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A comparison of autumn migration strategies in Robins *Erithacus rubecula* at a coastal and an inland site in southern Sweden.

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The biometrics, age ratio and timing of migration of Robins were compared during autumn migration at an inland and a coastal site 200 km apart. The proportion of adult birds was higher at the inland site. The time of peak of migration differed between the two sites by 9 days. The daily distribution showed that at the coastal site the birds made a land-fall at dawn, while at the inland site the migration continued during the morning.

Robins in the same visual fat class were heavier at the inland site, but their mean fat class was lower than at the coastal site. This would be expected if Robins inland were short-stage migrants and therefore do not need extensive fuel reserves. At the coastal site a higher proportion of the Robins are probably long-stage migrants.

The orientation of the Robins under clear skies was more south-westerly at the coastal site. The direction is significantly different from the mean azimuth of sunset at the coastal site only. Under totally overcast conditions the directions were more scattered at both sites, indicating the importance of visual cues for orientation.

It is well known that among nocturnal passerine migrants at coastal sites, islands or peninsulas the proportion of young birds is often exceptionally high (Mehlum 1981, Ralph 1981, Pettersson 1983). However, other differences between inland and coastal sites are relatively unexplored. They might include differences in the seasonal and daily distribution of birds, fat accumulation and orientation, which may give hints to the sort of migration strategies used over the inland and along the sea/coast, respectively.

This paper presents data on Robins *Erithacus rubecula* captured at an inland and a coastal site in southern Sweden during the autumn of 1990 (with some complementary data from 1989 and 1991). The Robins breeding in Scandinavia and Finland are migratory birds (nocturnal migrants). Their wintering areas are situated in south–western Europe and the Mediterranean region (Rehndahl 1966, Roos 1984, Pettersson *et al.* 1986, Cramp 1988). In Sweden the autumn migration starts in late August and then continues to the beginning of November. Robins are caught in large numbers at bird observatories in southern Sweden and are therefore well suited for studies of migration.

METHODS

Falsterbo Bird Observatory (55°12'N, 12°23'E) is situated on the southwestern point of Sweden (Fig. 1). The ringing site is the lighthouse garden, a small wooded area, surrounded by open fields. The inland locality at Uråsa, Väckelsång (56°41'N, 14°53'E) is located 200 km northeast of Falsterbo. The ringing site is a wooded area surrounding a small stream, while the surroundings consist of cultivated areas, pastures and a lake.

The bird ringing in autumn at Falsterbo Bird Observatory follows a standardized scheme which operates from 21 July to 10 November. In this study we have only considered Robins caught between 1 September and 20 October 1990. This period covers the main migration period of the Robin (90% of the seasonal total). At Uråsa the same period was covered. At both sites the same daily ringing programme was carried out, which means starting at 0430hr 1 – 20 September, at 0500hr 21 September – 5 October and at 0530 hr 6 – 20 October (Swedish standard time = Greenwich Mean Time + 1 hour). The ringing lasted at least 6 hours and was thereafter continued as long as more than 10 birds (of all species) were caught every hour. The number of nets used depended on the weather (strong winds or

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Appendix 1. The amount of mist-netting done each month during April to September 1981–1991, shown as units of 100 m netting days used. Japanese nets (4 – shelf, 2.75 m nominal height, 32 mm stretched mesh) were used throughout the study.

	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
April	0	6.5	14.8	14.6	12.2	10.9	21.3	20.5	25.3	22.4	11.7
May	0	10.1	18.3	10.8	13.3	16.1	27.6	21.3	37.3	26.0	19.4
June	0	12.3	15.2	9.9	12.6	17.4	18.5	27.6	26.1	25.9	19.4
July	2.1	13.9	19.9	17.5	16.8	20.0	21.7	32.5	39.6	31.7	27.0
August	17.7	25.7	28.9	31.1	31.5	27.9	36.5	34.8	35.0	48.6	52.6
September	15.6	12.9	17.3	13.1	15.3	23.0	20.3	36.0	25.5	38.1	22.9
Totals	35.4	81.4	114.4	97.0	101.7	115.3	145.9	172.7	188.8	192.7	153.0

Appendix 2. Recaptures in subsequent breeding seasons of Whitethroats initially captured as (a) adults or (b) juveniles. The total of adults captured in 1981 includes four birds also trapped in earlier years; the total for 1982 includes two adults trapped prior to but not in 1981.

