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Differences in fat deposits and wing pointedness between male and female Willow Warblers caught on spring migration at Ottenby, SE Sweden*

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Four major groups of Willow Warblers are distinguishable during spring migration at Ottenby, SE Sweden. South Scandinavian males (sm) and females (sf), North Scandinavian males (nm) and females (nf). Sm carry relatively more fat than both sf and nm, and nf carry more fat than sf and nm. Males have more pointed wings, but no wing shape difference was found between northern and southern populations. Morning trapping times differed between the sexes (males being caught earlier than females), in accordance with morphometric flight theory.

In this short contribution we present data on fat deposits in the Willow Warbler *Phylloscopus trochilus* during spring migration at Ottenby, SE Sweden. We also

describe wing-shape differences between the sexes and stress the importance of migration as a selective agent acting on morphological characters. In migrating birds the males generally return to the breeding area before the females, and birds from northern populations normally migrate later in spring than their southern conspecifics, thus passing the latter on their way northwards (e.g. Schüz 1971). The principal passage of males and females of different populations of the Willow Warbler at Ottenby is shown in Fig. 1, together with the populations' presumed breeding areas.

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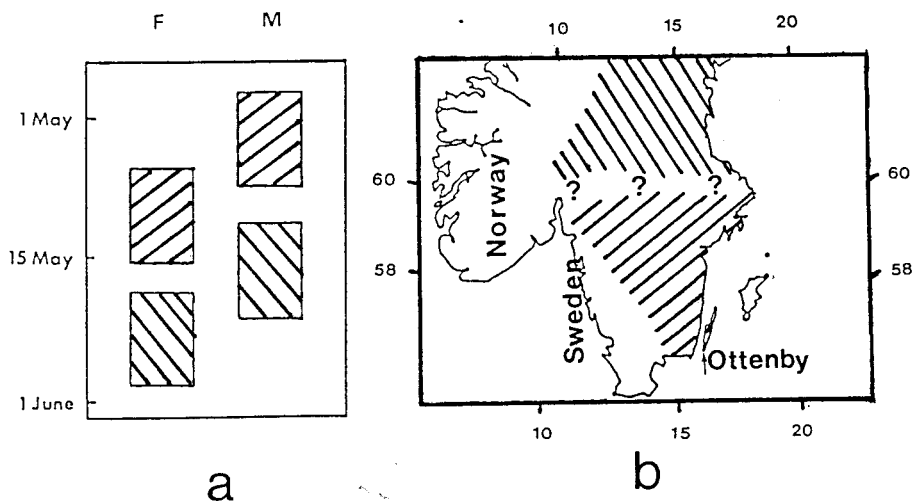


Fig. 1. (a) The principal passage, by sex, of southern and northern populations of Willow Warblers at Ottenby. The groups were identified on the basis of wing lengths (males 70–71 mm, females 64–65 mm, e.g. Tiainen 1982) (see Hedenström and Pettersson 1984). F = females, M = males. (b) Presumed breeding areas of birds of southern and northern populations caught at Ottenby. The ranges are approximate and indicate the birds' destinations in relation to the study site.

Material and methods

The data were collected within the standardized ringing scheme at Ottenby Bird Observatory (56°12'N, 16°24'E) in the springs of 1982–84. The field work at Ottenby starts on 15 March each year, about a month before the earliest Willow Warblers arrive (for details about ringing routines see Hjort et al. 1981). Wing length (method 3, Svensson 1975) was used to separate the sexes (Niemeyer 1969, Tiainen 1982). The wing lengths used were 64–65 mm for females and 70–71 mm for males. The amount of fat was classified on a seven-grade scale for each bird by a visual method modified from Busse and Kania (1970, cf. Pettersson and Hasselquist 1985). Weights were taken to the nearest 0.1 g using a 50 g Pesola spring balance. Linear regressions between weight and fat classes were calculated to estimate the mean fat-free live weight (corresponding to fat class 1). According to our method, birds in fat class 6, i.e. those with filled fat deposits, had on average 20.5% fat (of live weight; $n = 20$), and an average weight of 9.9 g. This is similar to birds classified as 'very heavy' at the Kurische Nehrung (55°12'N, 20°42'E); these weighed 22% more than lean birds (Dolnik and Blyumental 1967). Birds trapped prior to their crossing of the Sahara in autumn have weights similar to Ottenby birds in fat class 6 (cf. Moreau 1969, Finlayson 1981). We also calculated the potential flight ranges according to Pennycuik's (1975) method no. 1 (for passerines). For each group we entered mean fuel ratio (= fat index) and mean weight.

