

MOVEMENT PATTERNS OF EUROPEAN REED WARBLERS *ACROCEPHALUS SCIRPACEUS* AND SEDGE WARBLERS *A. SCHOENOBÆNUS* BEFORE AND DURING AUTUMN MIGRATION

NIKITA CHERNETSOV & NIKOLAY TITOV

Chernetsov N. & N. Titov 2001. Movement patterns of European Reed Warblers *Acrocephalus scirpaceus* and Sedge Warblers *A. schoenobaenus* before and during autumn migration. *Ardea* 89(3): 509-515.

The foraging movements of European Reed Warblers *Acrocephalus scirpaceus* and Sedge Warblers *Acrocephalus schoenobaenus* at migratory stopover sites were studied by comparing the frequency distribution of distances between capture-recapture localities of individual birds with a simulation model of a random distribution of movements. The results indicate that Reed Warblers have no defined home ranges before autumn migration, but move randomly or nearly randomly between localities at a stopover site. Reed Warblers and Sedge Warblers at migratory stopovers have home ranges that are too large to be exclusive territories. Previous studies have shown that Robins *Erithacus rubecula* and Wrens *Troglodytes troglodytes* have well-defined small home ranges at stopovers. It is suggested that the reason for these differences is due to the differences in feeding ecology of the species concerned, in particular the spatial distribution of their prey. Both Reed and Sedge Warblers forage on invertebrates, which are unpredictable in their distribution and in the timing of their occurrence.

Keywords: *Acrocephalus schoenobaenus* - *Acrocephalus scirpaceus* - home range - migration - foraging movements

Biological Station Rybachy, Zoological Institute, Rybachy 238535, Kaliningrad Region, Russia; E-mail: NChernetsov@bioryb.koenig.su



INTRODUCTION

The spatial distribution of foraging movements at migratory stopover sites is an important feature of an avian species migratory strategy. Some migrants are known to have temporary territories or at least small home ranges at stopovers (Szulc-Oleh 1965; Kodric-Brown & Brown 1978; Bibby & Green 1980, 1981, Carpenter *et al.* 1983; Mehlum 1983; Titov 1999a, b). In the Robin *Erithacus rubecula* and the Wren *Troglodytes troglodytes* it was shown that at migratory stopovers individuals that make prolonged stopovers have a smaller home range, rather than move randomly over a large area (Szulc-Oleh 1965; Mehlum 1983; Titov 1999a, b). Studies in Portugal showed that Pied Flycatchers *Ficedula hypoleuca* (Bibby & Green 1980) and European Reed Warblers *Acrocephalus*

scirpaceus occupied territories at stopovers, whereas Sedge Warblers *Acrocephalus schoenobaenus* did not (Bibby & Green 1981). The authors suggest that the reason is that European Reed Warblers forage on active, easily disturbed insects and have to defend their territories against conspecifics. Sedge Warblers feed mainly on aphids and do not need to defend their foraging ranges. More recent studies have shown, however, that the difference in foraging strategies between Reed and Sedge Warblers is not so clear-cut as they suggest (Chernetsov & Manukyan 1999, 2000).

Recent studies of the distribution of movements at migratory stopovers use neutral models (Titov 1999a). The method is to compare the frequency distribution of distances between capture localities of the same bird at a trapping site with a model which assumes random movements of a

bird within a study area. If the real data differ from the model then the bird's movements are considered to be non-random. This method does not show whether birds defend their home ranges, i.e. whether they obtain territories *sensu* Fretwell & Lucas (1970). We applied this method of neutral models to test the hypothesis that Reed and Sedge Warblers gain temporary individual home ranges at migratory stopovers. We also tested for the possible difference in this respect between moulting (local) and having completed moult (passage) European Reed Warblers.

MATERIALS AND METHODS

The trapping data from Rybachy, Courish Spit, Russia (55°09'N, 20°52'E) were analysed. The trapping was done within the framework of a joint research project of the Biological Station Rybachy and Vogelwarte Radolfzell (Germany). Trapping and handling routine followed the guidelines of the ESF programme (Bairlein 1995). A total of 73 mist-nets were used at the trapping station with

an area of ca. 0.6 ha (Fig. 1). Each bird was released within one hour of trapping and the number of the mist-net where a bird was trapped was always recorded. The same procedure was followed for recaptures; i.e. the locality of all captures was known for each bird. This enabled the creation of a frequency distribution of distances between capture localities of an individual bird.