Initial captures		*Totals recaptured in later years*									
Year	Total	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
(a) ADULTS											
1981	36	11	6	0	1	0	0	0	0	0	0
1982	79	–	12	1	0	0	0	0	0	0	0
1983	41	–	–	3	2	1	1	1	1	0	0
1984	19	–	–	–	4	2	1	1	0	0	0
1985	26	–	–	–	–	5	3	2	1	0	0
1986	36	–	–	–	–	–	10	3	4	2	0
1987	52	–	–	–	–	–	–	6	5	1	0
1988	40	–	–	–	–	–	–	–	8	0	1
1989	96	–	–	–	–	–	–	–	–	7	2
1990	38	–	–	–	–	–	–	–	–	–	1
1991	28	–	–	–	–	–	–	–	–	–	–
Totals	491	11	18	4	7	8	15	13	19	10	4
(b) JUVENILES											
1981	149	8	5	0	0	0	0	0	0	0	0
1982	341	–	18	2	2	1	0	0	0	0	0
1983	287	–	–	10	3	2	0	0	0	0	0
1984	123	–	–	–	4	1	0	0	1	0	0
1985	190	–	–	–	–	8	8	3	2	2	0
1986	300	–	–	–	–	–	31	11	10	4	1
1987	395	–	–	–	–	–	–	24	11	4	3
1988	242	–	–	–	–	–	–	–	20	7	3
1989	304	–	–	–	–	–	–	–	–	15	2
1990	151	–	–	–	–	–	–	–	–	–	3
1991	108	–	–	–	–	–	–	–	–	–	–
Totals	2590	8	23	12	9	12	39	38	44	32	12

