Habitat distribution during the post-breeding and post-fledging period in the Reed Warbler *Acrocephalus scirpaceus* and Sedge Warbler *A. schoenobaenus* depends on food abundance

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- Abstract

Habitat selection in Reed and Sedge Warblers in late summer and autumn was studied on the basis of trapping in several sites along the Courish Spit. The study revealed that during the period of post-breeding and post-fledging movements birds, especially juveniles, were strongly associated with patches where their preferred food, plum aphids, was most abundant. Both Reed and Sedge Warblers were much more abundant in wet reedbeds where more aphids were recorded, although many nests occurred in dry reed. The Reed Warbler re-distributed itself within reedbeds, whereas the Sedge Warbler moved into reed stands from breeding sites in nearby sedge and shrub, thus making a more significant shift in habitat selection between the breeding and post-breeding periods. The association of birds with concentrations of their prey suggests that the purpose of post-breeding and especially postjuvenile movements is to find sites which are most suitable for completing moult and pre-migratory fattening.

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Introduction

In the avian life cycle the period of post-fledging movement is usually defined as the time between parental independence and the onset of autumn migration. The post-breeding period in adults occurs between the end of parental care and autumn migration (Sokolov 1997). The pattern and scale of such movements may differ significantly even in taxonomically and ecologically similar species (Grüll & Zwicker 1981). Shifts in diet and habitat preference may also occur (Dolnik 1982, Ormerod 1990). The post-fledging period has previously been poorly studied, primarily due to methodological difficulties (Baker 1993, Vega Rivera et al. 1998). At this time birds are often inconspicuous, call infrequently, are more mobile and leave the study area quickly. The post-fledging period is of importance for survival of first-year birds and subsequent distribution during the following breeding season. Some passerines are believed to imprint future breeding areas during this period (Sokolov 1997).

The aim of the present study was to investigate the pattern of habitat selection in Reed Acrocephalus

scirpaceus and Sedge Warblers A. schoenobaenus during the period of post-breeding and post-fledging movements. The pattern was compared with the abundace of plum aphids *Hyalopterus pruni* which is an important prey species for Sedge and Reed Warblers (Bibby & Green 1981, Koskimies & Saurola 1985, the present paper). The hypothesis was tested that birds are more abundant at sites with higher aphid scores. The body mass of birds trapped at rich and poor sites were also compared.

Study area, material and methods

My study was conducted between July and September in 1997 on the Courish Spit in the Kaliningrad Region (Russia). Four study sites were chosen, located up to 26 km apart (Figure 1), where 'active trapping' of Reed and Sedge Warblers was done. During active trapping, mistnets are placed in the sample site, then several people walk towards the nets, flushing the birds into the nets. This method differs considerably from 'passive trapping' which is applied in standardised longterm trapping programs (Berthold & Schlenker 1975, Berthold et al.

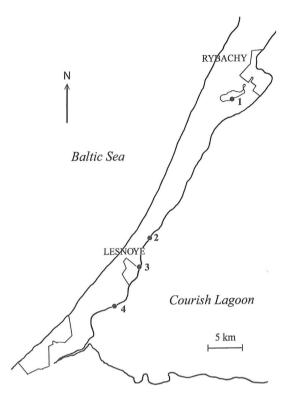


Figure 1. Map of the Courish Spit. Numbers 1–4 indicate the study sites.

Karta över Courish Spit. Siffrorna 1-4 anger studielokalerna.

1991, Bairlein et al. 1995), where the flushing of birds is not allowed. Active trapping permits only broad comparisons among trapping data. On the other hand, it allows quick and efficient trapping of birds in the sample area. This method is especially efficient in the afternoon, when the activity of the birds decreases and foraging activity is often restricted to a very limited locality. Moreover, birds are handled immediately after capture. Although no quantitative estimate of capture efficiency is available, when several successive attempts are done it becomes obvious that this method results in a high capture rate of available birds. In isolated patches of suitable habitats, active trapping enables the capture of the majority of birds present, even on the first attempt.

The following study sites were chosen (Figure 1):

Site 1 is a lake 2 km from the village of Rybachy (reedbeds along the southern shore).

Site 2 is situated in a reed bed along the shore of the Courish Lagoon, about 50 m broad, near the Museum of Nature of the National Park, 'Courish Spit'.

Site 3 is situated in a reed bed along the shore of a lagoon near the village of Lesnoye.

Site 4 is an extensive reedbed along the shore of a lagoon 7 km north of the start of the Courish Spit.