To run the simulations, net numbers generated by the random numbers' generator of FoxPro 2.0 software replaced the real net numbers. Both Reed and Sedge Warblers were much more frequently trapped in nets in the reedbed than in other habitats. The probability of 'captures' in a certain virtual net was related to the probability of capture in the real net with this number (model 2 from Titov 1999a). Subsequently the distribution of distances between simulated 'trapping localities' was computed. These simulated localities referred to the random movement distribution, when a bird moves around the study site without showing any preferences for a particular area(s) within it (and not avoiding any particular area(s), either). For each model, 10°000 distances were calculated. If multiple captures in real nets occur independently (i.e. recaptures are not biased towards shorter distances), no significant difference between real data and the model should be recorded. This would mean that home ranges of birds are at least as large as the study area. If recaptures occur significantly closer to the previous capture site than predicted by the model, home ranges smaller than the study area should be assumed.

Trapping data from 1994-1996 were included in the analysis, when the number of Reed and Sedge Warbler was highest. Due to rapid vegetation succession at the study site we did not pool the data over a longer period. Capture efficiency of individual nets altered over the years as willow scrub gradually replaced reed. Over three consecutive years the habitat change was not very great. First-year birds trapped from 15 July onwards were included in the analysis. The last birds leave the Courish Spit by mid October. Simulations were run separately for:

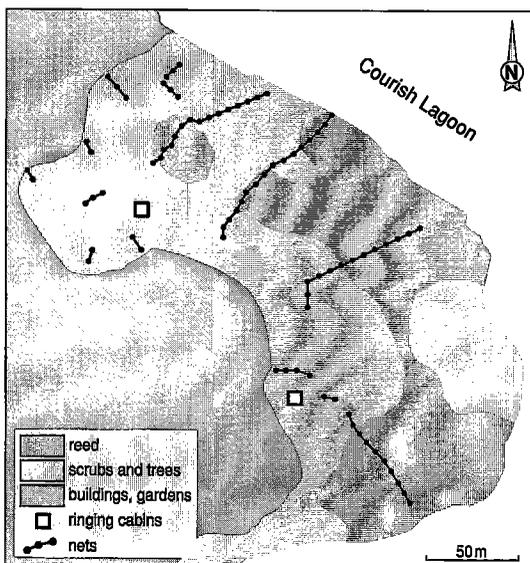


Fig. 1. Map of the study site.

- European Reed Warblers in post-juvenile moult;
- European Reed Warblers that have completed moult; and
- Sedge Warblers without growing feathers.

The first group includes mostly local European Reed Warblers, 25-30 to 55-60 d old, before the onset of autumn migration. In the Sedge Warbler post-juvenile moult is much abridged (though not completely; Fedorov 1990; Redfern & Alker 1996), therefore it is difficult to distinguish between local and passage individuals in this species.

RESULTS

Moulted European Reed Warblers trapped before the onset of autumn migration ($n = 1047$) showed a distribution of distances moved between capture localities that was clearly different from that predicted by the model (Kolmogorov-Smirnov test, $\lambda_{1047, 10000} = 2.27, P < 0.001$; Fig. 2). A detailed inspection of Fig. 2 shows that this difference from the model was due to less frequent captures within 40 m from the previous capture site, than predicted by the random movement model. With this part of the distribution excluded, the difference was not significant ($\lambda_{868, 7603} = 0.84, P = 0.50$). Captures of moulted European Reed Warblers before the onset of autumn migration are not concentrated in a certain area, the birds rather prefer to move widely across the trapping site. A weak trend to avoid the immediate vicinity of the previous capture site may be noted.

