. Ecol. Sociobiol. 38: 293-302.

Alerstam T. 1978. Reoriented bird migration in coastal areas: Dispersal to suitable resting grounds? Oikos 30: 405-408

Alerstam T. 1990. Ecological causes and consequences of bird orientation. Experientia 46: 405-415

Alerstam T. & Lindström Å. 1990. Optimal bird migration: the relative importance of time, energy and safety. In: Gwinner E. (ed.) Bird Migration: Physiology and Ecophysiology: 331-351. Springer, Berlin Heidelberg.

Baker R.R. 1983. The function of post-fledging exploration: a pilot study of three species of passerines ringed in Britain. Ornis Scand.224: 71-79.

Batschelet E. 1981. Circular Statistics in Biology. Academic Press, New York.

Bruderer B. & Liechti F. 1998. Flight behaviour of nocturnally migrating birds in coastal areas - crossing or coasting. J. Avian Biol. 29: 499-507.

Evans P.R. 1968. Reorientation of passerine night migrants after displacement by the wind. Br. Birds 61: 281-303.

Haartman L. von 1945. Umschlagende Zugrichtung beim Buchfinken *Fringilla c. coelebs* L., im Herbst. Ornis Fenn. 22: 10-16.

Haartman L. von, Bergman G. & Koskimies J. 1946. Beobachtungen über umschlagende Zugrichtungen der Bachstelze, *Motacilla a. alba* L., im Herbst. Ornis Fenn. 23: 50-62.

Ketterson E. & Nolan V. 1979. Seasonal, annual, and geographic variation in sex ratio of wintering populations of dark-eyed juncos (*Junco hyemalis*). Auk 97: 532-536.

Koskimies J. 1947. Über den Herbstzug der Bachstelze *Motacilla alba* in der Gegend von Helsinki. Ornis Fenn. 24: 61-79.

Lindström Å. 1990. The role of predation risk in stopover habitat selection in migrating bramblings, *Fringilla montifringilla*. Behav. Ecol. 1: 24-35.

Lindström Å. & Alerstam T. 1986. The adaptive significance of reoriented migration of chaffinches *Fringilla coelebs* and bramblings *F. montifringilla* during autumn in southern Sweden. Behav. Ecol. Sociobiol. 19: 417-424.

Mardia K.V. 1972. Statistics of Directional Data. Academic Press, London.

Moore F.R. & Young W. 1991. Evidence of food-based competition among passerine migrants during stopover. Behav. Ecol. Sociobiol. 28: 85-90.

Oring L.W. & Lank D. B. 1992. Sexual selection, arrival times, philopatry and site fidelity in the polyandrous spotted sandpiper. Behav. Ecol. Sociobiol. 10: 185-191.

Richardson W.J. 1978. Reorientation of nocturnal landbird migrants over the Atlantic Ocean near Nova Scotia in autumn. Auk 95: 717-732.

Richardson W.J. 1982. Northeastward reverse migration of birds over Nova Scotia, Canada, in autumn. Behav. Ecol. Sociobiol. 10: 193-206.

Sandberg R. 1994. Interaction of body condition and magnetic orientation in autumn migrating robins, *Erithacus rubecula*. Anim. Behav. 47: 679-686.

Sandberg R., Pettersson J. & Alerstam T. 1988. Why do migrating robins, *Erithacus rubecula*, captured at two nearby stop-over sites orient differently? Anim. Behav. 36: 865-876.

Siegel S. & Castellan N. J. 1988. Nonparametric Statistics for the Behavioural Sciences. McGraw-Hill, New York.

Wallraff H.G. 1991. Conceptual approaches to avian navigation systems. Experientia 46: 379-388.

SAMENVATTING

Trekvogels trekken soms tegen de overheersende trekrichting in. Hiervoor bestaan verschillende verklaringen: slecht weer, verdrifting door harde wind of oriëntatiefouten. Uit recent onderzoek bij Falsterbo aan de uiterste zuidpunt van Zweden blijkt, dat de zangvogels die daar tijdens de herfsttrek aankomen en dan geconfronteerd worden met de zee geregeld omgekeerde trek vertonen. Een aannemelijke verklaring is, dat ze terugkeren op zoek naar goede foerageergebieden om verder op te vetten. Daarna hebben ze voldoende brandstof om de trektocht over zee te maken. In deze studie werd onderzocht wat zangvogels doen, die tijdens de herfsttrek aan de grond kwamen in een gebied in het binnenland van zuid Zweden: het Kvismare vogelstation. Daartoe werden alle terugmeldingen geanalyseerd van 18 soorten zangvogels die in de herfst op Kvismare waren geringd en hetzelfde jaar nog werden teruggemeld. Er

waren maar heel weinig terugmeldingen die wezen op een tegengestelde trekrichting. Omgekeerde trek bleek in het binnenland veel zeldzamer dan aan de kust bij Falsterbo. Dit ondersteunt de eerder opgestelde verklaring dat zangvogels die op de trek geconfronteerd worden met een ecologische barrière tijdelijk omkeren op zoek naar goede foerageergebieden, om daarna de barrière te nemen.

