

## **Timing of spring migration, body condition, and fat score in local and passage populations of the Reed Warbler *Acrocephalus scirpaceus* on the Courish Spit**

Nikita Chernetsov

*Abstract:* Chernetsov, N. (1999): Timing of spring migration, body condition, and fat score in local and passage populations of the Reed Warbler *Acrocephalus scirpaceus* on the Courish Spit. *Avian Ecol. Behav.* 2:75-88.

I studied the timing of spring arrival of a local breeding population of Reed Warblers, along with body condition of arriving birds. In contrast to similar studies of Willow Warblers, the bulk of Reed Warblers arrived at their breeding grounds lean. However, some variation occurred between birds and also within the same individual in different years. This variation concerned both timing of arrival and body condition of arriving birds. It is suggested that the tendency towards year-to-year stability in the timing of arrival is affected, sometimes significantly, by environmental factors. I also suggest that Reed Warblers are usually able to locate the goal of their migration exactly, without spending much time searching for their breeding site.

*Key words:* Reed Warbler, spring migration, arrival, timing of arrival, body condition.

*Address:* Zoological Institute, Russ. Acad. Sci., Biological Station "Rybachy", Rybachy, Kaliningrad Reg., 238535, Russia. E-mail: nikita@scl356.spb.edu

### **1. Introduction**

Due to the difficulties of controlling individual birds, few studies discussing the timing of spring arrival along with factors such as body weight, fat score and gonadal development are available (Lapshin 1978, Sandberg 1996, Fransson & Jakobsson 1998, Potti 1998). Most instructive are those studies that present the data on arrival together with the pattern of transit migration and the physiological condition of arriving and passage birds.

Another important problem is how migrants finish their spring passage, i.e. how they locate the site of previous breeding attempts (adults) or natal areas (second-year birds) in spring (Sokolov 1997). According to recent thinking, migrants find their goal by moving in the system of polar co-ordinates (Wiltschko & Wiltschko 1978, 1998). According to this concept, navigation is very accurate, birds finding their goal without using local landmarks. Studies on the Courish Spit have shown that Pied Flycatchers know their migration goal to within approx. 1 km. They are able to find it easily in spring and usually do not halt near nest-boxes to the SW of their breeding/natal areas (Sokolov & Vysotsky 1990).

There are several reports concerning the consistency of individual timing and routes of spring migration in many passerines, incl. the Reed Warbler (Payevsky 1962, 1972). These reports are based on recaptures of marked individuals at the same site in different years. Some part of these data may refer to individuals arriving at their breeding sites.

Reaching the goal of migration involves termination of migration and migratory disposition. First spring captures of marked (breeding) individuals allow us to record their condition at the moment of completing migration. Higher body weight and fat score are indicators of migratory disposition that may be measured in the field (Biyumenthal 1971, Dolnik 1975).

Recent data show that some long-distance migrants arrive at their breeding grounds with considerable fuel reserves that are comparable with the reserves of conspecifics on migration (Sandberg 1996, Fransson & Jakobsson 1998). The existence of such a "safety margin" can be explained by unpredictable and often adverse weather in the breeding range at the moment of arrival. Insectivorous, long-distance migrants need fuel stores that would allow them to survive during a possible cold spell. Males may also utilise fat for development of the gonads (Fransson & Jakobsson 1998).

In this paper I discuss the timing of spring arrival of Reed Warblers *Acrocephalus scirpaceus* belonging to the breeding population of the Courish Spit and their body condition and fat stores at arrival. The hypothesis of a safety margin in arriving Reed Warblers is tested by comparing their condition with that of passage migrants.

## 2. Material and methods

I analysed the data from Rybachy (Courish Spit of the Baltic Sea) trapping station for the years 1992-1997. From 1993, the breeding population of the area was under constant control, involving regular nest searches and the trapping and ringing breeding birds and nestlings. The area is a mixture of willow *Salix* spp. scrub and reedbed *Phragmites australis* on the shore of Courish Lagoon. The bulk of the local Reed Warbler population bred in the trapping area or nearby. The nearest site with several nests was Lake Chaika (Mowenbruch) 1.5 km from the study site; the nearest site where Reed Warbler bred in numbers were reedbeds 20 km to the SW of Rybachy. Due to growing scrub which is gradually replacing reed, the breeding population is declining.

In this study the following birds were treated as locals:

- 1) that were ringed as breeding at the study site in previous years;
- 2) that were ringed at the study site as pulli or fledglings in previous years before the onset of autumn migration;
- 3) that were initially ringed in spring but subsequently retrapped at this site 20 or more days after ringing (incl. those retrapped in subsequent years).

Some individuals were repeatedly controlled over several years. A large number of nets (total length 511 m) distributed over a significant area gave a high probability of capturing arriving birds. If Reed Warblers are able to learn to avoid nets, this probably happens after the first capture of the season. In this paper I consider birds trapped before June 10 as arriving, though some Reed Warblers may arrive later. On July 1, 1998, a Reed Warbler without incubation patch or cloacal protuberance was trapped. It weighed 14.6 g and had fat score 6 on the 9-grade Kaiser (1993) scale. When tested in an Emien funnel this bird displayed nocturnal restlessness and NE orientation of activity, corresponding to the expected spring migratory direction. It was probably still in spring migratory state.

All local birds (as defined above) trapped before June 10 were included in the analysis of arrival pattern, apart from 13 females first-captured already with incubation patches. In the analysis of body mass only those captured before June 1 were included. I believe that from early June the probability of a time interval between arrival and first capture may arise. To be on the safe side, these birds were excluded from the analysis of body condition.