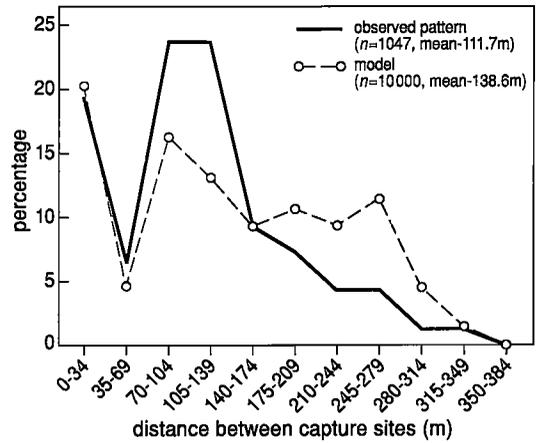


Fig. 2. Distribution of distances moved between capture localities by moulted European Reed Warblers.

In European Reed Warblers that have completed moult which were mainly passage migrants ($n = 97$), a different distribution is observed ($\lambda_{97, 10000} = 1.87, P < 0.002$; Fig. 3). The number of captures within 70-140 m from the previous capture site is significantly higher than predicted by the random movement model. At migratory stopovers European Reed Warblers have defined home ranges of large size but definitely smaller than the study site. In Sedge Warblers ($n = 294$) the proportion of captures less than 100 m from the previous capture location is higher than predicted by the model ($\lambda_{294, 10000} = 2.80, P < 0.001$; Fig. 4). This species, like migrating European Reed Warblers, have rather large home ranges.

We compared length of stay of pre-migratory and migrating European Reed Warblers and migrating Sedge Warblers at Rossitten Cape (cal-

Table 1. Length of stay in the study area and the approximate radius of the home range in Reed and Sedge Warblers at Rybachy.

	Length of stay, pre-migratory	days migratory	Home range pre-migratory	radius, m migratory
European Reed Warbler	17-19	ca. 3	>360 m	140 m
Sedge Warbler	-	2-4	-	100 m
Source	Chernetsov 1999	Chernetsov 1999	this study	this study

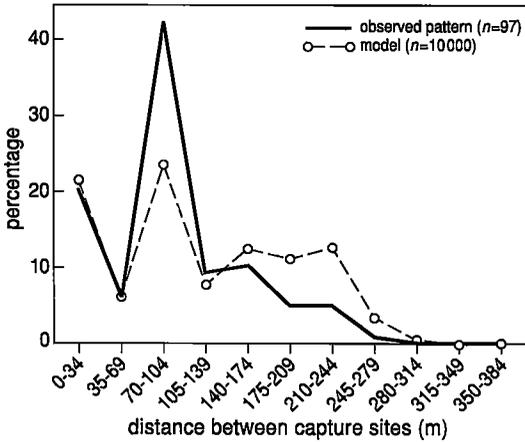


Fig. 3. Distribution of distances moved between capture localities by European Reed Warblers that have completed moult.

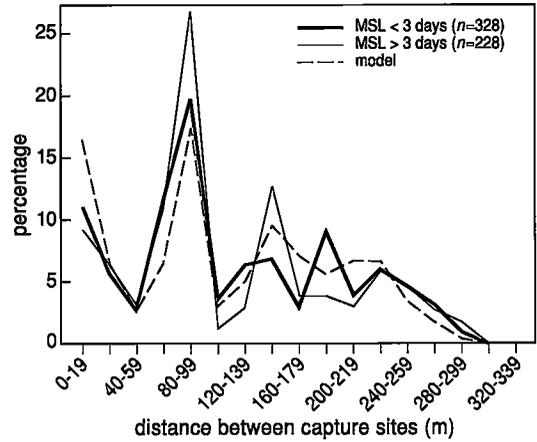


Fig. 5. Distribution of distances moved between capture localities by moulting European Reed Warblers with the minimum length of stay of 1-2 days and more than three days.

