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Juvenile dispersal in Reed Warblers *Acrocephalus scirpaceus* at night

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The aim of this study was to test whether juvenile dispersal in Reed Warblers *Acrocephalus scirpaceus* takes place at night. If this does occur then the questions arise: "in which part of the night, at what age and physiological condition do they disperse?" In 1999 on the Courish Spit on the Baltic we ringed large numbers of Reed Warbler pulli at three isolated reedbed sites. Each night from late July until mid September we tape-lured Reed Warblers in a habitat atypical of this species. The trapping site was nearly equidistant from the two main plots where pulli were ringed. Additionally, in 1997-1999 at one of the reedbed study sites Reed Warblers starting and ending nocturnal flights were captured in high nets while at the same site, during the daytime, birds were trapped in standard mist nets.
Our results suggest that juvenile dispersal of Reed Warblers takes place at night. The analysis of capture histories of ten birds ringed as pulli or just after fledging shows that: (1) age of birds during nocturnal movements was 33-49 days; (2) birds moved towards the NE and SW mainly during the last two hours before sunrise; (3) flight duration did not exceed 75 min; (4) all birds had low fuel stores and were in active moult; (5) nocturnal juvenile dispersal occurs by movements from one isolated reedbed area to another.

Key words: juvenile dispersal, Reed Warbler, tape luring, nocturnality, post-fledging movements, migration.

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1. Introduction

Juveniles of most bird species, show an urge to disperse (i.e. actively to change location), after they become independent of their parents. The possible biological significance of juvenile dispersal is to settle in new areas, to avoid competition and inbreeding, to regulate population density, to establish links with the future breeding sites, seeking new food sources and moulting sites (for reviews see Greenwood 1980, Greenwood & Harvey 1982, Bauer 1987, Sokolov 1991, 1997, etc.). Due to methodological difficulties (high post-fledging mortality, avoiding control, low probability of reporting from outside the study plot) many aspects of juvenile dispersal of many passerines remain poorly studied. Reed Warbler *Acrocephalus scirpaceus* is no exception. Few data are available on age of juvenile dispersal, the stages of moult, dispersal directions of individual birds, whether all the birds involved in dispersal or not, whether they move slowly through the vegetation or by flight at different distances, whether at day or at night, whether there is a gap between the end of dispersal and the onset of autumn migration, or what the impact is of different external and internal factors on dispersal distance and timing.

As breeding areas of Reed Warblers may form patches of isolated habitat, their dispersal be-

haviour may differ considerably from that shown by species inhabiting comparatively uniform habitats. In a study of post-fledging movements of juvenile Reed and Sedge Warblers *(Acrocephalus schoenobaenus)* at three sites in south-central Sweden, Nielsen and Bensch (1995) concluded that post-fledging dispersal of these species occurs "within the birds' main habitat, the birds slowly exploring the surroundings of the place of birth. The predominant direction of the dispersal might correspond to the general migratory direction". However, several recoveries of juveniles reported by these authors between two isolated reed areas, 8 km apart along the N-S axis, suggest that some individuals may move by one or several movements in non-migratory directions. That juvenile Reed and Sedge Warblers can disperse for considerable distances and in different direction, is shown by recoveries before the onset of autumn migration in other regions: e.g. in Britain (Insley & Boswell 1978), in Estonia (Chernetsov 1998), on the Courish Spit (Chernetsov 1999, Chernetsov & Mukhin, in press).

Reed Warblers are known to be nocturnal migrants (Cramp 1992). Nocturnal activity, though weak, starts in hand-raised caged individuals at the mean age of 36 days (Mukhin 1999). These observations, together with nocturnal captures of tape-lured juveniles in an atypical habitat in early August (Herremans 1990), suggest that post-fledging movements take place at night. In the latter case however the possibility cannot be excluded that nocturnal movements of juvenile Reed Warblers were related to autumn migration, not to dispersal. In order to indicate whether nocturnal movements of young Reed Warblers refer to dispersal or to migration, it is necessary to know the birds' natal site and age.

The aim of this study was primarily to find out whether juvenile dispersal occurs at night. If it does then at what part of the night, at what age and in what physiological condition do birds disperse, and what are peculiarities of dispersal behaviour compared with autumn migration.

The working plan was as follows: (1) To try to capture Reed Warblers ringed as pulli at departure from the natal site or directly during nocturnal flight. Knowing their (a) hatching date; (b) natal site; and (c) capture time, it would then be possible to detect dispersal age, direction and time of night; (2) To compare physiological condition (moult, body mass, fuel stores) of juveniles captured at night during the supposed dispersal and on autumn migration.

2. Study area, material and methods

To implement the study plan we first conducted marking of Reed Warbler pulli in three isolated reedbeds at different distances from each other. Secondly, at nearly every night between late July and mid September we tape-lured Reed Warblers in an atypical Reed Warbler habitat - on sand dunes covered by willow bushes and some small birches and pines. Capture location was nearly equidistant from the two main areas where pulli were marked. Thirdly, in one of reedbeds Reed Warblers starting and ending flight at night were captured in high mist-nets. At daytime, birds were trapped in standard mist-nets.

Nest searches and nestling marking were done in 1997-1999 on the Courish Spit at the three isolated reedbed sites. Two sites were in the vicinity of the village of Rybachy. Site one was on Rossitten Cape (Rybachy study plot). The overall area covered with reed is slightly less than 4 ha, but only 1.6 ha were suitable for breeding of Reed Warblers, The reedbed is compact, maximum distance between most distant sites is less then 500 m. About two-thirds of the Reed Warblers breed in the central part of the reedbed. Site two was the small Lake Chaika (Lake study plot) 1.5 km from the Rybachy (Fig. 1). The reed grows there along the shore of the lake in small patches, their overall area being ca. 0.5 ha. No other reedbeds are available for breeding of Reed Warblers near Rybachy.