Ringing routine followed the protocols of the ESF project (Bairlein et al. 1995). Fat was scored after Kaiser (1993). Birds were sexed according to the presence of incubation patch or cloacal protuberance during the breeding period, i.e. not at the first capture in spring.

When comparing the body condition of birds from different samples, often differing in wing chord, body mass was corrected for size. I calculated the relationship between wing chord and body mass in lean Reed Warblers. This was done to minimize the impact of fat stores on this relationship. On the Courish Spit mass depends on the wing length according to the following allometric equation:

$$\text{mass} = 1.06 * \text{wing}^{0.565}$$

Thus, when comparing condition of birds from different samples the value of mass was divided by  $\text{wing}^{0.565}$ .

## 3. Results

### 3.1. The pattern of arrival of local birds and of transit passage

The time elapsed between the capture of the season's first Reed Warbler and the capture of the first definitely local individual varied from 0 to 13 days; in 1993 the year's first Reed Warbler was a local bird (Tab. 1). During this period the number of Reed Warblers caught was very low (Fig. 1). Before the first wave of passage in the respective year (Tab. 1) a total of 26 birds was trapped (14%).

No significant difference was found between patterns of passage in transit migrants and the arrival of local birds (Fig. 1, Kolmogorov-Smirnov test,  $\lambda = 1.12$ ;  $p > 0.05$ ). Annual patterns of arrival and of passage also show that local birds usually arrived in the same period as when northern populations (migrants) passed through, at least before June 1 (Fig. 2).

I calculated proportions of local birds first-trapped during the waves of passage (high and rising

numbers of stopover migrants) and during inter-wave arrivals (low and declining numbers). In 1992-1995 respectively 88%, 86%, 71% and 89% of local birds were trapped during the waves of passage. However, in 1996 and 1997, 91% and 53% of local Reed Warblers were first-trapped during the inter-wave periods. Local birds probably do not always arrive with the main flow of migrants. They may also arrive during the periods when transit passage is weak.

Table 1. Time of arrival of local breeders and passage of northern birds.

Year	Date of the first capture	Date of the first capture of a local bird	Date of the first wave of passage
1992	-	-	12/5
1993	28/4	28/4	14/5
1994	4/5	7/5	17/5
1995	28/4	11/5	17/5
1996	24/4	7/5	21/5
1997	2/5	6/5	15/5

Note: In 1992 the trapping session commenced after the arrival of the first Reed Warbler, but before the first wave of passage.

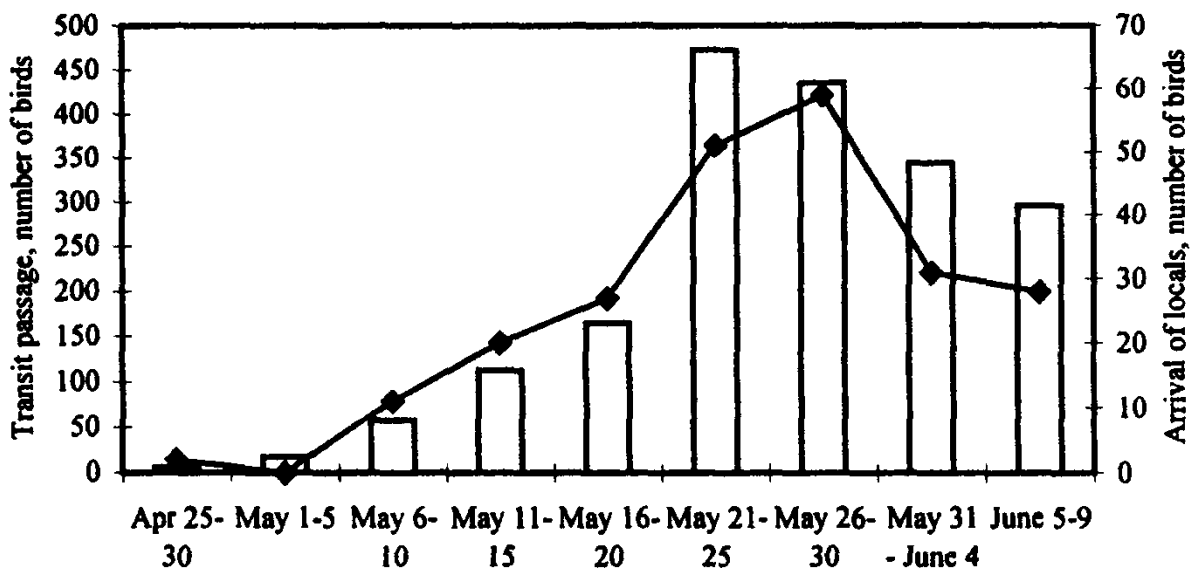


Figure 1. Patterns of transit passage (bars) and of arrival (line).

### 3.2. Sex-related timing of arrival

Sex-related difference in the timing of arrival was found to be on the edge of statistical significance (Fig. 3, Kolmogorov-Smirnov test,  $\lambda = 1.36$ ;  $p = 0.05$ ). In spite of earlier arrival of first males, median arrival dates of males (May 25) and females (May 26) were very close. Over the whole study period the earliest female was captured on May 7 (in 1992). However, local females did not occur in any numbers until the third 10-day period of May, together with the onset of intensive passage of migrants (Fig. 1, 2). This same pattern where local females generally arrive together (later) at the peak of migration has also been recorded for other species, e.g. in the Chaffinch *Fringilla coelebs* on the Courish Spit (Payevsky 1967) and in the Willow Warbler in NW Russia (Lapshin et al. 1981).

Figure 2. Patterns of spring arrival of locals (bars) and passage of northern populations (line).