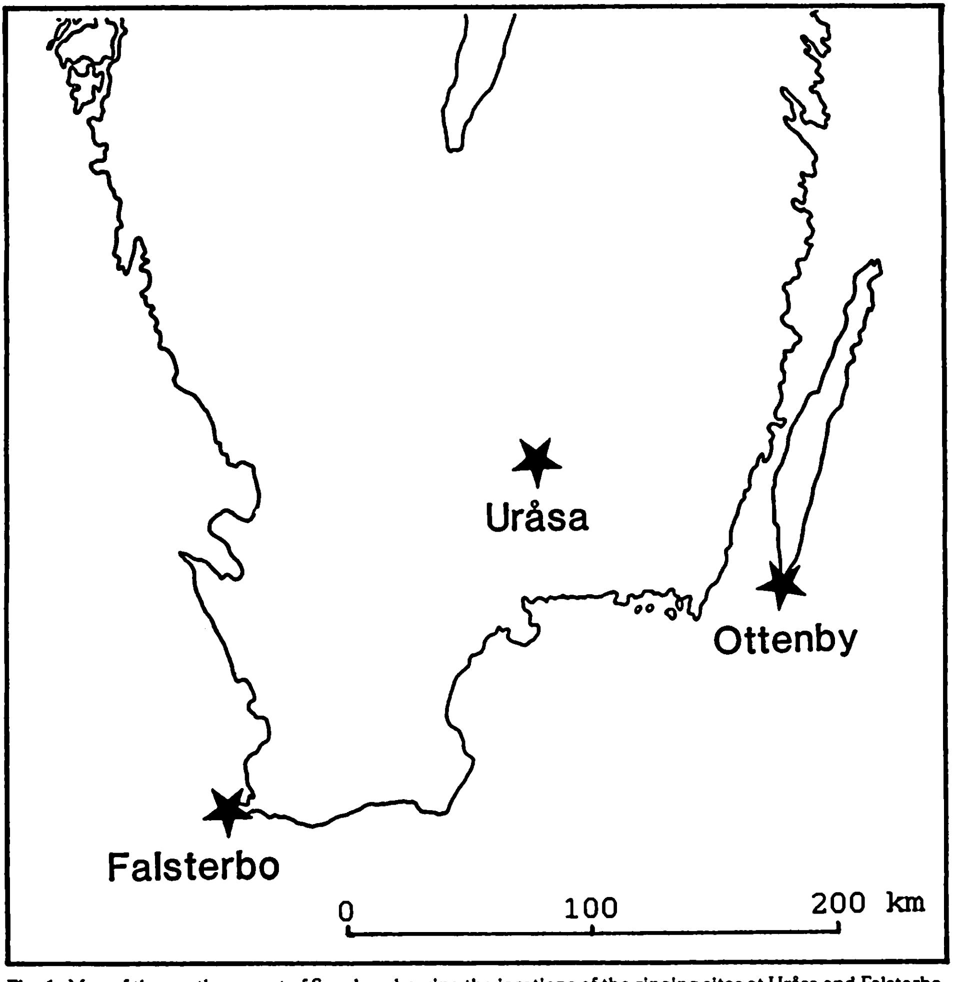

Fig. 1. Map of the southern part of Sweden showing the locations of the ringing sites at Uråsa and Falsterbo. The Ottenby Bird Observatory is also mentioned in the text.

risk of rain reduced the number). The maximum number of nets used was 21 and 18 at Falsterbo and Uråsa, respectively.

The Robins were aged according to Karlsson *et al.* (1986) using the presence of unmoulted greater coverts as the first criterion in 1st year birds. Wing length was measured to the nearest 1 mm according to method 3 (maximum chord, Svensson 1984). Fat deposits were estimated visually following the modified classification proposed by Pettersson & Hasselquist (1985). The birds were weighed to the nearest 0.1g with a 50g Pesola spring balance. Wing measuring and fat classification were calibrated regularly to avoid differences between observers.

The complete moult of the adult birds was classified on the basis of how long the flight feathers had grown, that is, the moult score described by Ginn & Melville (1983). The postnuptial moult of all juveniles was also recorded. Only birds which had finished or almost finished their moult (only sheath–remains left) were included in this analysis, i.e. all birds that were considered to be migrating. For birds recaptured at least one day after the previous capture, fat class, body mass and moult were registered anew.

Robins which were selected for tests in orientation cages were housed indoors with ability to follow the natural photoperiod. They were fed with an unlimited amount of mealworms and water. The orientation experiments were performed in the evening of the same day the Robins were caught. The birds were released immediately after the experiments were finished.

During the orientation experiments the birds were placed in modified Emlen-funnels (Emlen & Emlen 1966), where the birds could see approximately 160 degrees of the sky. The experiments were conducted in open fields and started ten minutes after sunset and lasted for 1 hour. The sloping walls of the funnels were covered with typewriter correction paper, on which the activity of the bird was registered as scratches. The mean orientation of each individual were calculated by using circular statistic methods (Batschelet 1981) based on the number of scratches recorded in each of the 24 sectors. Birds which had produced less than 40 scratches were considered as inactive and excluded from the analysis. To avoid unreliable orientation results a few birds were excluded from the analyses due to disorientation, based on a predetermined level of P=0.05 according to the Rayleigh test (Batschelet 1981). When comparing the orientation at the two sites the mean direction of the samples was calculated. The Rayleigh test was used to determine whether the mean direction of the sample differed from random. Mardia's one-way classification test was used to test the difference in scatter or mean orientation between samples (Mardia 1972).

The orientation tests at Falsterbo used in this analysis include birds tested during the study period in both 1989 and 1990, while orientation tests at Uråsa were performed in 1990 and 1991.

RESULTS

Age distribution

The proportion of adults captured at Falsterbo in autumn 1990 was 15% (n=2217), whereas at Uråsa it was 20% (n=201), a significant difference (χ^2_1=4.31, P<0.05). Among Robins caught at Uråsa between 1 and 25 September, 27% were adults, while between 26 September and 20 October the proportion of adults dropped to 11%. At Falsterbo the corresponding numbers were 9% and 20%, respectively.

Seasonal distribution

At Uråsa the peak of migrating Robins occured significantly earlier than at Falsterbo by approximately 10 days (Fig. 2). The difference in seasonal distribution between the two sites