To evaluate the degree of wing pointedness, the distance from the tip of primaries 5 and 9, respectively, to the wing-tip was measured to the nearest 0.5 mm, giving two different indices, I_5 and I_9 (Fig. 2). In long distance migrants the 9th primary (descendantly) will be longer, the 5th primary shorter relative to the wing-tip, resulting in a more pointed wing than in short distance migrants (Kipp 1958, 1959).

In order to look for possible differences in flight

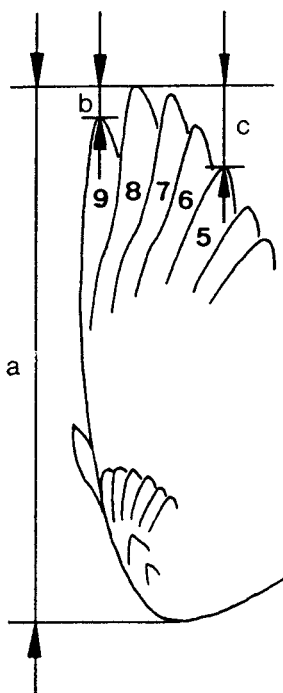


Fig. 2. Measurements used for calculating wing indices I_5 and I_9 . The primaries are numbered in descending sequence. $I_5 = (a-c)/a$; $I_9 = (a-b)/a$.

velocity between the sexes, capturing times for birds of different wing length were compared. Assuming that the birds take off from the southern coast of the Baltic Sea they have to cover at least 200 km before reaching Ottenby. With a flight speed of 30 km h⁻¹ (Tucker 1975) and neutral winds they will arrive at Ottenby during the morning hours if they start migrating after dusk on the preceding day.

Results

Tab. 1 gives fat-index data together with mean weights and potential flight ranges for four different groups of Willow Warblers in three years. As seen from Tab. 2 the between-group relations were the same in all three

Tab. 1: Fuel ratio, weight and potential flight range for different groups of Willow Warblers at Ottenby in 1982–84. The range calculations refer to Pennycuik's (1975) method No. 1. Mean fuel ratio (= fat index, fraction of the total body weight being consumed) and mean weight for each group were entered in the equation.

	Sampling period	n	Fuel ratio	S.D.	Mean weight (g)	S.D.	Flight range (km)
1982							
males	28 Apr– 7 May	126	0.1164	0.055	9.53	0.59	522
	13 May–22 May	85	0.0828	0.057	9.64	0.60	364
females	8 May–17 May	167	0.0986	0.055	8.31	0.52	437
	20 May–29 May	370	0.1049	0.065	8.38	0.60	467
1983							
males	26 Apr– 5 May	172	0.1020	0.058	9.13	0.58	453
	11 May–20 May	38	0.0835	0.060	9.59	0.64	367
females	7 May–16 May	210	0.0974	0.059	8.21	0.52	432
	22 May–31 May	136	0.1295	0.068	8.48	0.64	586
1984							
males	1 Apr–10 May	151	0.1400	0.064	9.32	0.68	638
	13 May–22 May	53	0.0963	0.070	9.43	0.71	427
females	6 May–15 May	167	0.0973	0.055	8.09	0.50	431
	18 May–27 May	116	0.1069	0.060	8.30	0.56	477

years, although the differences were not always statistically significant (8 out of 12 were). Males arriving early in spring had more fat than early arriving females. For late passing birds the situation was reversed, i.e. the females had the heaviest fat loads. Late passing females also had more fat than early females.

Wing-index I_s was less for males than for females in all three years (Tab. 3, $p < 0.001$, one-tailed Kolmogorov-Smirnov Two-sample Test, Siegel 1956). Hence,

the male Willow Warblers had a more pointed wing, in agreement with Kipp's (1958, 1959) principles. The other index, I_b was greater in males than in females in all three years (Tab. 3, $p < 0.05$, 0.01, and 0.001, respectively). Within the sexes, inter-populational variation in indices I_s and I_b were small and insignificant ($p > 0.05$). Tainen and Hanski (1985) recently reported wing-shape indices in accordance with our results.