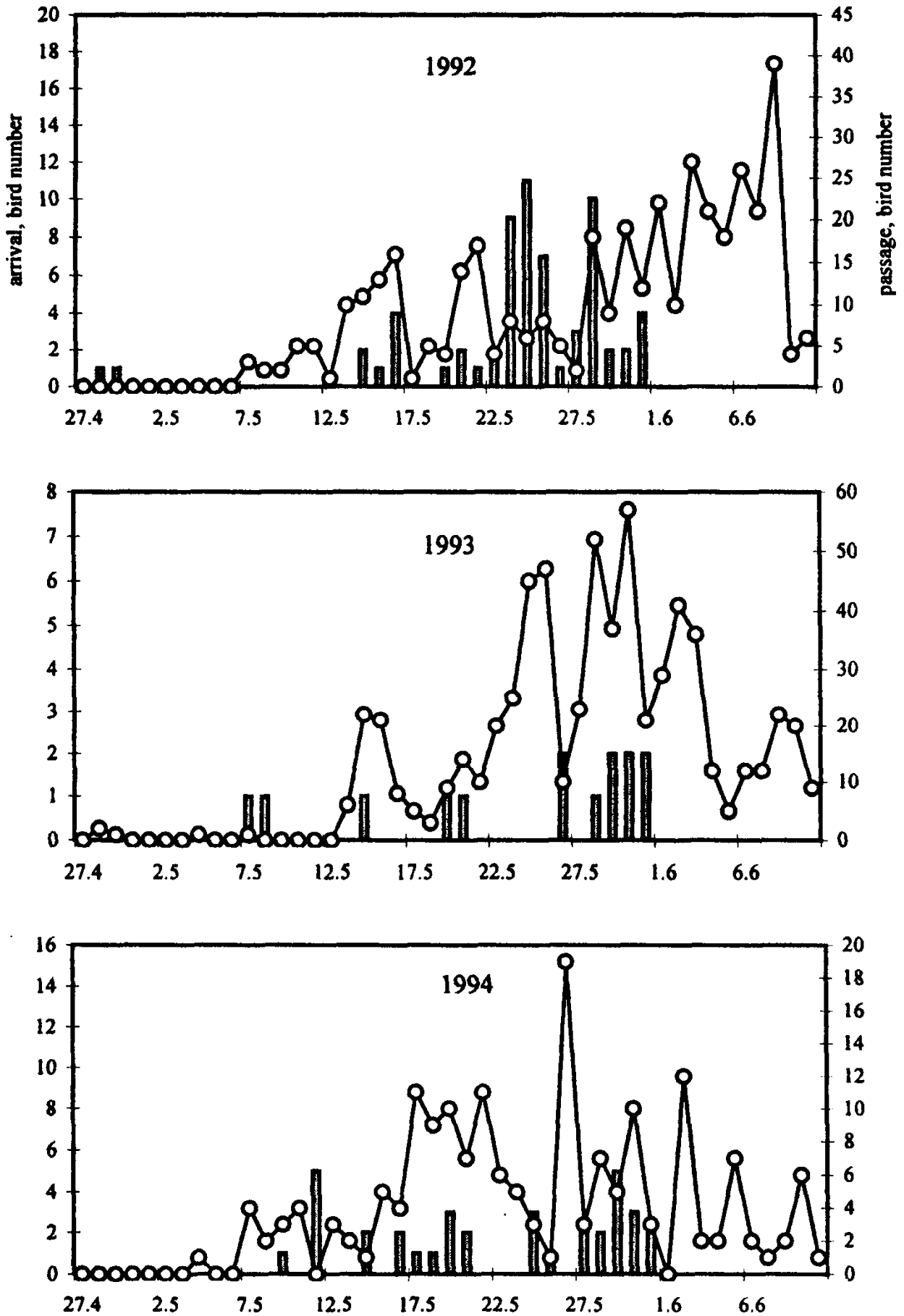
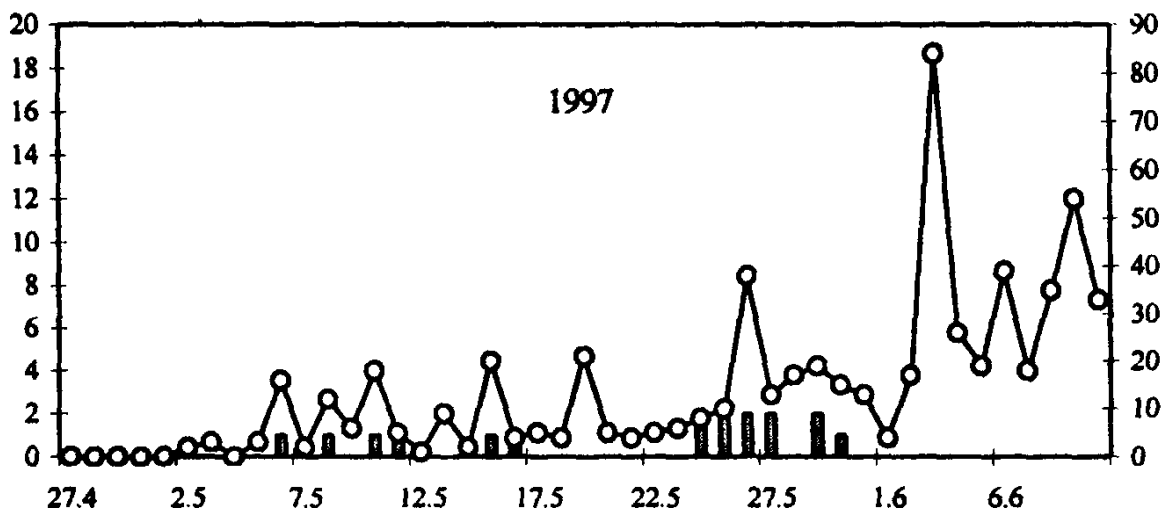