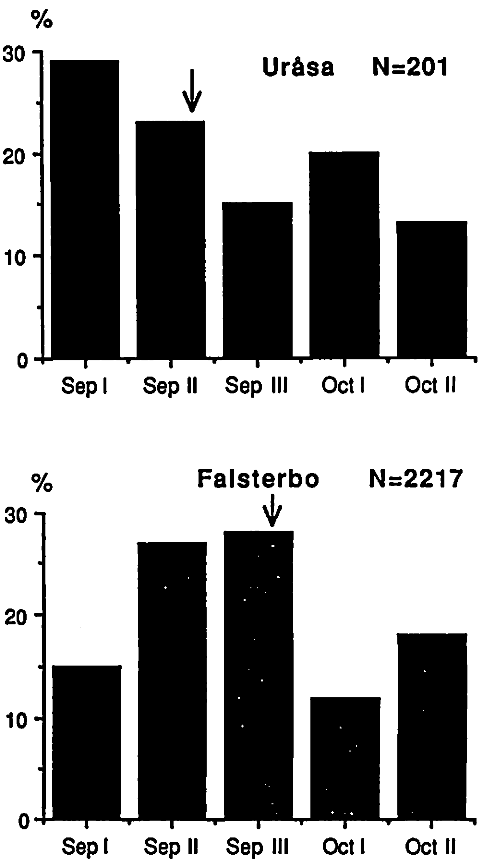

Fig. 2. Robins captured (percentage on ten-day periods) at Uråsa and Falsterbo 1 September – 20 October 1990. The arrows indicate median dates.

was significant (χ^2_4=50.4, P<0.001). Median dates were 18 September at Uråsa and 27 September at Falsterbo and this difference was significant (Median test, χ^2_1=16.42, P<0.001).

Daily distribution

The daily distribution of captured birds differed significantly between the two sites (Fig. 3, χ^2_5=23.0, P<0.001). At Uråsa there was a peak, although not very marked, during the first hour and then the Robins continued to

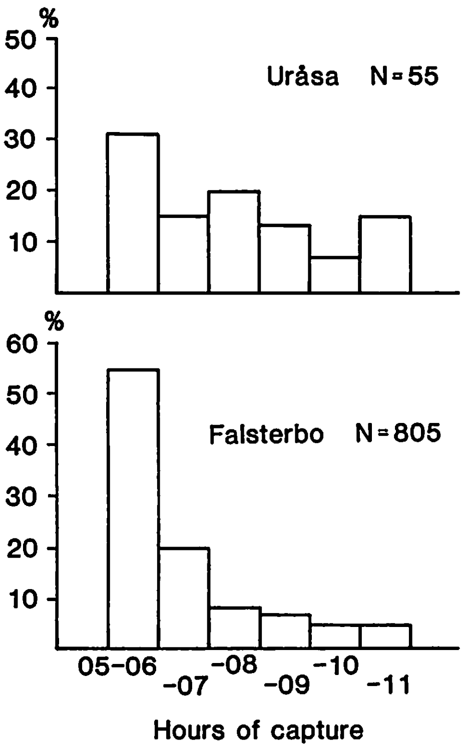

Fig. 3. Daily captures of Robins at Uråsa and Falsterbo (percentage on hours) 21 September – 5 October. This period was selected because the trapping efforts started on the stroke of an hour (0500 hrs). Only the six standard hours are included.

pass through the area all morning. At Falsterbo there was a conspicuous first hour peak when 55% of the daily total were caught.

Biometry

The mean wing length was very similar at the two sites (Falsterbo $\bar{x}$=73.2, s=1.87, n=1134; Uråsa $\bar{x}$=73.6, s=1.91, n=201). The difference was not statistically significant (z=1.26). Thus on average the birds were of the same size at the two sites.

The average level of visually estimated fat deposits at Falsterbo was 2.5 and at Uråsa 2.2 (Table 1). The fat class distributions differed significantly between the two sites when fat class 0 and 1 and also 5 and 6 were pooled in order to obtain equivalent groups (χ^2_4=37.3, P<0.001). The fat deposits of the birds at Uråsa increased during the season, but at Falsterbo the fat deposits were more constant over time (Fig. 4a). The mean body mass showed similar trends (Fig. 4b).

When fat deposits and body mass were compared a significant difference between the two sites was observed (Table 2, Fig. 5).

Birds caught at Uråsa retained a higher body mass level in each fat class compared to Falsterbo.