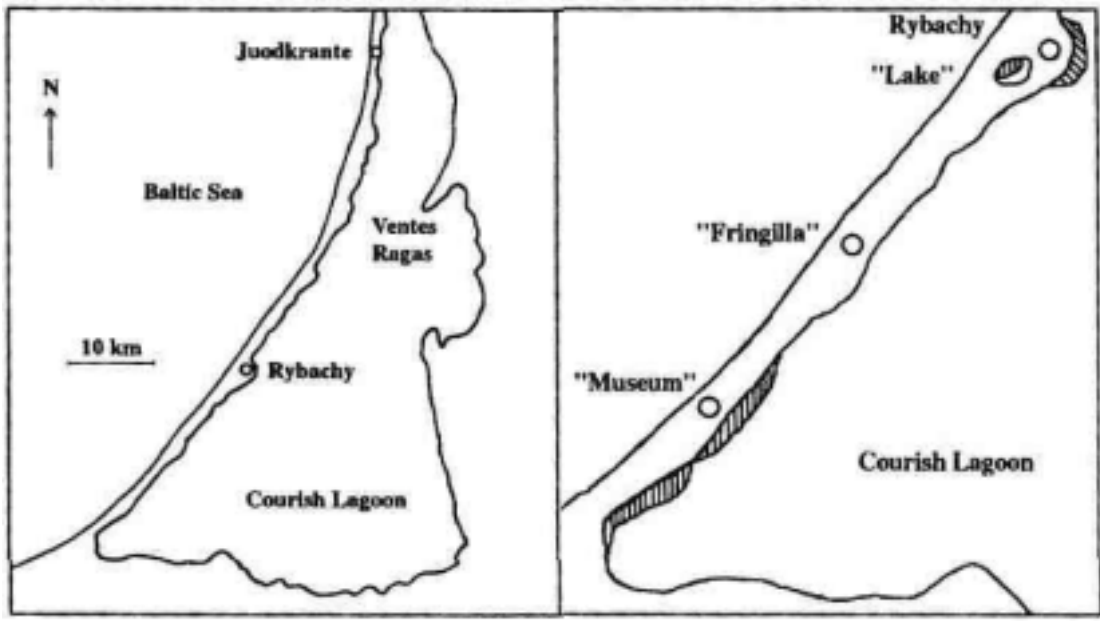

Figure 1. Map of study area. Reed stands are shaded.

Site three (Museum site, because of its proximity to the National Park "Courish Spit" Museum) is situated 14-17 km from the start of the Courish Spit, about 20 km to the SW from the first two areas (Fig. 1). The reedbed stretches for 2.5 km along the coast of Courish Lagoon and consists of 18 fragments of different size. The overall area is slightly less than 10 ha, but Reed Warblers breed only along a narrow coastal strip. No reed occurs on the shore of the lagoon between the Museum site and Rybachy emphasising the isolation of the Museum site from the sites to the NE. Towards the SW the reed strip, after a gap of 300-400 m, extends to the start of the spit. At all three sites, nest searches and nestling ringing was undertaken from the beginning of the breeding period until fledging of the last pulli (late May - late August) (Tab. 1).

Table 1. Timing of breeding and number fledgings of Reed Warblers at three study plots on the Courish Spit in 1999.

10-day periods	Rybachy			Lake			Museum		
	Nests with eggs	Eggs laid	Nestlings fledged	Nests with eggs	Egg-slaid	Nestlings fledged	Nests with eggs	Egg-slaid	Nestlings fledged
21.05-31.05	2	7					1	5	
1.06-10.06	13	53					1	4	
11.06-20.06	4	17		2	7		3	12	
21.06-30.06	7	27	6	2	9		4	16	8
1.07-10.07	5	18		1	4		10	39	3
11.07-20.07	5	17	11	1	4	4	5	20	3
21.07-31.07	4	13	10	2	7	2	2	5	26
1.08-10.08			10			4			30
11.08-20,08						7			8
21.08-31.08						3			
Total	40	152	37	8	31	20	26	101	78

Nocturnal tape-luring was undertaken between 22 July and 12 September 1999 at the trapping station "Fringilla", 23 km from the start of the Courish Spit. The site is situated in a transition gap between forest and high sandy dunes, covered with willow scrub with single small birches and pines. The width of this gap is about 100 m. Birds were trapped in 12 standard 7-m mist-nets that were opened at sunset and closed 30-40 min after sunrise. The nets were put in a rectangle with a tape lure at its centre. This consisted of a car tape player with two 20 W loudspeakers, oriented to the NE and SW at an angle of 45°. Songs of two species, Reed Warbler and Marsh Warbler *Acrocephalus palustris* were played continuously from sunset until sunrise (continuous 45 min loops of each species in sequence). The nets were checked by torchlight at the end of each hour after sunset throughout the night, and 60 and 30 min before sunrise. Trapped birds were weighed immediately after capture to the nearest 0.1 g. In the morning, other biometrical information was collected following the guidelines of ESF programme (Bairlein 1995). All birds captured at night were released within one hour after dawn within 250 m from the capture site.

Birds starting and ending nocturnal flight, at the trapping station "Rybachy" where nestlings were ringed, were trapped in high nets. The special mist-nets were put above the reed, tops of trees and bushes. Previously marked birds are controlled at the moment of nocturnal departure (or captured on landing). For more details see Bolshakov et al. (1999). High nets were opened 2 hours before sunset and closed on sunrise, except in situations of gale force wind. Nets were checked each hour by torch with a narrow, well-defined beam. During the first hour after sunset nets were checked twice, 45 and 65 min after sunset. At dawn, nets were also checked twice, 70 and 30 min before sunrise. The method was applied in 1997-1999 between mid July and late September.

Additionally we used the trapping data from Rybachy station in 1997-1999. Birds were captured in 73 standard mist-nets in reedbeds and scrub (see details in Titov 1999). All birds captured at Rybachy were ringed and biometrical data were taken following the standard methods of the ESF programme (Bairlein 1995).

To compare body condition of juvenile Reed Warblers accounting for their structural size, we used body condition index. This index was calculated as $m*w^{-794}$, m being body mass, and w - wing length (Titov & Chernetsov 1999).