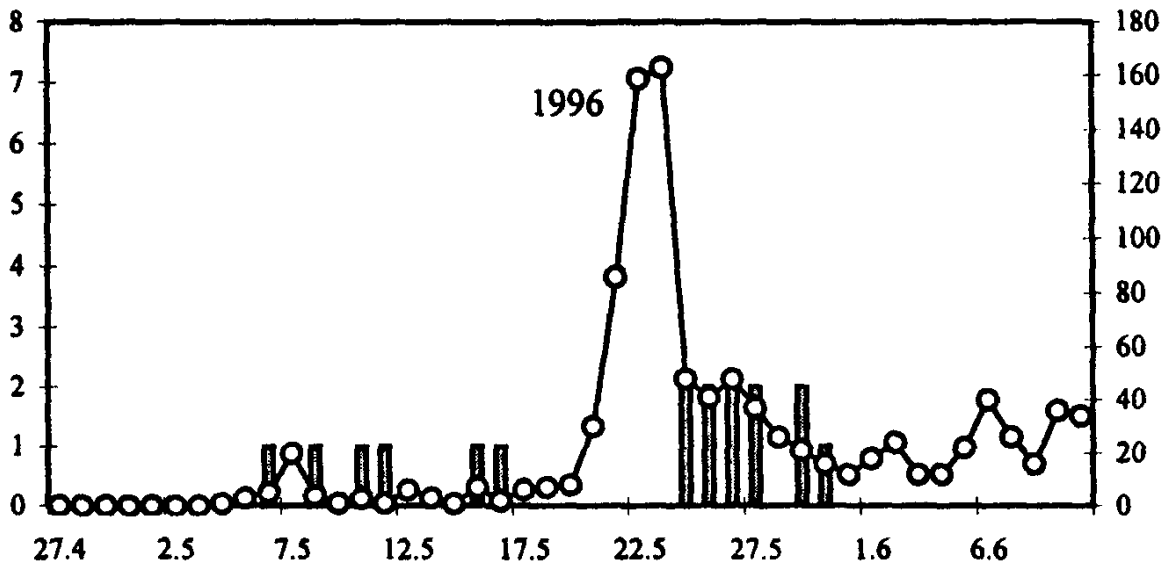
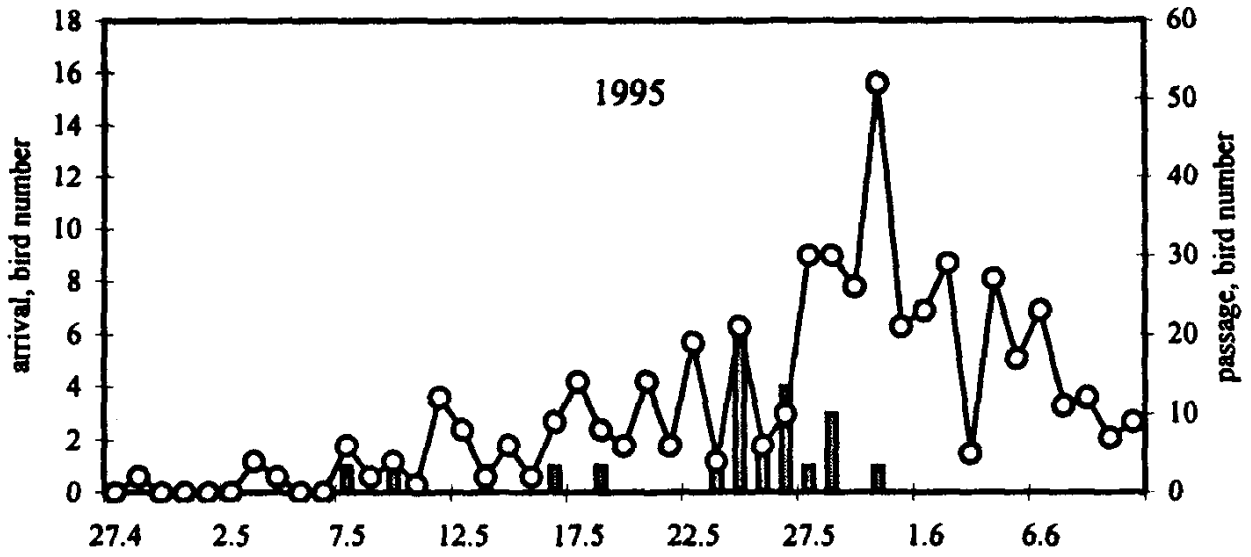