At site 4 birds were trapped both in the reedbed on the shore and in the water, up to 60–70 metres into the lagoon. The first session took place on 8 July, and the last on 22 September when numbers of *Acrocephalus* warblers dropped dramatically. A total of 11 sessions were conducted, three in July, five in August, and three in September. Although only a rough comparison was possible, every attempt was made to keep the effort similar across all sites, and greater than tenfold differences in counts were assumed to indicate distinct trends.

All trapped birds were ringed, aged and sexed. Wing–length was measured and fat and muscle scores were taken. Fat scoring followed Kaiser (1993). Moult scoring followed the standard procedure of the ESF programme (Bairlein et al. 1995) which allows to distinguish between the beginning of moult, active moult, finishing moult, and completed moult.

Before and between trapping sessions the study areas were searched for nests of *Acrocephalus* warblers and young were later ringed in the located nests. A total of 378 ringed Reed Warblers and ten Sedge Warblers fledged.

In parallel with bird trapping, estimates of plum aphid abundances were done at each site. Plum aphids are believed to be the main prey of the Sedge Warbler in Europe in late summer and autumn (Bibby & Green 1981, Koskimies & Saurola 1985). In the diet of the Reed Warbler plum aphids are considered to be less important (Bibby & Green 1981). Methods of aphid collection and estimation of abundance followed Shaposhnikov (1952). In every sample site the number of colonies on 20 reed stems was counted, along with the number of plum aphids in 20 colonies. Average number of aphids in a colony was used as an estimate of aphid abundance.

Results

Aphids

Aphid abundance is presented in Table 1 and shows a clear distinction between sites with low or zero aphid counts (dry sites) and those with consistently high counts (wet sites). Study sites can thus be divided into two groups, those practically without aphids (sites 2 and 4 [dry]) and those with aphids

	Site Lokal				
Dates Datum	1 (wet)	2 (wet)	3 (dry)	4 (dry)	4 (wet)
18 July	_	_	_	14 ± 8	_
22 July	-	-	_	23 ± 22	-
3 August	50 ± 41	_	0	0	-
9 August	61 ± 41	_	0	0	-
18 August	57 ± 41	110 ± 16	0	17 ± 5	108 ± 31
22 August	55 ± 35	80 ± 50	0	0	152 ± 42
31 August	106 ± 74	130 ± 52	0	0	175 ± 70
4 September	95 ± 26	135 ± 46	0	0	102 ± 54
12 September	61 ± 22	53 ± 24	0	0	77 ± 18
20 September	48 ± 12	70 ± 39	0	0	72 ± 47

Table 1. Mean aphid scores (\pm SD) at each site between July and September in 1997. *Genomsnittligt bladlusindex* (\pm SD) vid de olika lokalerna mellan juli och september 1997.

present (sites 1, 2, and 4 [wet]). At site 4 (dry) the aphid colonies were recorded until mid August but subsequently disappeared, probably due to high temperatures in late July and August. No colonies were recorded at site 3. Humid conditions prevailed at the remaining sites, and high aphid counts were evident.

Reed Warbler

A total of 97 adults were trapped, and the totals for each site are shown in Table 2. In July and early August nearly all adults were caught near their nests and numbers were similar at dry and wet sites (46 and 43 birds respectively). After 10 August, when the majority of birds were in pre-migratory state, only eight adults were trapped, of which seven were at wet sites where aphids were abundant. During this last period, adults remaining in the breeding area concentrated in places where aphids were abundant. The average body mass (\pm SD) of adults trapped after 10 August was 14.1 \pm 1.24 g (n=8).

Of the 85 juveniles, 13% were trapped in the vicinity of nests at an age when not able to fly properly and probably still dependent of their parents (eleven birds still having flight feathers growing and post-juvenile moult commencing). The remaining birds were caught after gaining independence. Of the juveniles trapped when in an advanced stage of moult, more than 90% were trapped at wet sites with aphids (69 out of 73). For example, at site 4 the reedbeds along the shore (where all nests were

Table 2. Total number of Reed and Sedge Warblers trapped at each site during 1997. The trapping effort was similar across sites (see text).

Totalt antal fån	gade rörsångare	e och sävsångare	vid de olika	lokalerna	under 1997.

Site	Soil type	Reed Warbler <i>Rörsångare</i>		Sedge Warbler	
Plats	Markförhållanden			Sävse	ångare
		adult	1st year	adult	1st year
1	wet / blött	31	33	6	38
2	wet / blött	17	22	0	7
3	dry / torrt	14	1	0	0
4 (dry)	dry / torrt	32	4	0	2
4 (wet)	wet / torrt	2	24	0	28

situated) and in the lagoon were about 30–80 metres apart. From late July and onwards, aphids occurred on the reed in the lagoon, but not on those along shore. Thus, immediately after gaining independence, juveniles moved to the lagoon reeds containing aphids (Table 1). Ten juvenile Reed Warblers ringed as nestlings were subsequently recaptured, eight of them at wet sites.