Moult was recorded after the techniques adopted in the ESF project (Bairlein 1995). Moult progress was recorded (beginning moult, active moult and end of moult), and the number of moulting body-feathers (0, <20, >20). For more convenient analysis of moult data, each birds was placed in one of the seven state of plumage categories:

O - remiges and restrices growing, but body-moult not yet started;

1 - juvenile plumage, less than one-third of body-feathers post-juvenile with <20 moulting body-feathers;

2 - beginning of body-moult, > 20 moulting body-feathers;

3 - one-third to two-third of body-feathers post-juvenile;

4 - over two-thirds of body-feathers post-juvenile, number of growing body-feathers >. *20;*

5 - moult nearly completed, number of growing body-feathers < 20;

6 - juvenile moult completed.

Statistical treatment of moult and fat score data was done by ridit analysis (Fleiss 1986, Bardin 1998). The whole period of research was divided into three sections: 28 July -8 August, 9-20 August, 21 August - 11 September.

3. Results

3.1. Breeding period of Reed Warblers in 1999

In 1999 at Rybachy site 32-34 pairs of Reed Warblers bred. This number was the lowest since regular population studies started in 1993. At Lake and Museum sites the number of breeding pairs was close to the long-term average, about 10 and 75-80 pairs, respectively.

In 1999, Reed Warblers started their breeding season in the study area in late May -early June. The earliest laying the first egg was recorded on 23 May. First young fledged in the last 10-day period of June (the first brood fledged on 23 June). The majority of juveniles fledged between 11 July - 10 August (Tab. 1). Last fledglings were recorded in the second half of August (the latest brood fledged on 21 August). At Rybachy site breeding success was ca. 3 times lower than at the lake and Museum sites. This was caused by a very high nest predation rate at Rybachy.

3.2. Analysis of nocturnal captures 3.2.1. General characteristics of nocturnal tape-luring results

Though we played recorded songs of both Reed and Marsh Warblers, only Reed Warblers were captured at night in high numbers: 182 individuals (33 adults and 149 juveniles). Only five Marsh Warblers were trapped (one adult and four juveniles). The small numbers of this species were due to its low breeding density on the Courish Spit. At three study plots only one Marsh Warbler nest was found.

The first juvenile Reed Warblers were captured on 28 July, the last ones on 5 September (Fig. 2).

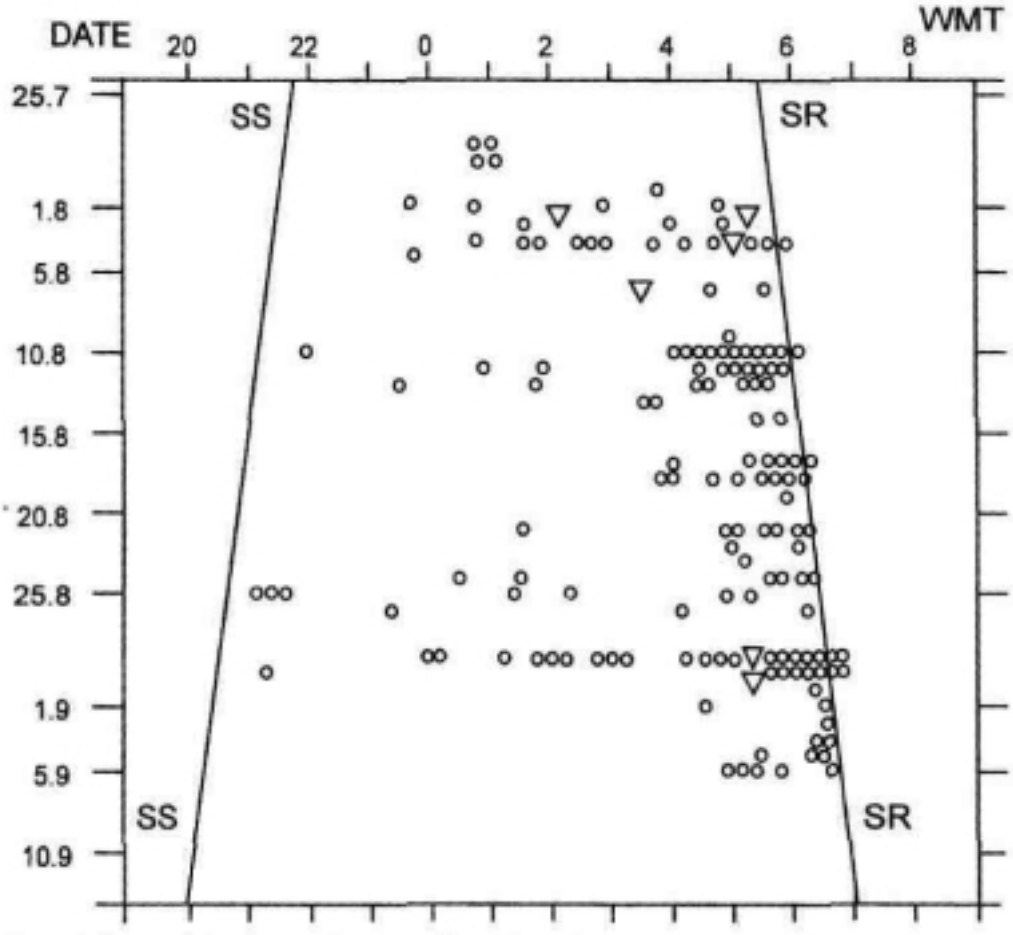

Figure 2. Temporal distribution of captures of juvenile Reed Warblers (tape-luring). Circles refer to birds without rings, triangles - ringed birds. SS - sunset, SR - sunrise. WMT - winter Moscow time.

The mean body mass of captured juveniles increased through the season, but the difference was not significant (Tab. 2, 3). However, mean body condition index of first-autumn birds trapped in late July - early August was significantly lower than in the two subsequent periods (Tab. 2, 3).

Table 2. Mean body mass and condition index of juvenile Reed Warblers tape-lured at night.

Period	Mean body mass ± SD, g (n)	Mean condition index ± SD
28.07 - 8.08	12.4 ± 1.43 (29)	0.435 ± 0.0395
9.08 - 20.08	12.7 ± 1.23 (48)	0.454 ± 0.0421
21.08 - 5.09	13.0 ±1.29 (72)	0.466 ± 0.0439

Table 3. Significance levels of differences between mean body masses and condition indices of Reed Warblers tape-lured in different periods.