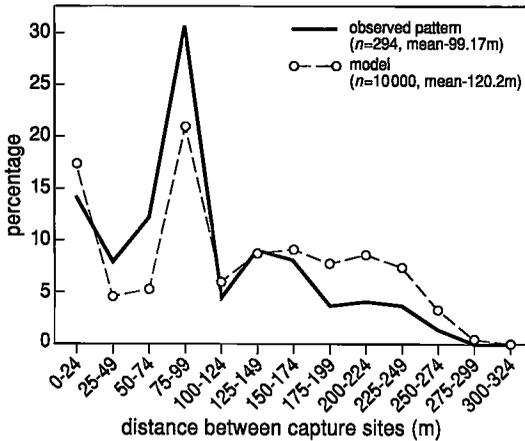


Fig. 4. Distribution of distances moved between capture localities by Sedge Warblers without growing feathers.

culated after capture-mark-recapture models) (Chernetsov 1999), and the radius of their home ranges in respective periods (Table 1). It is possible that European Reed Warblers, during their rather long stay visit a large area, whereas during short periods of time, comparable with the length of migratory stopovers, their home range is much smaller. To test for this possibility, we calculated

the frequency distribution between capture localities of moulting birds with a time elapsed between capture events not exceeding two days (Fig. 5). This distribution was not significantly different from the distribution for birds with a minimum stopover length of more than three days ($\lambda_{328, 228} = 0.95, P > 0.10$). This means that wide movements across the study site are not the result of a long stay at the study site, but occur within a short period of time.

DISCUSSION

During the post-fledging foraging movements before the onset of autumn migration European Reed Warblers do not possess well defined home ranges, their size is comparable with the area of the trapping site (ca. 0.6 ha). Territorial behaviour is not possible as the same area is a home range for many individuals. Movements within the preferred habitat, and change of the habitat during the post-fledging period are typical of *Acrocephalus* warblers (Ormerod 1990; Chernetsov 1998; Honza *et al.* 2000). During this period, birds seem

to be moving actively, which can be important for solving orientation tasks, habitat exploration, searching for future breeding sites (Sokolov 1997; Fedorov 2000), as well as for foraging optimisation (Vega Rivera *et al.* 1998; Chernetsov 1998). This can be a reason for broad movements of moulting European Reed Warblers.

Our results for the migratory period are different from those obtained for the Robin and the Wren at the same site (Titov 1999b). The latter two species occupied small home ranges that were 'probably defended at least by Robins'. Our data for the European Reed Warbler (no small defended ranges) also differs with the results from Portugal (Bibby & Green 1981) and from Sweden (G. Walinder in Schaub & Jenni 2000).

Territorial behaviour is known to be costly in terms of time and energy (for a review see: Dolnik 1995). For it to be favourable, the benefits must outweigh the costs. Costs of defending a home range seem to be justified in Robins and Wrens (Titov 1999b), but not in *Acrocephali*, either during the pre-migratory period or at migratory stopovers. What may account for this difference? One of possible explanations is that Robins on migration utilise resources that are uniformly distributed. Indeed, on the Courish Spit Robins mainly take terrestrial invertebrates that have a more or less uniform spatial distribution, they are not selective when feeding (Titov 2000). In such case obtaining and defending a territory may bring a short-term benefit, namely help to maximise the feeding rate (Begon *et al.* 1986). On the Courish Spit both Reed and Sedge Warblers utilise prey, which is locally superabundant but unpredictable in their distribution and the timing of their occurrence. These are mainly chironomids, aphids and the community of insects that are ecologically connected with aphids (Chernetsov & Manukyan 1999, 2000). It may be worth noting that during the breeding season neither Reed nor Sedge Warblers hold separate feeding territories (Catchpole 1972). Birds that utilise patchily distributed and unpredictable prey may not need to obtain individual home ranges or territories for maximising their feeding rate. The bulk of the population may do

better by adopting the floater strategy (Bairlein 1996).

If this suggestion is correct, the difference between the short distance movements of European Reed Warblers at migratory stopovers in Iberian Peninsula and on the Courish Spit may be explained by the difference in foraging ecology between these regions (Bibby & Green 1981, Chernetsov & Manukyan 1999), and possibly by variation between years.