A total of 58 juveniles were caught at late stages of moult and the first one was trapped on 9 August. The first juvenile Reed Warbler showing completed moult was caught on 17 August and alltogether 24 juveniles with completed post-juvenile moult was captured. All individuals that had completed moult were trapped at wet sites. The average body mass of these birds was 14.7 \pm 1.42 g (n=24), i.e. slightly higher than the average body mass of adults. I compared body mass of juveniles at advanced stages of moult (medium moult, end of moult, moult finished) in different habitats. At the dry sites the average mass was 12.4 \pm 0.57 g (n=4), and for wet sites 13.6 \pm 1.58 g (n=67). The difference was not significant (t=2.49, p>0.10).

Sedge Warbler

A total of six adults and 75 juveniles were trapped, all but two (juveniles) at wet sites (Table 2). The average body mass of adults $(13.8\pm0.41 \text{ g})$ was only slightly greater than for juveniles $(13.0\pm1.38 \text{ g},$ n=69, wet sites). The body mass of the two juveniles caught at Lesnoye (dry site) were 12.6 g and 12.9 g, respectively. The abbreviated post-juvenile and postnuptial moult has limited effect on the physiological status and fat index of Sedge Warblers (Chernetsov 1996), therefore moulting and non-moulting juveniles were combined in calculations. No Sedge Warblers ringed as nestlings were subsequently recaptured.

Discussion

The patterns of occurrence of Reed and Sedge Warblers within the reedbeds are similar during the postbreeding and post-fledging periods. Adults are mainly trapped in the vicinity of nests in breeding habitats. Once parental care ceases, it is likely that adult birds quickly put on fat and begin migration. Early onset of autumn migration in adult Reed and Sedge Warblers has been reported from many sites in Europe and Asia (Insley & Boswell 1978, Gavrilov 1980, Koskimies & Saurola 1985, Leivits & Vilbaste 1990, Chernetsov 1996). This paper suggests that a few adult Reed Warblers after breeding move from the breeding sites to wet reedbeds with richer food supply. The summer of 1997 was unusually hot and dry at the Courish Spit, and breeding sites dried out and probably became unsuitable for foraging.

Post-fledging movements of juveniles are more pronounced than post-breeding movements in adults. Both Reed and Sedge Warblers were concentrated in places where food was abundant. In reedbeds near Peterhof (St. Petersburg region), juvenile Reed Warblers move from dry reedbeds where most nests are situated, into wet reedbeds, where aphids are much more numerous (V. A. Fedorov, pers. comm.). As food sources are variable and "spatially heterogeneous" (aphid abundance may differ by several orders of magnitude between sites only 50–100 metres apart), the distribution of birds within reedbeds is patchy.

Although the Reed Warbler re-distributes itself during the pre-migratory period within the speciesspecific habitat (reedbeds, pure or mixed stands), the Sedge Warbler exhibits a more significant shift in habitat selection, from breeding sites in sedge and scrub vegetation into reedbeds (Koskimies 1991, Cramp et al. 1992). Such a shift has been previously reported for this species (Ormerod 1990, Koskimies 1991).

In the absence of high aphid concentrations Sedge Warblers may utilise alternative prey species (Grosch 1995, Chernetsov 1998), although the exploitation of locally superabundant prey is the main foraging strategy of both Reed and Sedge Warblers (Chernetsov & Manukyan, in prep.). On the Courish Spit *Acrocephalus* warblers forage on aphids, their invertebrate predators and parasites. This corresponds to the report from Estonia where *Hyalopterus pruni* is an important prey for both Sedge and Reed Warblers (Mäll 1995).

Body mass of both Reed and Sedge Warblers was higher than reported from a number of Baltic and Scandinavian sites (Leivits & Vilbaste 1990, Celmins 1990, Hall 1996). Individuals that had completed moult may accumulate much fuel for migratory flights at sites with abundant prey. It should be noted however that differences in body mass of birds within the same habitat, at sites differing in prey abundance, suggest that considerable variation in the condition of individual birds occur within sites. Juveniles capable of tracking locally superabundant food sources have an advantage for performing energy–consuming moult (Reed Warbler) and premigratory fattening (both species). Within site variation in average body mass of birds complicate comparisons of body mass of birds between geographically distant sites (Bibby & Green 1981, Bairlein 1991, Chernetsov 1996).