Figure 2. Continued



### 3.3. Age-related timing of arrival and body condition in males

Of 75 males trapped, their age was known, 59 of them being old birds (i.e. after second year, EURING age 6) and 16 being second-year birds (EURING age 5). Timing of their arrival differed (Fig. 4, Kolmogorov-Smirnov test,  $\lambda = 1.62$ ;  $p < 0.05$ ), old males arriving earlier.

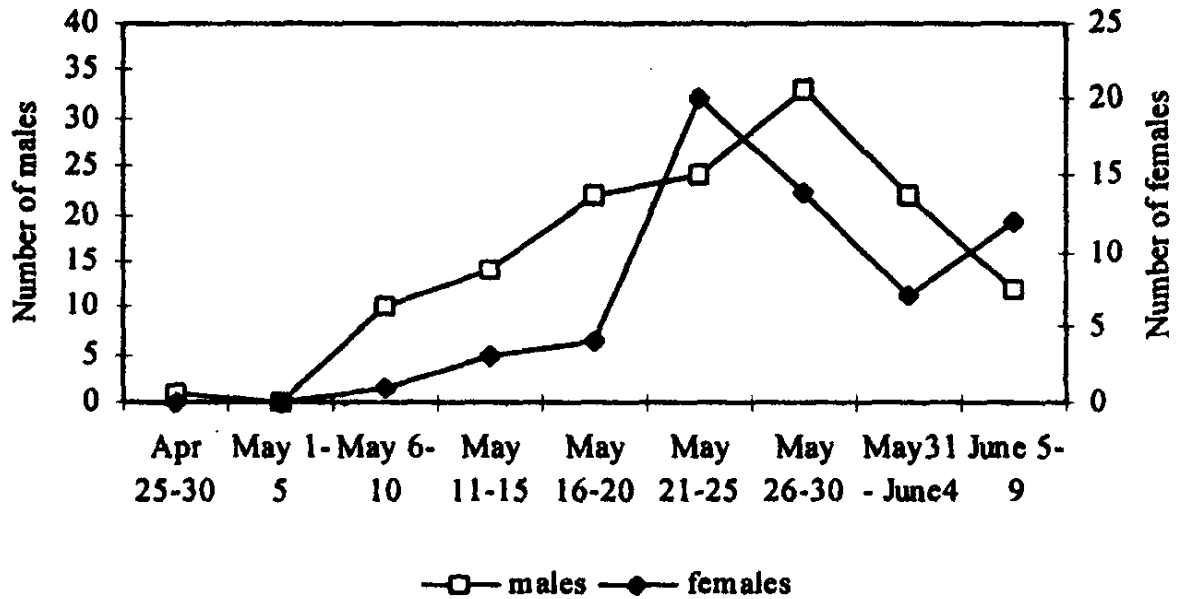


Figure 3. Arrival of local males and females.

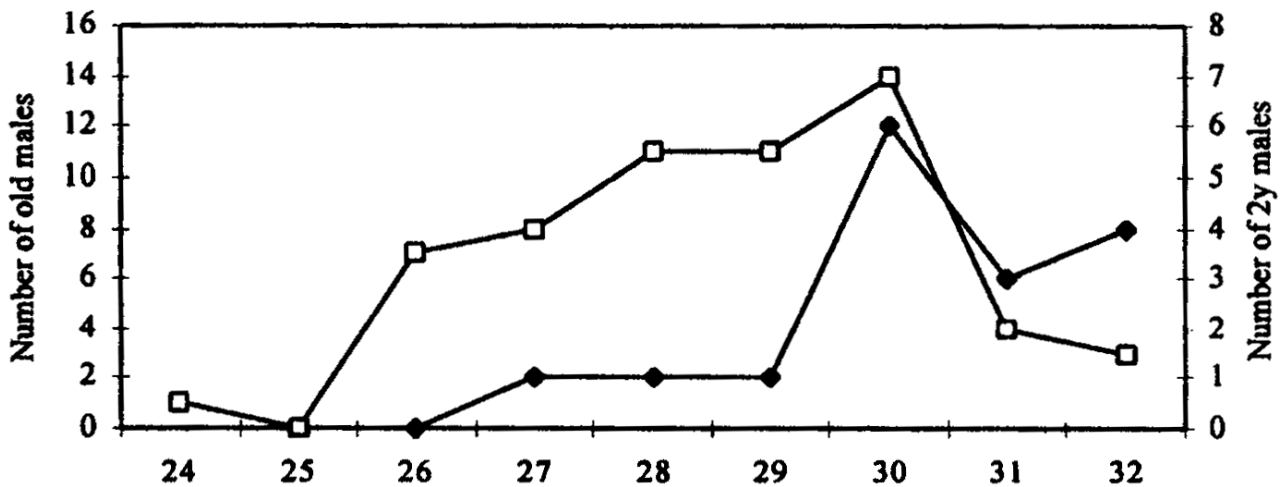


Figure 4. Arrival of local old and second-year (2y) males.

Wing length of second-year (2y) males ( $67.56 \pm 1.63$ ,  $n = 16$ ) was slightly higher than in old males ( $68.42 \pm 1.68$ ,  $n = 59$ ), though the difference was barely significant:  $t = 1.88$ ,  $p = 0.068$ . Condition index showed no age-related variation (2y:  $10.65 \pm 0.51$ ,  $n = 16$ ; older birds:  $10.86 \pm 0.57$ ,  $n = 59$ ; t-test:  $t = 1.4$ ,  $p > 0.10$ ).

### 3.4. Body condition and fat score in arriving locals and in passage birds

Body weight of passage Reed Warblers was found to be higher than that of arriving locals. The difference in wing length, migrants being slightly longer-winged, was not significant (Tab. 2A, 2B). Passage birds were those trapped before June 1 in the same season as locals included in the analysis. A

half of arriving local Reed Warblers weighed 9 - 11.4 g, i.e. as much as during non-productive phases of the annual cycle. In contrast, in some years more than half of transit birds weighed over 12 g.

Table 2A. Body mass, wing length, and condition index of arriving locals and passage birds.

	Passage	Locals		
		all	males	females
n	874	179	110	45
Body mass, g	11.88 ± 0.85	11.54 ± 0.73	11.76 ± 0.65	11.08 ± 0.63
Wing length, mm	67.65 ± 1.72	67.60 ± 1.87	68.17 ± 1.64	66.19 ± 1.39
Condition index	10.98 ± 0.75	10.67 ± 0.64	10.82 ± 0.58	10.37 ± 0.59

Table 2B. Significance levels.