Received 27 April 1998, accepted 11 November 1998
Corresponding editor: Bruno J. Ens

APPENDIX

Number of recoveries (n), mean angles of orientation (α), vector lengths (r), distances in km and medians and ranges of date of capture of migration movements of birds ringed at Kvismare Bird Observatory during autumn migration and recovered within the same calendar year shortly after capture ≤ 14 days) or later > 15 days), respectively. Significance levels are according to the Rayleigh test (Batschelet 1981).

Species	Period (days)	α	r	P	Distance Range (km)	Distance Median (km)	Date Range (dd, mm)	Date Median (dd, mm)	n
(A) Short-distance migrants									
Coal Tit *Parus ater*	≤ 14	-	-	-	-	-	-	27 Sep	0
	> 15	168°	-	-	(169)	169			
	1								
Blue Tit *Parus caeruleus*	≤ 14	182°	-	-	(437)	437	2 Aug-23 Sep	16 Sep	1
	> 15	212°	0.64	0.04	20-459	398			8
Great Tit *Parus major*	≤ 14	-	-	-	-	-		7 Aug	0
	> 15	226°	-	-	(5)	5			1
Siskin *Carduelis spinus*	≤ 14	183°	-	-	(475)	475	31 Jul-18 Sep	11 Sep	1
	> 15	207°	0.98	0.02	1008-2400	1358			4
(B) Temperate migrants									
Dunnock *Prunella modularis*	≤ 14	-	-	-	-		-	13 Sep	-
	> 15	210°	-	-	(1781)	1781			1
Robin *Erithacus rubecula*	≤ 14	-	-	-	-	-	9 Jul-30 Sep	21/22 Sep	0
	> 15	214°	0.99	0.0001	1287-3129	2232			8
Song Thrush *Turdus philomelos*	≤ 14	-	-	-	-	-		14 Sep	0
	> 15	213°	-	-	(2244)	2244			1
Redwing *Turdus iliacus*	≤ 14	-	-	-	-	-	11 Jul-13 Sep	12 Aug	0
	> 15	209°	0.96	0.004	1561-2747	1969			6
Reed Bunting *Emberiza schoeniclus*	≤ 14		-	-	-	-	7 Jul-20 Sep	3 Aug	0
	> 15	214°	0.99	0.0001	10-2152	1530			58
(C) Tropical migrants									
White Wagtail *Motacilla alba*	≤ 14	254°	-	-	(7)	7	22 Jul-13 Sep	8/9 Aug	1
	> 15	175°	0.71	n.s.	9-2665	346			5
Yellow Wagtail *Motacilla flava*	≤ 14	200°	-	-	(449)	449	2 Aug-23 Aug	10/11 Aug	1
	> 15	206°	-	-	(1122)	1122			1
Sedge Warbler *A. schoenobaenus*	≤ 14	198°	0.93	0.0001	109-1532	448	7 Jul-12 Sep	2 Aug	14
	> 15	197°	0.92	0.0001	9-2017	859			47
Reed Warbler *A. scirpaceus*	≤ 14	218°	0.89	0.0001	15-1414	303	7 Jul-27 Sep	8/9 Aug	39
	> 15	216°	0.95	0.0001	10-2941	906			123
Whitethroat *Sylvia communis*	≤ 14	169°	-	-	(337)	337	20 Jul-31 Aug	9 Aug	1
	> 15	160°	0.95	n.s.	108-563	336			2
Garden Warbler *S. borin*	≤ 14	227°	0.55	n.s.	22-719	596	7 Aug-31 Aug	15 Aug	4
	> 15	242°	0.90	0.04	533-2791	1522			4
Blackcap *S. atricapilla*	≤ 14	197°	-	-	(349)	349	- -	20 Aug	1
	> 15	-	-	-	-	-			-
Willow Warbler *Phylloscopus trochilus*	≤ 14	161°	0.87	n.s.	361-563	557	24 Jul-31 Aug	12/13 Aug	3
	> 15	197°	0.87	0.001	346-2777	1139			11
Pied Flycatcher *Ficedula hypoleuca*	≤ 14	238°	0.76	n.s.	12-452	232	27 Jul-15 Aug	28/29 Jul	2
	> 15	223°	0.99	n.s.	874-2161	1518			2