Another reason for the observed difference may be the very high numbers of Robins at stopovers on the Courish Spit in some days during migration (Titov 1999b). The pressure of competitors may force birds to obtain exclusive feeding ranges. In Reed and Sedge Warblers in autumn day-to-day variation in trapping figures is less pronounced (Chernetsov 1999). Together with earlier passage season and better food supply it may allow these species to forage non-territorially, without carrying costs of territorial behaviour. We however believe that this explanation is less likely as the bulk of Robins obtain territories 1-2 days after arrival when the number of stopover migrants declines (Titov 1999b). Northern Wheatears *Oenanthe oenanthe* at stopovers on Helgoland (North Sea) stopped defending temporarily territories when the number of conspecifics became too high (Delingat & Dierschke 2000, and pers. comm.). It is more likely that the cause of inter-specific difference in the strategy of territory exploitation at stopovers is the difference in foraging strategy, which is linked to the unpredictable prey distribution.

ACKNOWLEDGEMENTS

We are grateful to Casimir Bolshakov for the facilities of the Biological Station Rybachy that allowed us to carry out this study. We would like also to thank all volunteer bird-ringers who participated in the trapping project and helped to collect the data analysed here. Martin Griffiths improved the English and made some important comments on the manuscript. Two anonymous referees made many valuable suggestions that helped us to improve the earlier draft greatly.

REFERENCES

- Bairlein F. 1995. European-African Songbird Migration Network: Manual of field methods. Vogelwarte Helgoland, Wilhelmshaven.
- Bairlein F. 1996. Ökologie der Vögel. Gustav Fischer Verlag, Stuttgart.
- Begon M., Harper J.L. & C.R. Townsend 1986. Ecology. Individuals, Populations and Communities. Blackwell Sc. Publ., Oxford.
- Bibby C.J. & R.E. Green 1980. Foraging behaviour of migrant Pied Flycatchers, *Ficedula hypoleuca*, on temporary territories. J. Animal Ecol. 49: 507-521.
- Bibby C.J. & R.E. Green 1981. Autumn migration strategies of Reed and Sedge Warblers. Ornis Scand. 12: 1-12.
- Carpenter F.L., D.C. Paton & M.A. Hixon 1983. Weight gain and adjustment of feeding territory size in migrant Rufous Hummingbirds. Proc. Nat. Acad. Sci. USA 80: 7259-7263.
- Catchpole C.K. 1972. A comparative study of territory in the Reed Warbler (*Acrocephalus scirpaceus*) and Sedge Warbler (*A. schoenobaenus*). J. Zool., London 166: 213-231.
- Chernetsov N. 1998. Post-breeding and post-fledging movements in the Reed Warbler (*Acrocephalus scirpaceus*) and Sedge Warbler (*A. schoenobaenus*) depend on food abundance. Ornis Svecica 8: 77-82.
- Chernetsov N. 1999. Migration strategies of *Acrocephalus* warblers within Europe. Unpubl. Ph.D. thesis, Zoological Institute, St.Petersburg [in Russian].
- Chernetsov N. & A. Manukyan 1999. Feeding strategy of Reed Warblers *Acrocephalus scirpaceus* on migration. Avian Ecol. Behav. 3: 59-68.
- Chernetsov N. & A. Manukyan 2000. Foraging strategy of the Sedge Warbler (*Acrocephalus schoenobaenus*) on migration. Vogelwarte 40: 189-197.
- Delingat J. & V. Dierschke 2000. Habitat utilization by Northern Wheatears (*Oenanthe oenanthe*) stopping over on an offshore island during migration. Vogelwarte 40: 271-278.
- Dolnik V.R. 1995. Energy and time resources in free-living birds. Nauka Press, St.Petersburg [in Russian].
- Fedorov V.A. 1990. Sedge Warbler - *Acrocephalus schoenobaenus*. In: Rymkevich T.A. (ed.) Moults of passerines of north-western USSR: 85-88. Leningrad Univ. Press, Leningrad [in Russian].
- Fedorov V.A. 2000. Factors affecting breeding and natal dispersal in the Great Reed Warbler (*Acrocephalus arundinaceus*). Vogelwarte 40: 279-285.
- Fretwell S.D. & H.L.L. Lucas 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheor. 19: 16-36.
- Honza M., Literák I., Pavelka J. & J. Formánek 2000. Postbreeding occurrence of the Marsh Warbler *Acrocephalus palustris* in reedbed areas in the Czech Republic and its migration to Africa. Ökol. Vögel (Ecol. Birds) 22: 119-129.
- Kodric-Brown A. & J.H. Brown 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality in migrant Rufous Hummingbirds. Ecology 49: 285-296.
- Mehlum F. 1983. Resting time in migrant Robins *Erithacus rubecula* at Store Færder, outer Oslofjord, Norway. Fauna norv. Seria C, Cinclus 6: 62-72.
- Ormerod S.J. 1990. Time of passage, habitat use and mass change of *Acrocephalus* warblers in a South Wales reedswamp. Ring. & Migr. 11: 1-11.
- Redfern C.P.F. & P.J. Alker 1996. Plumage development and post-juvenile moult in the Sedge Warbler *Acrocephalus schoenobaenus*. J. Avian Biol. 27: 157-163.
- Schaub M. & L. Jenni 2000. Fuel deposition of three passerine bird species along the migratory route. Oecologia 122: 306-317.
- Sokolov L.V. 1997. Philopatry of Migratory Birds. In: Turpaev T.M. (ed.) Phys. Gen. Biol. Reviews 11: 1-58. Harwood Acad. Press, Amsterdam.
- Szulc-Oleh B. 1965. The resting period of migrant Robins on autumn passage. Bird Study 12: 1-7.
- Titov N. 1999a. Individual home ranges in Robins *Erithacus rubecula* at stopovers during autumn migration. Vogelwelt 120: 237-242.
- Titov N. 1999b. Home ranges in two passerine nocturnal migrants at a stopover site in autumn. Avian Ecol. Behav. 3: 69-78.
- Titov N. 2000. Interaction between foraging strategy and autumn migratory strategy in the Robin *Erithacus rubecula*. Avian Ecol. Behav. 5: 35-44.
- Vega Rivera J.H., J.H. Rappole, W.J. McShea & C.A. Haas 1998. Wood thrush postfledging movements and habitat use in northern Virginia. Condor 100: 69-78.