The association of birds with prey concentrations suggests an important role of food for the understanding of patterns in post-fledging movements of *Acrocephalus* warblers. The purpose of these movements is to locate sites most suitable for providing resources to complete moult and pre-migratory fattening. My study on the *Acrocephalus* warblers supports the suggestion that foraging optimisation plays a role in determining post-fledging movements (Mikhejev 1961, Vega Rivera et al. 1998).

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Sammanfattning

Habitatutnyttjande under efterhäckningstiden hos rörsångare Acrocephalus scirpaceus och sävsångare A. schoenobaenus i relation till riklig tillgång på föda.

Efterhäckningstiden är en dåligt studerad period i fåglarnas årscykel, framförallt beroende på metodologiska svårigheter (Baker 1993, Vega Rivera et al. 1998). Under efterhäckningstiden för fåglarna ett tillbakadraget liv, och är inte lika hårt knutna till ett visst område som under häckningstiden, vilket gör dem svårare att följa i fält. Efterhäckningsperioden är dock ingalunda en parentes i årscykeln – då utförs flera aktiviteter som är viktiga för den fortsatta överlevnaden (ruggning och fettpålagring inför flyttningen) och förberedelser inför den kommande häckningssäsongen (sökande efter möjliga häckningsplatser).

Studien genomfördes mellan juli och september 1997 vid Courish Spit (Kaliningrad, Ryssland). Fyra studieområden valdes inom ett område som spänner 26 kilometer i nordsydlig riktning längs Östersjöns sydöstra strand (Figur 1). På dessa platser utfördes "aktiv" fångst av rörsångare och sävsångare. Med aktiv fångst avses här att nät sattes upp i vassmiljö, varefter de fåglar som gömde sig i vegetationen skrämdes in i näten. Denna metod har visat sig mycket effektiv vad gäller att fånga lokala fåglar som ofta har små födosöksområden. Parallellt med nätfångsten räknades förekomst av bladlöss (Hvalopterus pruni) vid de olika lokalerna. Tidigare under samma säsong hade de fyra lokalerna noggrant genomsökts efter bon av Acrocephalus sångare.

Av Tabell 1 framgår att tillgången på bladlöss var mycket högre bland vass som stod blött jämfört med vass på torrlagd botten. Totalt fångades 97 adulta rörsångare (Tabell 2). I juli och början av augusti

fångades adulta fåglar framförallt i närheten av sina bon, och antalet var jämnt fördelat mellan våta och torra lokaler (46 respektive 43 fåglar). Efter 10 augusti fångades endast åtta adulta rörsångare, av vilka sju fångades vid de våta lokalerna som också höll höga tätheter av bladlöss. Av de 85 juvenila rörsångarna, fångades 13% i närheten av bon medan de fortfarande var beroende av sina föräldrar. Av de juveniler som fångades vid högre ålder när ungfågelruggning var väl framskriden, fördelade sig 93% på de våta lokalerna. Kroppsvikten för fåglarna på de torra lokalerna var något lägre än vid de våta lokalerna (12,4±0,57, n=4 mot 13,6±1.58, n=67) men skillnaden var inte signifikant (t=2.49, P>0,1). Totalt fångades sex adulta och 75 juvenila sävsångare, alla utom två (juvenila) vid de våta lokalerna (Tabell 2). Medelvikten för adulterna (13,8±0.41 g, n=6) var endast något högre än för juvenilerna (13,0±1.38, n=69).

Rörsångarna och sävsångarna visade på en likartad fördelning mellan vassområden under efterhäckningsperioden. Båda arterna visade de högsta tätheterna där födan var riklig. Även om rörsångaren ändrar sin fördelning inom vassområdena mellan häcknings- och efterhäckningstiden, visar sävsångaren en mer radikal habitatvalsförändring, eftersom den framförallt häckar i annan strandvegetation än vass.

I frånvaro av höga bladluskoncentrationer måste sävsångaren utnyttja andra byten, även om utnyttjandet av lokalt superabundanta byten är den vanliga födosöksstrategin får både rörsångare och sävsångare (Chernetsov och Manukyan opubl.). Associationen mellan dessa sångare och bladluskoncentrationer pekar på betydelsen av födan för förståelsen av t.ex. unfågelrörelser hos *Acrocephalus* sångare. Orsaken till dessa rörelser kan vara att finna platser med lämpliga resurser för att genomföra ruggningen och fettpålagring inför flyttningen (Mikhejev 1961, Vega Rivera et al. 1998).