	Passage vs. locals	Local males vs. females
Body mass	t = 4.96 p < 0.001	t = 3.02 p < 0.001
Wing length	t = 0.33 p > 0.10	t = 7.59 p < 0.001
Condition index	t = 5.12 p < 0.001	t = 4.39 p < 0.001

I compared fat scores of locals and passage migrants by ridit analysis (Fleiss 1986, Bardin 1998). As in 1992-1993 fat scoring followed Biyumenthal & Dolnik (1962), this scale was used for comparisons. Ridit average in locals was 0.342 db 0.0215; z = 7.35;

p < 0.0001. Fat score 0 was recorded in 61% of locals and 36% of migrants,

Weight corrected for size was higher in local males than in females. Body condition of local males was better than that of females (Tab. 2A, 2B).

In passage migrants, but not in arriving local breeders, significant inter-annual variation in body weight and wing length was recorded (Tab. 3). The data are too scarce for differential analysis between sexes. Inter-annual variation of body weight in passage migrants was not related to the variation of the median date of passage (Tab. 3).

Table 3. Inter-annual variation of wing length, body mass, and condition index in local breeders and passage migrants.

Year	n	wing length, mm	body mass, g	condition index
Passage migrants				
1992	154	67.67 ± 1.60	11.91 ± 0.86	11.01 ± 0.80
1993	309	67.68 ± 1.77	11.83 ± 0.78	10.94 ± 0.70
1994	116	67.26 ± 2.00	12.09 ± 0.91	11.20 ± 0.84
1995	268	67.18 ± 1.67	12.05 ± 0.92	11.18 ± 0.80
1996	429	67.55 ± 1.65	11.78 ± 0.91	10.92 ± 0.80
1997	172	67.88 ± 1.76	11.99 ± 0.71	11.07 ± 0.63
ANOVA		F <sub>5, 1471</sub> = 5.87; p < 0.001	F <sub>5, 1471</sub> = 6.48; p < 0.001	F <sub>5, 1471</sub> = 7.32; p < 0.001
Local breeders				
1992	27	67.93 ± 1.86	11.51 ± 0.73	10.61 ± 0.63
1993	64	67.95 ± 1.67	11.50 ± 0.70	10.61 ± 0.61
1994	14	66.00 ± 2.14	11.29 ± 1.03	10.58 ± 0.98
1995	35	67.39 ± 1.87	11.67 ± 0.69	10.82 ± 0.58
1996	22	67.52 ± 1.79	11.63 ± 0.62	10.76 ± 0.51
1997	17	67.62 ± 1.65	11.58 ± 0.67	10.71 ± 0.59
ANOVA		F <sub>5, 178</sub> = 2.91; p = 0.016	F <sub>5, 178</sub> = 0.69; p = 0.63	F <sub>5, 178</sub> = 0.68; p = 0.64

### 3.5. Individual inter-annual variation in the timing of arrival, body mass and fat score of arriving birds

Nineteen local breeders were controlled at arrival in two different years, five birds in three years and two birds were controlled four times. Variation in the timing of arrival reached 17 days towards earlier arrival and 15 days towards later arrival (Tab. 4). No consistent trend towards earlier or later arrival was revealed with growing age.

The mass of these birds, measured between years, varied from +1.1 to -2.3 g, although in 83% the variation was less than 1 g. No consistent trend was recorded. I did not find any relationship between changes in the arrival date and arrival mass ( $r = 0.06$ ;  $p > 0.10$ ).

#### Discussion

The phenology of arriving birds (locals) and of passage birds (migrants) are similar when pooled over the whole study period (Fig. 1). In four years 71-88% of local birds arrived at the Courish Spit during the main waves of passage. However, in other years up to 91% of locals arrived during inter-wave periods (Fig. 2).

Table 4. Date of first capture, body mass, and fat score of individual birds in different years. Fat scores after Biyumental & Dolnik (1962).

Ring No	Sex	Age	Date	Time	Fat	Mass	Change of date	Change of mass
609008	F	IND	07/05/92	10	2	10.5		
	F	AD	28/04/93	8	1	10.0	-9	-0.5
609017	I	IND	08/05/92	13	1	11.8		
	M	AD	23/05/93	5	1	11.5	15	-0.3
609052	M	IND	13/05/92	7	1	11.0		
	M	AD	15/05/93	14	2	12.0	2	1
609061	M	IND	13/05/92	17	2	12.6		
	M	AD	16/05/93	5	2	11.4	3	-1.2
609076	M	IND	14/05/92	6	1	10.9		
	M	AD	14/05/93	11	2	12.0	0	1.1
609086	F	IND	14/05/92	10	1	10.2		
	F	AD	25/05/93	6	1	11.8	11	0.4
	F	AD	11/05/95	6	1	10.7	-14	-0.7
	F	AD	25/05/96	5	0	11.0	14	0.3
609139	M	IND	16/05/92	5	1	10.8		
	M	AD	24/05/93	5	1	11.0	8	-0.2
	M	AD	11/05/95	21	1	11.6	-13	0.6
	M	AD	13/05/96	15	0	11.9	2	0.3
609146	I	IND	16/05/92	5	1	11.3		
	M	AD	29/04/93	8	1	11.3	-17	0
609150	M	IND	16/05/92	7	1	11.5		
	M	AD	22/05/93	20	2	12.6	8	1.1
609193	F	IND	20/05/92	5	1	10.9		
	F	AD	23/05/93	17	2	12.9	3	2
	F	AD	26/05/94	7	2	10.6	3	-2.3
609197	M	IND	20/05/92	5	1	11.9		
	M	AD	28/05/93	8	2	11.7	8	-0.2
609262	M	IND	22/05/92	6	1	11.2		
	M	AD	11/05/95	6	3	12.1	-11	0.9
	M	AD	09/05/96	11	0	11.4	-2	-0.7