	Mean mass	Mean condition index
28.07 - 8.08 vs. 9.08 - 20.08	t-0.85 p>0.05	t - 2.01 p < 0.05
9.08 - 20.08 vs. 21.08 - 5.09	t- 1.24 p>0.05	t " 1.44 p > 0.05
28.07-8.08vs.21.08-5.09	t - 1.84 p > 0.05	t-3.38 p<0.01

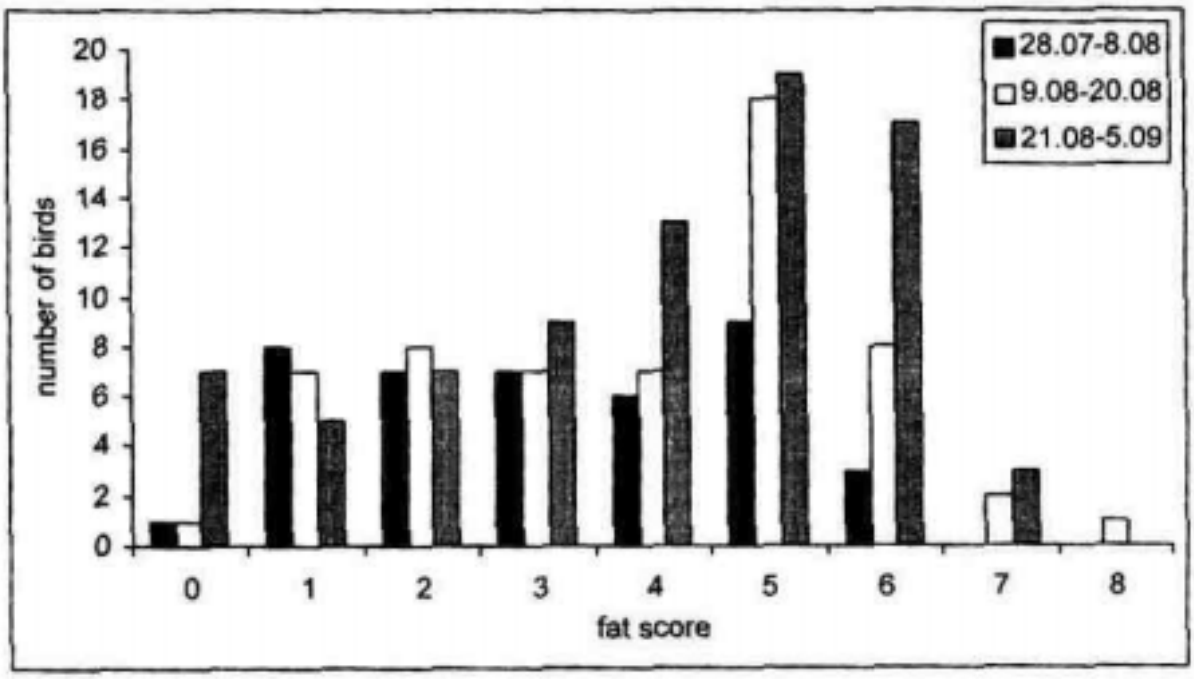

Figure 3. Frequency distribution of fat scores of juvenile Reed Warblers tape-lured at night in different periods.

In late July - early August, Reed Warblers had significantly lower fat scores that in late August - early September. No significant difference was found between other periods (Fig. 3, Tab. 4).

No juveniles in state of plumage categories 0, 1, or 2 were captured (Tab. 5). All birds were at least in the middle of juvenile moult (category 3). In late July - early August, the proportion of such birds was 14.8%. In the bulk of birds trapped during this period (81.4%), moult was advanced more than one-half or nearly completed (categories 4 and 5). Only one individual out of 27 had completed moult (category 6). In mid August the proportion of Reed Warblers with completed moult reached 42.6%, in early September -66.1% (Tab. 5).

Table 4. Differences in fat scores of Reed Warblers tape-lured in different periods.

	28.07-8.08 vs. 9.08-20.08	21.08-5.09 vs. 28.07-8.08	21.08-5.09 vs. 9.08-20.08
Ridit average	0,605	0,386	0,486
S.E.	0,058	0,055	0,049
Z	1,814	-2,085	-0,286
P	>0,05	<0,05	>0.05

Note: S.E. - standard error of ridit average. Z - statistical test for differences in ridit averages . Table 5. Numbers of juvenile Reed Warblers tapelured at night in different stages of body-moult.

Moult category*	28.07 - 8.08	9.08 - 20.08	21.08 - 5.09
0			
1			
2			
3	4		
4	11	16	11
5	11	11	11
6	1	20	43

Note: * for description of moult categories sec Material and Methods.

3.2.2. Juvenile Reed Warblers marked as pulli and recaptured by tape-luring

Checks of nests with marked pulli showed that in 1999, at Rybachy study plot 37 marked birds fledged, at the lake plot - 20 and at the Museum plot - 78 (Tab. 1). Three birds, one from each study plot, was recaptured by tape-luring. Three more ringed juveniles were recaptured. Two of them were previously ringed on the Courish Spit at Rybachy and at Juodkrante, and one at Ventes Ragas on the eastern coast of the Courish Lagoon at 12, 41 and 44 km to the NE from the tape-luring site, respectively (Fig. 1, Tab. 6). Capture histories of these six young birds showed the following.

1. Birds ringed as nestlings were in the age of 43-49 days after hatching at nocturnal recapture.
2. Five out of six birds were recaptured to the SW, and one to the NE from natal (ringing) sites. One individual (AX 000436) was first recaptured 9 km to the SW from its natal site, and 8 days later it was recaptured at daytime in the natal area.
3. Five birds were trapped during the two last hours before sunrise, one bird three hours before sunrise.
4. Fat score did not exceed 3 in birds captured at night (mainly 0 - 2), body mass varied between 11.0 - 12.2 g (mean 11.4 ± 0.44 g). All birds were in active moult (categories 3 and 4).

Table 6. Capture histories of Reed Warblers marked as pulli and recaptured by tape-luring.