Recaptures

At Uråsa the mean period between first capture and last recapture was 5.9 days. There was a tendency for Robins to deposit more fat the longer they stayed and the later in the season it was (Table 3). At Falsterbo the mean first capture – last recapture interval was 2.4 days. Even if birds stayed for longer periods they did not increase their fat deposits. Most of the birds stayed less than 5 days and decreased in fat deposits and body mass (Table 3). The difference in time distribution of recaptures between Uråsa and Falsterbo was statistically significant when comparing the number of birds recaptured within and after 5 days,

Table 1. Fat class distribution and mean body mass in Robins captured at a coastal site (Falsterbo) and an inland site (Uråsa) respectively 1 September – 20 October 1990.

Site	*n*	*Fat class*								*Mean body mass*	*s*
		0	1	2	3	4	5	6	x̄	(g)	
Falsterbo	1016	90	121	254	348	130	70	3	2.5	15.47	1.02
Uråsa	201	10	68	53	40	16	9	5	2.2	16.33	1.03

Table 2. Significance levels for differences in mean body mass/fat class (two-tailed t-test) in Robins captured at Falsterbo and Uråsa. Samples shown in Table 1.

Fat class	*t*	*df*	*P*
0	3.78	98	<0.001
1	9.96	187	<0.001
2	11.14	305	<0.001
3	5.29	386	<0.001
4	4.48	144	<0.001
5	3.57	77	<0.001

respectively (χ^2_1=12.2, P<0.001). When considering body mass changes there was a significantly higher proportion of birds decreasing in body mass at Falsterbo (out of 59 recaptured Robins, 42 were losing and 15 were gaining body mass) than at Uråsa (out of 37 recaptured Robins, 18 were losing and 18 were gaining body mass, χ^2_1=5.41, P<0.05).

Orientation

The orientation tests (Fig. 6) showed differences in the behaviour of the birds at the two sites and there was also a difference between the birds orientation due to cloud cover. At Uråsa the Robins oriented on average in a westerly direction (the mean vector, α=276°, r=0.47, n=30, P<0.002) under clear skies (less than 4/8 of the sky covered with clouds). Under total overcast (more than 7/8 of the sky covered with clouds) the mean direction was SSW but not significant (α=201°, r=0.33, n=25, P=0.06). Under clear skies the mean direction was not significantly different from the mean direction of sunset (difference = 4°, 95% confidence interval = +30°, Batschelet 1981).

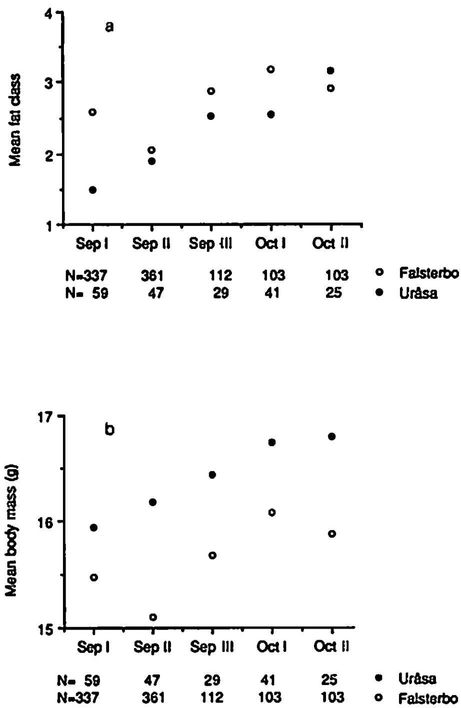

Fig. 4. (a) Mean fat level per ten-day period in Robins at Uråsa (•) and Falsterbo (o) 1 September – 20 October 1990. Sample sizes shown below. (b) Mean body mass per ten-day period in Robins at Uråsa (•) and Falsterbo (o) 1 September – 20 October 1990. Sample sizes shown below.

At Falsterbo the mean orientation of the Robins under clear skies was WSW (α=253°, r=0.75, n=57, P<0.001). Under total overcast conditions the birds did not show a significant

Table 3. Changes of fat level and body mass in recaptured Robins at Uråsa and Falsterbo. The mean change of fat and body mass is indicated for the three different groups of Robins: recaptured 1–5 days, 6–10 days and more than 10 days after first capture.