609406	F	IND	26/05/92	5	1	11.1		
	F	AD	24/05/96	5	0	10.8	-2	-0.3
609428	F	IND	28/05/92	5	1	11.8		
	F	AD	24/05/93	6	3	12.2	-4	0.4
609484	I	AD	29/05/92	19	1	11.8		
	M	AD	28/05/93	12	1	11.4	-1	-0.4
609509	I	IND	30/05/92	7	1	11.0		
	F	AD	29/05/95	5	2	11.1	-1	0.1
639900	M	IND	20/05/93	5	1	11.8		
	M	AD	18/05/95	9	1	12.3	-2	0.5
	M	AD	18/05/96	16	0	12.2	0	-0.1
640302	M	SAD	30/05/94	17	1	11.0		
	M	AD	20/05/95	6	1	10.9	-10	-0.1
	M	AD	24/05/96	5	0	10.9	4	0
640393	M	AD	14/05/95	12	2	12.5		
	M	AD	07/05/96	6	0	11.7	-7	-0.8
641031	M	IND	23/05/93	5	1	11.0		
	M	AD	29/05/94	8	2	11.4	6	-0.4
641037	I	IND	23/05/93	7	1	10.0		
	I	AD	07/05/94	8	2	9.0	-16	-1
641087	F	IND	24/05/93	8	1	10.8		
	F	AD	24/05/95	6	1	10.8	0	0
641116	M	IND	25/05/93	5	2	11.7		
	M	AD	26/05/94	8	1	11.7	1	0
641117	F	IND	25/05/93	5	2	10.8		
	F	AD	16/05/95	6	2	11.4	-9	0.6
	F	AD	23/05/96	5	0	11.1	7	-0.3
641226	I	IND	28/05/93	6	2	11.5		
	I	AD	16/05/95	6	1	11.7	-12	0.2
642544	M	SAD	29/05/94	20	1	12.2		
	M	AD	27/05/95	6	3	12.6	-2	0.4

Although first local males arrive before first females, median arrival dates of both sexes are similar (Fig. 3, section 3.2). Obvious difference in the timing of arrival was recorded only between second-year and older males, the latter arriving earlier (Fig. 4). A similar pattern has been noted for a number of other avian species (Payevsky 1985).

A study of arrival of Pied Flycatchers to a Spanish breeding area did not reveal any hereditary component in the variation of arrival dates (Potti 1998). The author suggests that inter-annual fluctuation in the conditions that are met during spring migration cause what he calls "environment noise" which is more pronounced than any possible genetic variation in the timing of arrival. Potti (1998) believes that in his population there are no "costs of being too early". In a Mediterranean population such costs may indeed be negligible, if any. Observations in the eastern Baltic suggest that in more northern areas such risks do exist for many insectivorous birds, incl. flycatchers and *Acrocephalus* warblers. When the weather is adverse (cold spells, rain) Pied Flycatchers change their feeding techniques, collecting a larger proportion of food from the ground; many take ants (Formicidae) (Chernetsov, unpubl.). In male Great Reed Warblers mortality between arrival at the breeding grounds and start of breeding may be very significant (Fedorov 1998).

First-arriving birds, mainly older males, are subject to a high risk of food shortage in the case of low temperature and low availability of insects. This is however compensated for by the opportunity to occupy better territories. The timing of arrival to the breeding site, like many other life traits, is likely

to be an evolutionary stable strategy.

Inter-annual fluctuations in the timing of arrival and of condition of arriving migrants, both on the population and on the individual level, are explained by the "environment noise"; synoptic situations favourable for migration (see: Richardson 1978, 1990, Alerstam 1990) occur in different seasons in different years. Weather on the migratory route may enhance or inhibit migration (for examples of arrested migration see: Bolshakov & Rezvyi 1998, Sokolov et al. 1998).

On the Courish Spit body mass, body condition and the proportion of fat individuals among local Reed Warblers having completed migration were significantly lower than in passage conspecifics. In contrast with our results, in Willow Warblers arriving at breeding sites on Gotland and in Swedish Lapland, higher fat scores were recorded, comparable with fat stores recorded in passage individuals (Sandberg 1996, Fransson & Jakobsson 1998). Willow Warblers arriving at the southern tip of Gotland landed after a flight over the Baltic Sea. They may have needed fat stores for the following reasons: (1) overshooting or missing the goal, causing the necessity to take prolonged flights over the sea; (2) the possibility of facing adverse weather conditions when flying over the Baltic; (3) unfavourable foraging conditions on the island after arrival, etc. In any of these cases birds with low fat stores would likely perish. In Lapland high fat stores among arriving migrants are easier to explain; they are most probably an adaptation for unpredictable weather conditions in high latitudes (Sandberg 1996).

The lack of significant inter-annual variation in the condition of Reed Warblers completing spring migration together with the presence of such variation in passage birds is especially interesting. The mechanism of finishing spring migration seems to be stable between the years. The bulk of birds reach the breeding site in different years in a similar physiological condition, i.e. with low fuel stores. However, some Reed Warblers do arrive with high mass, and not infrequently are high mass and fat score recorded in an individual that in another year arrives lean (Tab. 4).

Data suggesting both similar timing of migration between different years (Tab. 4, see also Payevsky 1962) and those suggesting considerable variation are available. It is a matter of preference to emphasize similarity or variation. The absolute stability of individual arrival dates is hardly possible, as it would be feasible only if the environment was stable. Moreover, it seems to be of no adaptive value, as stable and early arrival to a northern breeding site would be too risky due to inter-annual variation of weather conditions (Sokolov et al. 1998).

I suggest that there is a general trend to stability which is disturbed by external factors, or "environmental noise". However, a fraction of the population may show no tendency to stability. These birds arrive when the chances of survival are low. Usually up to 88% of Reed Warblers arrive at their breeding sites on the Courish Spit when northern populations are still on migration over the same area. This suggests that: (1) migration of passage birds and those approaching their migration goal occurs under similar meteorological conditions; (2) birds locate the goal very precisely and do not spend much time searching for their "home".