Ring number	Date	Hour after sun-set (for night captures)	Capture method *	Capture loca-tion	Fat score	Body mass, g	Moult category	Age, days **
AX000330	22.06		Nest	"Rybachy"				8
	13.07		Net	"Rybachy"	2	12.3		29
	16.07		Net	"Rybachy"	1	12.0	2	32
	20.07		Net	"Rybachy"	2	11.8	2	36
	23.07		Net	"Rybachy"	1	11.8	3	39
	1/2.08	+5	Tape lures	"Fringilla"	1	11.0	4	49
AX000430	23.07		Nest	"Museum"				7
	29/30.08	+9	Tape lures	"Fringilla"	0	11.1	4	45
AX000436	26.07		Nest	"Lake"				8
	29/30.08	+9	Tape lures	"Fringilla"	0	11.3	4	43
	08.09		Net	"Rybachy"	2	11.4	5	51
VV94702 (& V017625)	19.07		Net	Ventes Ragas				
	1/2.08	+8	Tape lures	"Fringilla"	2	11.5	4	
XS91510	23.07		Net	"Rybachy"	2	12.5	2	
	26.07		Net	"Rybachy"	1	12.3	2	
	6/7.08	t-7	Tape lures	"Fringilla"	3	12.2	3	
VX15502 (+V017631)	29.07		Net	Juodkrante				
	2/3.08	+8	Tape lures	"Fringilla"	2	11.2	4	

Notes: * Nest - ringed as pullus; Net - captured at daytime in standard nets; Tape lures - tape lured at night. ** - only for birds with known hatching date.

3.2.3. Capture histories of birds after nocturnal tape-luring (all captures)

Out of 143 juvenile Reed Warblers, that were initially marked when tape-lured, two birds were recaptured 12 km to the NE from the site of nocturnal capture. One bird (V 017647) captured at "Fringilla" on 4 August one hour after sunset, was twice recaptured in standard nets at Rybachy on 7 and 11 August. At nocturnal capture at "Fringilla" the bird weighed 12.2 g, had fat score 2 and was in active moult (category 4). At Rybachy on 7 and 11 August, it weighed 13.6 g and 15.1 g, respectively, had fat scores 4 and 6, respectively and by the end of its stay at Rybachy, this bird had nearly completed body-moult.

Another Reed Warbler (V 017816) was tape-lured on 13 August at "Fringilla" two hours before sunrise. At capture it weighed 13.2 g, had fat score 3 and was in active moult (category 4). After 22 hours, it was recaptured in the sixth hour after sunset at Rybachy in high nets, nearly 7 m above the ground. Its body mass has decreased by 1.0 g. On 17 August, this bird was again captured at Rybachy at daytime in standard nets. Its body mass at this captured was 12.9 g.

3.2.4. Reed Warblers marked as pulli and recaptured in high nets

Of all nestlings, ringed at Rybachy in 1997-1999, four were recaptured in high nets in the hatching year (Tab. 7). At the moment of nocturnal departure their age was 33-43 days, mass varied between 10.4 - 11.6 g, fat score was 0 to 2. All birds were in active moult (categories 3 and 4).

Three birds were captured two hours before sunrise, one three hours before sunrise. Between fledging and nocturnal capture, all birds were repeatedly recaptured at daytime in standard nets. In all moulting Reed Warblers captured at night, body mass showed a tendency to decrease with increasing age. This could be caused by decreasing water index of body tissues with the progress of juvenile moult (Dolnik 1975).

4. Discussion

A most important function of juvenile dispersal is search of the site of future breeding. The position of the future breeding site relative to the natal site obviously largely depends on the direction and distance of juvenile dispersal. It was shown in many passerine longdistance migrants that the bulk of birds settle within several kilometres from their natal sites. However a fraction of individuals may breed at large distances from their hatching areas, up to several dozens of hundreds of kilometres. Direction from breeding sites to natal sites also varies broadly, but some long-distance migrants show a trend to breed further south from the natal site, towards the direction of autumn migration (for reviews see: Sokolov 1991. 1997).

Table 7. Captures of Reed Warblers, marked as pulli, in high nets at Rybachy.

Ring number	Date	Hour after sunset (for nocturnal captures)	Capture method *	Fat score	Body mass, g	Category of plumage state	Age, days
XS 21331	09.07.97		Nest				8
	02.08.97		Net	0	11.5	2	32
	8/9.08.97	+8	High net	0	10.4	3	38
XS 21437	25.07.97		Nest				6
	09.08.97		Net	1	12.2	0	21
	19.08.97		Net	1	11.6	3	31
	23/24.08.97	+8	High net	2	11.4	4	35
AX 000329	22.06.99		Nest				8
	12.07.99		Net	1	12.2	1	28
	16.07.99		Net	0	12.1	2	32
	20.07.99		Net	2	12.4	3	36
	26.07.99		Net	1	11.9	4	42
	27/28.07.99	+7	High net	1	11.2	4	43
AX 000487	04.08.99		Nest				10
	21.08.99		Net	0	13.6	2	27
	23.08.99		Net	0	11.5	3	29
	29/30.08.99	+8	High net	2	11.6	4	35

Note: * Nest - ringed as pulli; Net - captured at daytime in standard nets; High net - captured in high nets.

Reed Warblers often breed in reedbed patches that may be situated at considerable distance from each other, thus the pattern of their juvenile dispersal may differ from the pattern shown by species that inhabit relatively uniform large forest habitats. It was suggested that during post-fledging dispersal, *Acrocephalus* warblers prefer to move within reed stands (Nielsen & Bensch 1995). However it remains uncertain how birds disperse when reed patches are isolated. In such a situation Reed Warblers would have to leave the natal area during post-fledging dispersal, or make only short movements within the small patch.

Long-term study of breeding biology of Reed Warblers, including the ringing of nestlings and control of breeding adults at Rybachy and at Museum study plots showed that some birds hatched at the Museum, bred at Rybachy (Fedorov, unpubl.). Thus, at least some Reed Warblers make natal dispersal for ca. 20 km to the NE.