Site	*1–5 days*			*6–10 days*			*>10 days*		
	Fat	Body mass	*n*	Fat	Body mass	*n*	Fat	Body mass	*n*
Uråsa									
1–20.9	0	–0.3	8	+0.8	–0.1	6	+1.3	–0.6	4
21.9–20.10	+0.5	+0.2	13	+1.5	+0.2	4	+2.5	+0.4	2
Falsterbo									
1–20.9	–0.3	–0.3	42	+1.3	+0.6	3			
21.9–20.10	–0.8	–0.6	10	–0.7	+0.2	3			

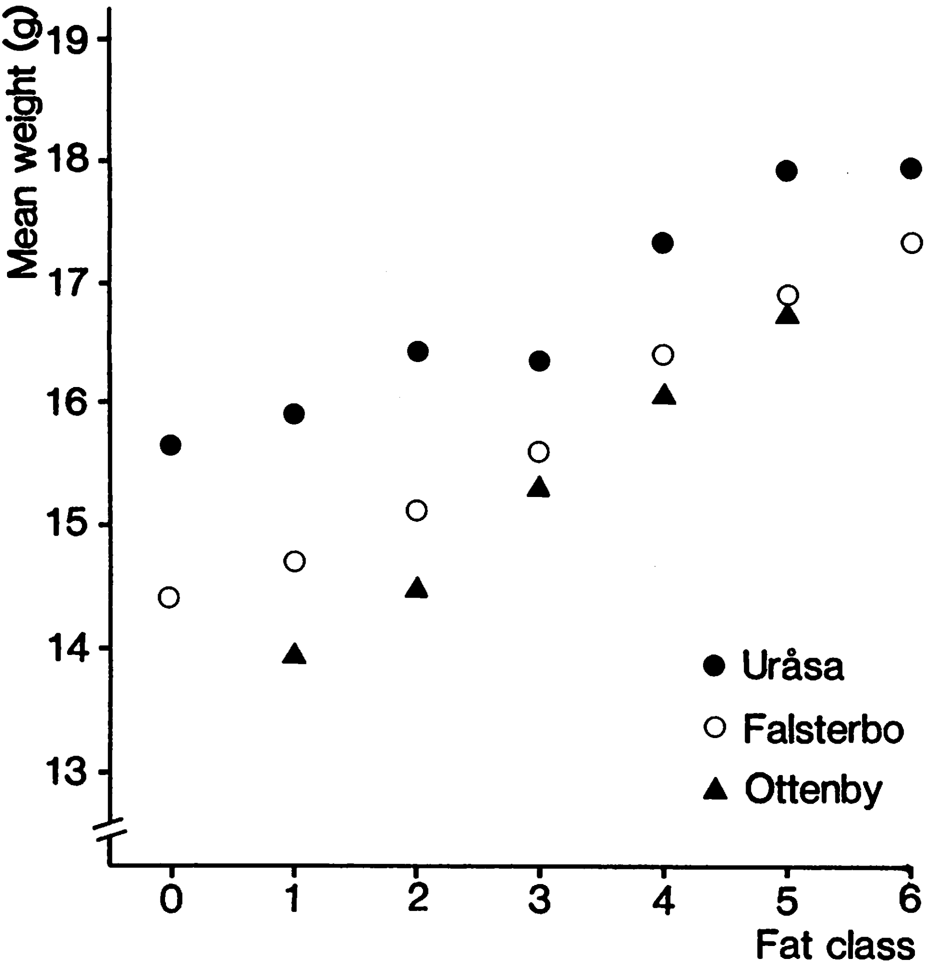

Fig. 5. Mean body–mass in each fat class in Robins captured at three ringing sites in southern Sweden in autumn 1990: Uråsa (dots), Falsterbo (circles) and (for comparison) Ottenby (triangels).

mean orientation but there was a tendency of a NE–SW axis. The mean direction under clear skies was significantly different from the direction of sunset (difference=21°, 95% confidence interval = ±12°, Batschelet 1981).

There was no statistically significant difference between the mean directions under clear skies at Uråsa and Falsterbo (Mardia's one–way classification test).