On 40 days out of 58 in 1980–84 when five or more birds of each sex were caught, males were, on average, caught earlier in the day than were females. The difference was statistically significant ($p < 0.003$, one-tailed Binomial Test, Siegel 1956). The mean difference in capturing time between the sexes was 15 ± 6 (SE) min and the median difference 12 min.

Tab. 2: Fat index relations between different groups of Willow Warblers (data extracted from Tab. 1). Significance levels refer to pairwise Mann-Whitney U-tests (Siegel 1956). σ_1 = early passing males, σ_2 = late passing males, φ_1 = early passing females, φ_2 = late passing females. Significance levels: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, ns = not significant.

1982	$\sigma_1 > \sigma_2$ ***	$\sigma_1 > \varphi_1$ **	$\varphi_2 > \sigma_2$ **	$\varphi_2 > \varphi_1$ *
1983	$\sigma_1 > \sigma_2$ ns	$\sigma_1 > \varphi_1$ ns	$\varphi_2 > \sigma_2$ ***	$\varphi_2 > \varphi_1$ ***
1984	$\sigma_1 > \sigma_2$ ***	$\sigma_1 > \varphi_1$ ***	$\varphi_2 > \sigma_2$ ns	$\varphi_2 > \varphi_1$ ns

Tab. 3. Wing indices (I_s and I_b) for male and female Willow Warblers at Ottenby in 1982–84. Differences tested with one-tailed Kolmogorov-Smirnov two-sample test (Siegel 1956). Significance levels as in Tab. 2.

		I_s	I_b	n
1982	males	89.11	92.42	160
	females	89.60***	92.14*	174
1983	males	89.70	91.73	205
	females	90.22***	91.31**	186
1984	males	89.36	91.93	221
	females	89.74***	91.30***	120

Discussion

A study using only one sampling spot may be biased in various ways. For instance, the populations involved may have distances of different length before they reach their respective breeding grounds after having passed Ottenby, and their previous migration may have taken place along different routes (Hedenström and Pettersson 1984). With this in mind we will present some possible interpretations of the fat-level results. The early males' relatively large fat deposits may serve as an energy reserve while food is still scarce and demands are great. Maximum activity seems to be connected with singing and territorial fighting just after arrival (Slagsvold 1977). In the northern population, the females had larger fat deposits than the males in spite of their later arrival (when invertebrate food normally is more abundant). The period between arrival and onset of breeding is short in the north, so the females may need large re-

serves immediately upon their arrival. In the Pied Flycatcher *Ficedula hypoleuca*, females of a North Finnish population arrived with 14% fat that was depleted during the nest-building and incubation phases (Ojanen 1984). Other explanations of the differences in the size of the fat deposits are also possible. As pointed out to us by T. Alerstam, the fat level is high in the first group of birds (early males), then decreases in mid-May (early females and late males) and finally increases again (late females). The decrease in fat level in mid-May coincides with peak migration, and may reflect competition at resting sites. Still another possibility is that variations in food abundance during the migration period might account for the variations in fat levels.

The difference in wing shape between the sexes may have evolved because of selection for fast migration in the males; to arrive early is probably more important to males than to females as the males have to occupy a favorable territory to attract a mate. Hence, we think that the longer and more pointed wing in males has evolved through intra-sexual competition. An equally pointed wing may not be so useful for the females, that do most of the nest building and feeding of the young (Järvi 1983, Arvidson 1984) and therefore must move more efficiently through dense vegetation (cf. Lederer 1984).

That males on migration fly faster than females is supported by the observed differences in capturing time at Ottenby (mean 15 min). Assuming a preceding flight of 200 km before arrival at Ottenby and applying the formula for flight speed of Tucker (1975), we calculated theoretical flight times for birds with wing-spans and weights typical of the two sexes (wing-span: 0.185 m for males and 0.175 m for females; weight: 9.4 g for males and 8.3 g for females; means of male and female groups in Tab. 1). We found a difference in flight time of 10 min between the sexes. Thus, a theoretical approximation and observations in the field yield results of the same order of magnitude. This supports the flight velocity hypothesis on the assumption that the birds arrive directly from the southern coast of the Baltic Sea.

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