Unfortunately, the available material does not allow me to discuss this important problem in more detail.

#### Acknowledgements

I am much indebted to Dr. Casimir Bolshakov who inspired me to write this paper. Constructive criticism and suggestions of Dr. Vladimir Payevsky and Dr. Leonid Sokolov helped a lot to improve earlier drafts. Lyndon Roberts kindly improved the English.

#### References

- Alerstam, T. 1990. Bird Migration. Cambridge Univ. Press, Cambridge.
- Bairlein, F. Jenni, L., Kaiser, A., Karlsson, L., Noordwijk, A., Peach, W., Pilastro, A., Spina, F., & G. Walinder. 1995. European-African Songbird Migration Network. Manual of field methods. Wilhelmshaven.
- Bardin, A.V. 1998. The application of ridit analysis to subcutaneous lipid data (using daily fat deposit variation in the great tit *Parus major* during winter as an example). Russ. J. Ornithol. Express-issue 49: 17-24 (in Russian).
- Biyumenthal, T.I. 1971. The development of the autumnal migratory state in some wild passerine birds: bioenergetic aspect. In: Bykhovsky, B.E. (ed.) Ecological and physiological aspects of bird migration.

- Nauka Press, Leningrad: 111-182 (in Russian).
- Biyumenthal, T.I. & V.R. Dolnik. 1962. Field estimation of energetic condition in birds. *Ornitologiya* (Moscow) 4: 394-407 (in Russian).
  - Bolshakov, C.V. & S.P. Rezvyi 1998. Time of nocturnal flight initiation (take-off activity) in the European Robin *Erithacus rubecula* during spring migration: visual observation between sunset and darkness. *Avian Ecol. Behav.* 1: 37-49.
  - Dolnik, V.R. 1975. Migratory disposition in birds. Nauka Press, Moscow (in Russian).
  - Fedorov, V.A. 1998. To the problem of polygyny in passerines: the case of the Great Reed Warbler *Acrocephalus arundinaceus*. In: Zoological Sessions. Annual Reports 1997. Abstracts. Zoological Institute, St.Petersburg: 45-46 (in Russian).
  - Fleiss, J.L. 1986. Statistical methods for rates and proportions. John Wiley & Sons, NY.
  - Fransson, T. & S. Jakobsson. 1998. Fat storage in male Willow Warblers in spring: Do residents arrive lean or fat? *Auk* 115: 759-763
  - Kaiser, A. 1993. A new multi-category classification of subcutaneous fat deposits on song birds. *J. Field Ornithol.* 64: 246-255.
  - Lapshin, N.V. 1978. Peculiarities of spring migration of Willow Warblers in north-western Russia. Abstracts 2nd All-Union Confer. Bird Migration, part 2. Alma-Ata: 85-86 (in Russian).
  - Lapshin, N.V., Rezvyi, S.P. & C.V. Bolshakov 1981. Spring migration of Willow Warblers (*Phylloscopus trochilus* L.). In: Ecology of birds in Ladoga area. Leningrad Univ. Press, Leningrad: 86-100 (in Russian).
  - Payevsky, V.A. 1962. Stability of individual timing and routes of seasonal movements in birds. In: Proceed. 3rd All-Union Ornithol. Confer., part 2. Lvov Univ. Press, Lvov: 131-132 (in Russian). Payevsky, V.A. 1967. The composition of the Chaffinch population migration across the Baltic area.
  - Comm. Baltic Commission Study Bird Migr. 4: 59-68 (in Russian with English summary). Payevsky, V.A. 1972. Individual variation of temporal and territorial distribution in some passerine birds during migration. Comm. Baltic Commission Study Bird Migr. 7: 3-17 (in Russian with English summary).
  - Payevsky, V.A. 1985. Demography of birds. Nauka Press, Leningrad (in Russian). Potti, J. 1998. Arrival time from spring migration in male Pied Flycatchers: individual consistency and familial resemblance. *Condor* 100: 702-708.
  - Richardson, W.J. 1978. Timing and amount of bird migration in relation to weather: a review. *Oikos* 30: 224-272.
  - Richardson, W.J. 1990. Timing of bird migration in relation to weather, undated review. In: Gwinner, E. (ed.) Bird Migration: physiology and ecophysiology. Springer, Berlin - Heidelberg – New York: 78-101.
  - Sandberg, R. 1996. Fat reserves of migrating passerines at arrival on the breeding grounds in Swedish Lapland. *Ibis* 138: 514-524.
  - Sokolov, L.V. & V.G. Vysotsky 1990. The accuracy of the spring migration navigation in the adult and subadult Pied Flycatchers (*Kcedula hypoleuca*) and Chaffinches (*Fringilla coelebs*) at the Courish Spit of the Baltic Sea. *Baltic Birds* 5 (2): 163-167.
  - Sokolov, L.V. 1997. Philopatry of Migratory Birds. Hardwood Acad. Publishers, Amsterdam. Sokolov, L.V., Markovets, M.Yu., Shapoval, A.P. & Yu.G.Morozov. 1998. Long-term trends in the timing of spring migration of passerines on the Courish Spit of the Baltic Sea. *Avian Ecol. Behav.* 1:1-21.
  - Wiltschko, W. & R. Wiltschko 1978. A theoretical model for migratory orientation and homing in birds. *Oikos* 30: 177-187.
  - Wiltschko, W. & R. Wiltschko 1998. The navigation system of birds and its development. In: Animal Cognition in Nature. Academic Press: 155-199.