Many migrant passerines are known to establish the link with their future breeding site during juvenile dispersal during the first few weeks after they achieve independence (usually by the age of 30-50 days) (Löhrl 1959, Haukioja 1971, Morton et al. 1991, Sokolov 1991, 1997). Juvenile Reed Warblers probably disperse and choose their future breeding sites during the same period, according to our data on young birds ringed in different years at Museum as pulli and recovered 20 km to the NE in standard mist-nets at Rybachy. The age of two birds at recapture was 33 and 35 days, and of the others between 40 and 50 days (mean 43.7 days, SD = 4.6, n = 16) (Chernetsov & Mukhin, in press).

How did Reed Warblers recaptured at 33-50 days, cover 20 km of woodland without reed stands (Fig. 1) between hatching and recovery sites? One possibility could be that during dispersal, Reed Warblers may move through habitats other than reed. This is however not supported by the capture data from Rybachy-type large stationary traps and mist-nets at "Fringilla" trapping station. Rybachy-type traps are oriented along the NE-SW axis, along the spit on the border of scrub and forest (for a detailed description of traps see: Dolnik & Payevsky 1976). The traps are open 24 hrs, mist-nets are situated in the scrub near the traps. During more than 40 years of trapping in summer and autumn, as few as 30 juvenile Reed Warblers were captured, whereas other long-distance migrants are captured annually in large numbers during this period (Sokolov et al. 2000). Of these 30 Reed Warblers, only 18 were trapped in late July - August, others in September and October.

We thus suggest that during juvenile dispersal. Reed Warblers fly between reed patches. Nocturnal tape-luring data from "Fringilla" lead us to expect that these movements may occur at night.

Low fat scores and active moult in all marked birds, trapped in late July - mid August, strongly support the assumption that their movements were short-range and did not indicate autumn migration. Assuming that tape-lured birds started their migratory flights from ringing sites 9-44 km from "Fringilla", and their flight speed was ca. 10 $m\text{-}s^{-1}$ (Alerstam 1990), their flying time in still air was only 15 - 75 min.

In 1999, the first Reed Warbler nestlings fledged in our study plots in late June -early July. Thus most juveniles tape-lured in late July - early August, should not be older than 50 days. As the bulk of Reed Warblers started to fledge as late as in mid July, birds aged 50 days and less could not contribute a high proportion of nocturnal captures until mid August. In late August and early September their proportion was much smaller than the proportion of birds in older age.

Our data thus strongly support the idea of Herremans (1990) that dispersal of first-autumn Reed Warblers may take place at night.

The data on 16 juvenile Reed Warblers ringed as pulli at the Museum plot and recaptured at Rybachy at the age of 33-50 days (Chernetsov 1999, Chernetsov & Mukhin, in press), and on ten birds captured at night allow the estimation of the physiological condition of birds dispersing from their natal sites. All of them are in active moult (categories 3 and 4), had low fuel stores (fat scores 0-3) and body mass not exceeding 12.8 g.

Recaptures of birds marked as nestlings provide data for valuable further analysis and discussion of nocturnal captures of unmarked Reed Warblers (see section 3.2.1). Using the data on moult, fuel stores, body mass and capture time of marked birds as a "dispersal criterion", we can try to estimate the proportion of dispersing individuals in tape-lured captures. In late July - early August it

was 39.3%, in mid August 29.2%, and in late August -early September 13.9% (Fig. 4). Thus even in the end of July and beginning of August, estimated proportion of dispersing birds is below one-half of all captured Reed Warblers. It is at the moment not possible to deduce, which type of movement captures of other birds refer to. It is worth noting that 64 out of 149 birds (43%) had completed juvenile moult and probably started the proper autumn migration. Last captures at the natal sites of juveniles ringed as pulli suggest that as few as 2-3% of Reed Warblers complete juvenile moult at their natal sites, and only about 1.5% accumulate fuel stores typical of migratory disposition (Chernetsov 1999). It is not improbable that a proportion of birds begin their autumn migration already at the last stages of moult.