DISCUSSION

Age distribution and timing

Many bird observatories are, because of high concentrations of migrating birds, placed along coasts or at islands and peninsulas. A biased age ratio is apparent at these places, where not more than 9 to 15% are adult birds (Mehlum 1981, Ralph 1981, Pettersson 1983). In contrast, Dunn & Nol (1980) found that at an

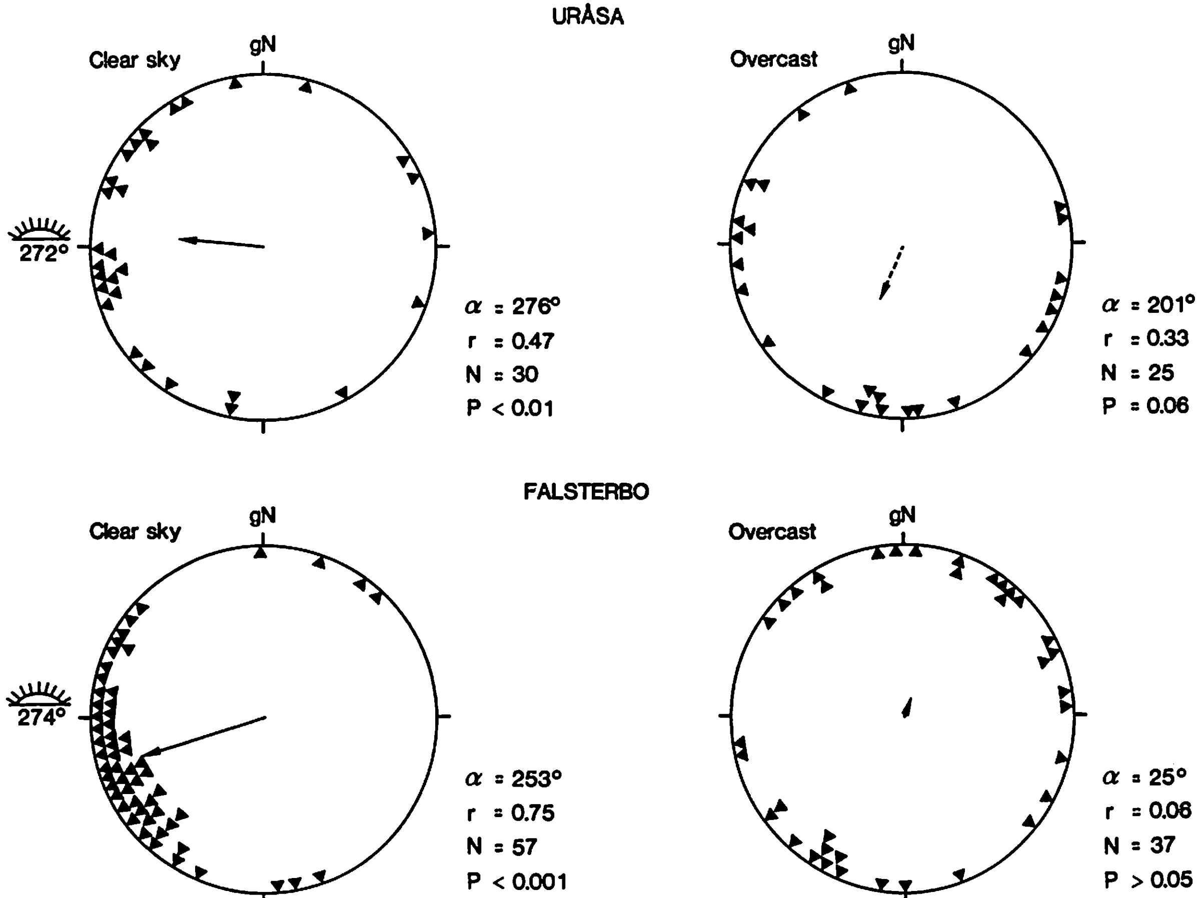

Fig. 6. Autumn orientation of Robins under clear skies and total overcast at Uråsa and Falsterbo. The mean azimuth of the sun 40 min. after sunset (i.e. in the middle of the test hour) is indicated (clear skies). Each symbol represents the mean direction of one individual bird. The mean vector (α) of the sample is represented by an arrow. The length of the arrow (r) is drawn relative to the radius of the circle = 1 (the length of the arrow is proportional to the mean vector length, r). Significance levels are according to the Rayleigh test.

inland site or at illuminated installations, 24% of the examined birds (mostly warblers) were adults.

The results of our study show a higher proportion of adult Robins at the inland site during the autumn migration. The proportion of 20% is close to the 25–30% expected for a stable Robin population (Lack 1965). It appears that adult and juvenile Robins use different migration strategies. Both age groups pass coastal points during migration, but most adult and experienced birds avoid stopping there.