SAMENVATTING

Kleine Karekieten *Acrocephalus scirpaceus* en Rietzangers *Acrocephalus schoenobaenus* werden in het najaar van 1994-96 gevangen met mistnetten in een moerasgebied bij Rybachy in Rusland. Elk mistnet had een eigen nummer en bij elke vangst werd het mistnetnummer genoteerd. Dat maakte het mogelijk om de afstand tussen twee opeenvolgende vangsten van een zelfde individu te berekenen. Uitgaande van de vaste locaties van de netten en rekening houdend met het feit dat de Rietzangers en Kleine Karekieten vooral gevangen werden in de netten in het rietland, kon een verde-

ling van vangafstanden worden berekend indien de individuen zich volkomen toevallig door het terrein zouden verplaatsen. Deze modelverdeling kon daarna vergeleken worden met de waargenomen verdeling. Voor ruiende Kleine Karekieten verschilden de twee verdelingen nauwelijks, al waren korte afstanden significant ondervetegenwoordigd. Dit betekent dat individuen zich door het hele terrein verplaatsten en mogelijk de plek meden waar ze net gevangen waren. Kleine Karekieten en Rietzangers die klaar waren met de rui, hadden een beperktere actieradius. Het is mogelijk dat deze beperktere actieradius te maken heeft met de korte verblijfsduur van doortrekkende Kleine Karekieten en Rietzangers. De actieradius van ruiende Kleine Kare-

kieten vertoonde echter geen verband met de geschatte verblijfsduur. Hoewel individuele Kleine Karekieten en Rietzangers op doortrek niet het gehele gebied gebruikten, waren hun individuele home ranges overlappend en veel groter dan de in hetzelfde gebied gevangen Roodborsten *Erithacus rubecula* en Winterkoninkjes *Troglodytes troglodytes*, die waarschijnlijk tijdelijke voedsel-territoria verdedigden. De auteurs suggereren dat dit verschil in gedrag terug te voeren is op het verschil in voedselkeus. (BJE)

Received 1 September 2000, accepted 21 May 2001
Corresponding editor: Bruno J. Ens