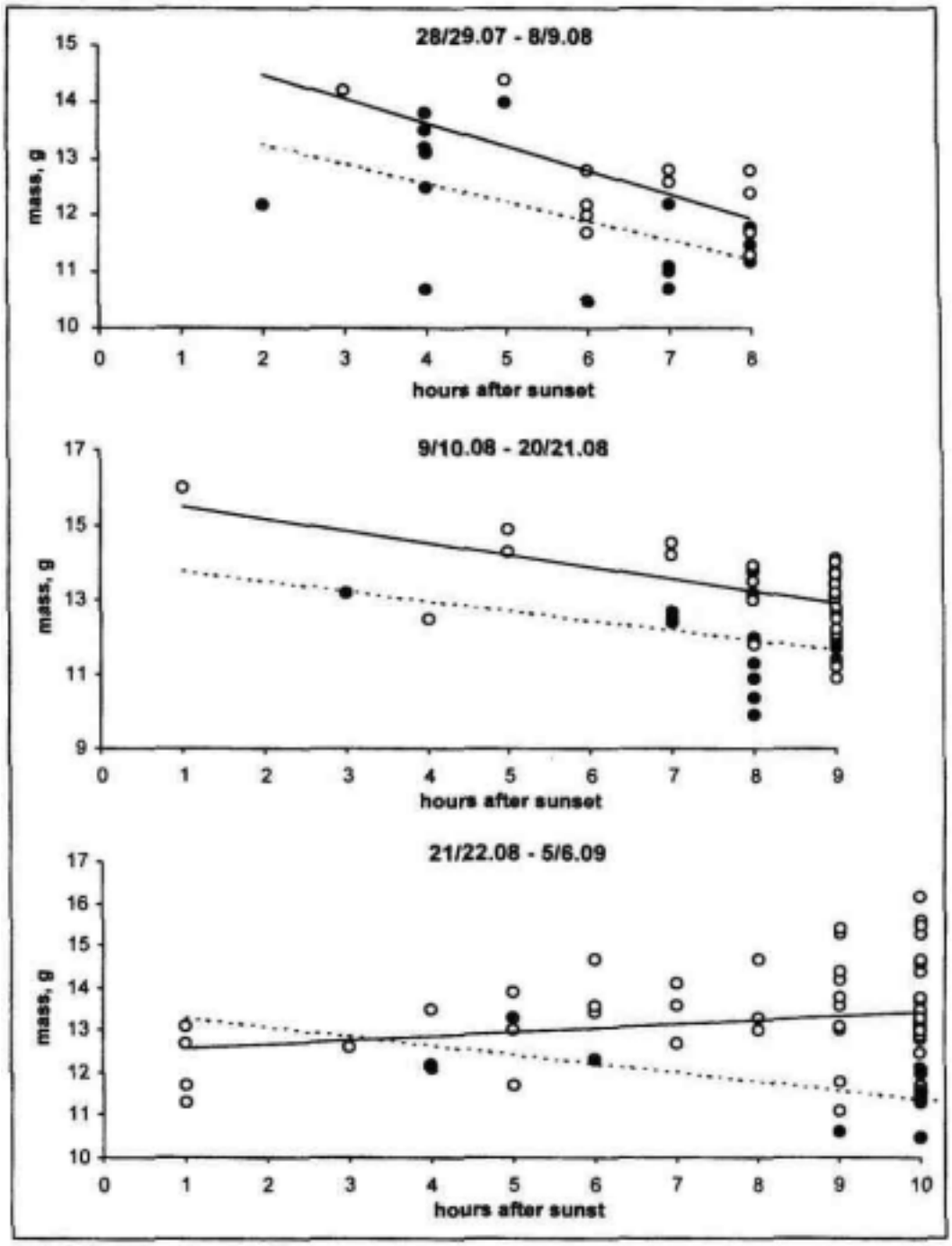

Figure 4. Body masses of Reed Warblers captured in different periods in different parts of the night. Open circles - birds with completed moult, filled circles - birds in moult. The unbroken line shows the trend of body mass in relation to capture hour in birds with completed moult, dashed line - the same for birds in moult.

Our studies and literature data show that Reed Warblers have a very protracted breeding period. It is caused by the high rate of nest predation and by the fact that a fraction of birds are double-brooded (Cramp et al. 1992). Due to all this, at the time when young from early broods can already start autumn migration, their conspecifics from late broods only reach the age of juvenile dispersal. This severely hampers differentiation between dispersing and migrating juveniles on the basis of nocturnal tape-luring. However, on the basis of our recapture data of birds of known age, and assuming that many Reed Warblers which were captured at night in active moult were dispersing, we can begin to define some of the characteristics of dispersal.

At what part of the night do birds disperse? Five out of six juvenile Reed Warblers with known natal (or marking) site, were tape-lured at "Fringilla" during the last two hours before sunrise. One more marked bird was captured there three hours before sunrise. As already shown above, their flight duration between ringing (marking) and recapture sites could not exceed 75 min. Thus it is reasonable to assume that both start and ending of nocturnal Hights took place at the end of the night. This is also supported by capture data of departing birds in high nets when three were trapped two hours before sunrise and one — three hours before sunrise. According to the pooled tape-luring data, 33 out of 45 birds in active moult (73.3%) were captured during the last three hours before sunrise.

The tendency for the bulk of Reed Warblers to make their juvenile dispersal at the end of the night could be due to better opportunities to select a good site for landing. Further, our observations show that in late July - early August, a fraction of adult male Reed Warblers (probably those making repeat or second breeding attempts) start to sing several hours before sunrise. It allows juveniles that make dispersal flights just before dawn to use not only visual cues for habitat selection (Degen & Jenni 1990, Jenni 1996), but the vocalisation of adult males, too.

However several facts suggest that post-fledgling movements may take place in other parts of the night as well. A juvenile Reed Warbler (V 017647) was tape-lured at "Fringilla" two hours after sunset. Three days later it was recovered 12 km to the NE. The other bird V 017816 was initially captured at "Fringilla" at dawn, and 22 hours later it was recaptured at Rybachy in high nets in the sixth hour after sunset. This could be either the departure for a new flight, or landing after its departure from "Fringilla" where it possibly spent the day.

We compared the temporal pattern of captures of birds in moult and birds that had completed moult and were probably on autumn migration. During the whole study period, Reed Warblers with completed moult were tape-lured during the whole night. The bulk of birds (78.1%) were captured during the last three hours before sunrise. Until mid August, birds trapped in the beginning and middle of the night were on average heavier than those captured in the last two hours. In the period 21 August - 5 September, quite to the contrary, Reed Warblers were heavier in the end of the night. The reason for this was probably a high proportion of passage individuals that ceased flight in the morning with rather high fuel loads.

Does dispersal occur during one or several nights? Of birds that were recaptured in daytime after a nocturnal capture at Rybachy 12 km to the NE, one (V 017816) remained there for four days, the other (V 017647) for seven days. The second bird increased its mass during its stay from 12.2 to 15.1 g, fat score increased from 2 to 6, the moult was nearly completed. So rapid and steep increase of body mass and fuel stores, and moult completion within only seven days in a juvenile is astonishing. Most probably, it was caused by very rapid development of migratory disposition in this bird.

Of 16 juvenile Reed Warblers that were marked in nests at Museum plot, and later recaptured at

Rybachy, 11 were trapped at the latter site once, and five - more than once. The following minimum stay durations were recorded: 2, 4, 13, 17 and 28 days. Thus at least in some birds dispersal movements take place in a short time, maybe in the form of one of several nocturnal hops. Unfortunately, there is no information available about how individual birds disperse for large distances.

Between 28 July and 20 August 1999, a total of 188 first-autumn Reed Warblers were captured and marked at Rybachy. As many local juveniles had been ringed earlier as nestlings, the majority of these birds had probably immigrated from other areas. None of them was subsequently tape-lured at "Fringilla".

Out of 78 Reed Warblers, ringed as pulli at Museum plot, only one was recaptured 12 km to the NE. Out of 57 birds that fledged at Rybachy three were recaptured at night to the SW from the natal site.

It is possible that the low number of nocturnal captures of Reed Warblers from the Museum plot was caused not only by a tendency to disperse towards the migratory direction (Nielsen & Bensch 1995). The reason could be the comparatively low number of nestlings ringed at Museum. Besides, Reed Warbler habitats at Rybachy are compact compared with those at the Museum site, where our study plot was only a part of extensive reedbeds. At Museum, juvenile Reed Warblers have good possibilities of moving within that area. Thus a large proportion of birds may need to leave the Rybachy area to achieve successful dispersal.