The observed difference in the seasonal distribution with the peak of migration occurring nine days earlier at Uråsa than at Falsterbo may indicate a very slow overall migration speed, about 22km per day. The Robins migrate either in very short stages or rest for several days between migration flights. Hildén & Saurola (1982) calculated a mean autumn migration speed of 60 km/day for Finnish Robins on the basis of ringing recoveries. With this speed it would only take 3–4 days to reach Falsterbo from Uråsa.

The daily distribution of captured Robins was more evenly spread at Uråsa than at Falsterbo. This may be due to a steady passage of birds, i.e. continued daytime migration through the forested inland areas (cf. Gauthreaux 1978). At Falsterbo the peak at dawn is a "fall" of Robins, which are confronted with a migration barrier (the Baltic Sea). Most Robins move away from the ringing site within two or three hours after dawn, and after that only few new ones arrive.

Fat – body mass relationships

Robins captured at Uråsa increased their visual fat deposits and their body mass during the season, while the Robins captured at Falsterbo showed a more constant level. The level of fat deposits was higher at Falsterbo than at Uråsa during September while it was the other way around in mid–October (Fig. 4a).

At Uråsa the Robins were on average heavier in each fat class than at Falsterbo (Fig.5). When Robins from Falsterbo and Ottenby were compared (Karlsson *et al.* 1988) Robins from Falsterbo were heavier in each fat class. The differences between Uråsa and Falsterbo were greater than between Falsterbo and Ottenby.

These findings are well in accordance with the theories of different migration strategies in Robins captured at Ottenby and Falsterbo Bird Observatories presented by Karlsson *et al.* (1988). Their explanation was that birds migrating over open sea need extensive fat reserves for a longer flight, i.e. they have adapted a long–stage migration strategy. The majority of the Robins at Ottenby belong to this category. On the other hand, birds migrating over land do not need the same amount of fat because of the possibility of resting along the route (short–stage migration strategy). At Falsterbo most of the Robins belong to this category, especially during September. The Robins at Uråsa should accordingly be short–stage migrants (less fat than Ottenby and Falsterbo Robins) at least during September. The change to fatter birds in October can then be interpreted as if the birds were changing migration strategy towards the end of the migration period. This was also supported by the recaptured birds, which increased their fat deposits especially in the late part of the season (Table 3).

A comparison of the body contents of migrating Robins from Ottenby and Falsterbo (Åkesson *et al.* 1992) showed that birds of the same visual fat class and wing length had relatively more fat at Falsterbo than at Ottenby, but this was not the major reason for the difference in body mass. When comparing lean Robins they had reduced their fat–free body mass and the flight muscle mass at Ottenby but not at Falsterbo. The water content did not differ between the two sites. Åkesson *et al.* suggest that these findings may be related to the different migration strategies used: mainly long–stage migrants at Ottenby, mainly short–stage migrants at Falsterbo. Unfortunately we have no data on body contents of the Robins captured at Uråsa, but the suggestion that Uråsa Robins mainly are short–stage migrants is supported by the differences in fat–body mass relationships as shown in Fig.5.

Orientation

The orientation of Robins at Uråsa (clear skies) showed a westerly mean direction which was not different from the direction of the sunset. At Falsterbo (clear skies) the mean direction was west–southwest, i.e. more corresponding to the normal migratory direction and the mean angle of orientation was significantly different from the sunset azimuth.

Earlier orientation experiments with Robins at Falsterbo during autumn migration showed a westerly or northwesterly mean direction (Sandberg *et al.* 1988). Sandberg suggests that the reasons behind this behaviour could be either escape responses (birds trying to escape from the orientation cages towards the brightest part of the sky), or a response to get a clear view of the sunset (birds may need to actually see the direction of the sunset to assess a appropriate migratory direction). Furthermore, this orientation may be related to a weak motivation to migrate or it may be associated with reorientation to more suitable resting grounds.

The relevance of these suggestions is not fully known, but Sandberg (1991) found experimental evidence for the importance of visual cues in the lower part of the sky for the orientation of Robins. However, priorities among orientation cues may differ depending on the migratory situation encountered.

This may explain the differences between the results of the tests at Uråsa and Falsterbo under clear skies, and also the very scattered orientation under total overcast at both sites.

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