The bird AX 000430 was ringed as nestling at the Lake plot and then tape-lured at "Fringilla". It was captured at night in the age of 43 days 9 km to the SW from its natal site, and 8 days later recaptured 1.5 km from the natal site. Why this bird returned to the hatching area is not clear. It could be reversal of direction during dispersal, or returning from an unsuitable habitat to the familiar natal area reedbed.

5. Conclusions

The aim of many studies of juvenile dispersal in migratory passerines is to estimate the distance between natal and first breeding sites. The mechanisms of the dispersal process in individuals birds attracts less attention primarily due to methodological difficulties of monitoring birds moving long distances. In some cases, the problem is tackled by working in completely or partially isolated study plots. As shown by our results, in species like Reed Warblers, an additional problem may be that some birds disperse at night. There are good reasons to believe that many juvenile Reed Warblers make comparatively long-distance nocturnal dispersal flights. We cannot exclude the possibility that other *Acrocephali* may also disperse from the natal areas at night. In this way young birds with flight abilities impaired by active moult, may minimise the risk of predation during daytime flight. It is also possible that during nocturnal dispersal, birds may develop and calibrate their orientation mechanisms.

In this study, we attempted to find out at what age, at what time and in what condition young Reed Warblers make nocturnal dispersal flights. Other questions including what proportion of birds disperse at night, at what altitude, whether time and distance of dispersal vary among siblings, between early and late broods, and between populations, and what external and internal factors control this event, require further study.

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References

Alerstam, T. 1990. Bird Migration. Cambridge Univ. Press.

Bairlein, F. 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 *Pmus major* during winter as an example). RUSS. J. Ornithol. Express-issue 49: 17-24 (in Russian with English summary.)

Bauer, H.-G. 1987. Geburtsortstreue und Streungsverhalten junger Singvogel. Vogelwarte 34: 15-32.

Bolshakov, C.V., Bulyuk V.N., Sinelschikova A.Yu. 1999. Flight initiation of nocturnal passerine migrants from a stopover site: the method of ringed birds and its possibilities. Abstracts Confer. "100 Years Bird Ringing", Helgoland: 27.

Chernetsov, N. 1999. Migratory strategies of *Acrocephalus* warblers within Europe. Unpubl. Ph.D. thesis, Zoological Institute, St.Petersburg (in Russian).

Chernetsov, N. & Mukhin, A. 2001. The possible endogenous basis of juvenile dispersal in the Reed Warbler, *Acrocephalus scirpaceus.* The Ring. In press.

Cramp, S. (ed.). 1992.The Birds of the Western Palaearctic. Vol. VI. Cambridge: Cambridge University Press.

Degen, T. &Jenni L.1990. Biotopnutzung von Kleinvögeln in einem Naturschutzgebiet und im umliegenden Kulturland während der Hcrbstzugzeit. Orn. Beob. 87: 295-325.

Dolnik, V.R. 1975. Migratory Disposition of Birds. Nauka Press, Moscow (In Russian).

Dolnik, V.R. & Payevsky, V.A. 1976. Rybachy-type trap. In: Ilychcv, V.D. (ed.). Ringing in the study of bird migrations in the USSR. Nauka Press, Moscow: 73-81 (in Russian).

Fleiss, J.L. 1986. Statistical methods for rates and proportions. John Wiley & Sons Ltd., N.Y.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28: 1140-1162.

Greenwood, P.J. & Harvey, P.H. 1982. The natal and breeding dispersal of birds. Ann. Rev. Ecol. Sysfc 13:1-21.

Haukioja, E. 1971. Short-distance dispersal in Reed Bunting *Emberaa schoemclus.* Omis Fenn. 48:45-67.

Herremans, M. 1990. Body-moult and migration overlap in Reed Warblers *(Acrocephalus scirpaceus)* trapped during nocturnal migration. Lc Gerfaut 80: 149-158.

Insley, H.& Boswell R.C. 1978. The timing of arrivals of Reed and Sedge Warblers at south coast ringing sites during autumn passage. Ring. & Migr. 2: 1-9.

Jenni, L. 1996. Habitatwahl nachtziehender Kleinvögel bei Bodennebel. J. Omithol. 137: 425-434.

Löhrl, H. 1959. Zur Frage des Zeitpunktes einer Prägung auf die Heimatregion beim Halsbandschnäpper *(Kcedula albicollis).* J. Ornithol. 100: 132-140.

Morton, M.L., Wakamatsu M.W., Pcreyra M.E., Morton G.A. 1991. Postfledging dispersal, habitat imprinting and philopatry in a montane, migratory sparrow. Ornis Scand. 22: 98-106.

Mukhin, A. 1999. Nocturnal restlessness in caged juvenile Reed Warblers *Acrocephalus scirpaceus.* Avian Ecol. Behav. 3: 91-97.

Nielsen, B. & Bensch, S. 1995. Post-fledging movements of juvenile Rccd Warblers *Acrocephalus scirpaceus* and Sedge Warblers *Acrocephalus schoenobaenus.* Ornis Svecica 5: 125-131.

Sokolov, L.V. 1991. Philopatry and Dispersal of Birds. Proceed, of the Zool. Inst. 230, Leningrad (in Russian).

Sokolov, L.V. 1997. Philopatry of Migratory Birds. In: Phys. Gen. Biol. Reviews. Vol. 11: 1-58. Har-wood Acad. Publ., The Netherlands.

Sokolov, L.V., Yefremov, V.D., Markovets, M.Yu., Shapoval, A.P. & Shumakov, M.E. 2000. Monitoring of numbers of passage populations of passerines over 42 years (1958-1999) on the Courish Spit of Baltic Sea. Avian Ecol. Behav. 4: 31-53.

Titov, N. 1999. Fat level and temporal pattern of diurnal movements of Robins *(Erithacus rubecula)* at an autumn stopover site. Avian Ecol. Behav. 2: 89-99.

Titov, N. & Chernetsov, N. 1999. How body mass should be compared to structural size when calculating condition index? Avian Ecol. Behav. 3: 111-113.