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Factors affecting breeding and natal dispersal in the Great Reed Warbler *(Acrocephalus arundinaceus)*

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Breeding and natal dispersal of the Great Reed Warbler *(Acrocephalus arundinaceus)* were studied in the southern part of the Pskov Region and on the Courish Spit on the coast of the Baltic Sea. As with many other species, adults are more likely to return to their breeding sites after successful reproduction than after breeding failure. As a rule, after several (usually two) unsuccessful breeding-attempts, adults will desert the nesting area. The following year, such birds did not return to the initial breeding site but chose instead the place to which they subsequently migrated. In young birds, a relationship has been noted between dispersal and what previously has happened to them as nestlings. It seems that the tendency to disperse is affected, at least partially, by hardships (e.g. poor feeding conditions) suffered prior to fledging.

Key words: Great Reed Warbler *(Acrocephalus arundinaceus)*, breeding dispersal, natal dispersal.

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1. Introduction

Previous ringing results have already shown that adult birds of migratory species exhibit a high degree of site fidelity. It is also well known that some young birds return to their natal area. However, there is a body of evidence to show that both adult and young individuals can switch from breeding or natal sites or undergo breeding or natal dispersal in accordance with GREENWOOD's terminology (1980).

Various factors are known to affect bird dispersal. For example, adult birds of many species are more likely to return to their breeding site after a successful breeding season than otherwise (e.g. VON HAARTMAN 1949, DARLEY et al. 1977, FREER 1979, HÖTKER 1982, ORING & LANK 1982, GRATTO et al. 1985, JAKOBER & STAUBER 1989). Furthermore, there is evidence that such behavioural variations should primarily be associated with higher dispersal rates rather than with mortality (e.g. VON HAARTMAN 1949, FREER 1979, SHIELDS 1984). The details of such breeding success-dependent dispersal remain however somewhat unclear.

A much-postulated theory of negative site fidelity relates to juvenile (postfledging) dispersal. This term is taken to mean the movement of young birds, after they have become independent, from the fledging areas to alternative sites. With migratory species these new sites, not the fledging area, become the departure and arrival points in autumn and spring. In the case of sedentary species they become permanent home ranges. Many authors have suggested the existence of such a mechanism (e.g. KLUIJVER 1935, JOHNSTON 1956, LÖHRL 1959, SOKOLOV 1976, 1991, BERNDT & WINKEL 1979).

The purpose of this paper is to show the relationship between dispersal and breeding success in the Great Reed Warbler. The data on natal dispersal in this species will be also presented along with the results taking account of individual conditions during the nestling period.

2. Study Areas and Methods

The Great Reed Warbler was studied in southwest of the Pskov Region between 1983–89 and on the Courish Spit on the Baltic coast from 1993 to 1999. In the Pskov Region, the control area was located at Lake Sebezhskoe (56.18 N, 28.30 E). The entire area of reeds here exceeded 4 hectares. However, only about 1.5 hectares of reeds were suitable nesting habitat for Great Reed Warblers. A more detailed description of this area maybe found elsewhere (FEDOROV in press).

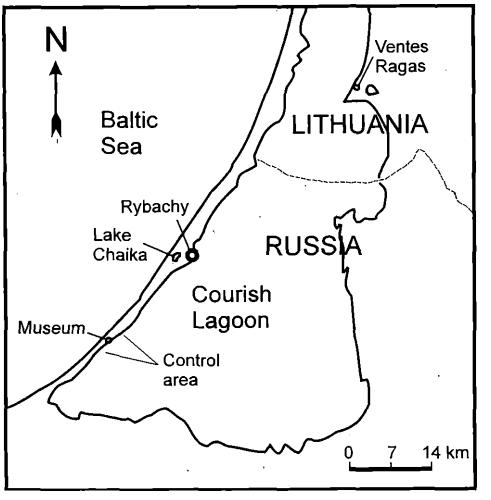

Fig.: Study area on the Courish Spit. – Untersuchungs-Region auf der Kurischen Nehrung.

Every year between 14 and 22 male Great Reed Warbler bred in the area of which 1 to 5 were bigynous. The breeding density in this area was higher (sometimes much higher) than in most other parts of Lake Sebezhskoe and on other lakes of the district. It appeared that breeding conditions for this species were close to optimal in this site.

The main control area on the Courish Spit (Fig.) was situated about 15 km from its southern origin (55.05 N, 20.40 E) and is termed "The Museum area", because of its proximity to the National Park "Curonian (Courish) Spit" Museum. The reed beds here stretched for about 2.5 km along the Courish Lagoon shore and consisted of 18 different-sized plots. The total area of reeds was about 9.5 hectares. Over the study period 40 to 60 female and 25 to 46 male Great Reed Warblers nested in this area, every year producing bi- and trigynous individuals.

Birds were also controlled at the "Rybachy" field station and at Lake Chaika, situated 1.5 km away from Rybachy. These two sites were situated about 20 km away from the Museum area (Fig.). At the Chaika Lake, the areas of reed beds were not extensive. Annually, 3–5 male Great Reed Warblers bred there of which 1–2 were possibly polygynous. At "Rybachy", the reeds were quite extensive, but the habitat was not suitable for this species and so, usually, only 2–3 pairs bred there, though there were 5 pairs in 1998.

Reeds were absent along a 20-km stretch of the Lagoon shoreline between Rybachy and the Museum area. Thus, the Museum area was strongly isolated to the northeast. To the southwest, after a break of 300–400 m, reeds stretched down to the beginning of the Spit.

The main method of research was to trap birds in the control areas in a variety of ways and, subsequently, to ring and individually mark them. The status of each bird could be detected by regular observation which also helped in the location of nests.

At the Sebezhskoe Lake, regular mist-netting throughout the entire control area was carried out from mid July till end of August, which made it possible to trap both local birds and individuals moving in from elsewhere. In the Museum area of the Courish Spit, birds were caught mainly at the nest and so wandering birds could be trapped only by chance. At Rybachy, the field station maintains a system of mist-nets in the reed beds which functions every year from the end of March until the beginning of November (for a detailed description of this field station see TITOV 1999). Several Great Reed Warblers dispersing from the Museum area were caught in these nets.

In every nest found, chicks were ringed according to their hatching sequence. In some nests it was determined directly: nestlings were marked after hatching. In the others the sequence of hatching was defined according to the stage of nestling development.

The greater part of nests received close attention: they were visited regularly and all the details of nestling growth and development were recorded. Sometimes few visits were paid to nests (for ringing of nestlings and trapping of adults only), but all the nests were checked just before and after fledging. It was necessary to ascertain breeding success, because the probability of predation for Great Reed Warbler nests is at its maximum just before fledging (FEDOROV 1988, and in press). During the course of the study in the Museum area, over one hundred successfully fledged young Great Reed Warblers were ringed in each year: a min. in 1997 of 107 and a max. in 1995 of 155. The overall total was 750 for the whole period from 1993 to 1998.

For statistical analysis, the χ^2test (two-tailed) was used. On one occasion the expected value in 1 cell was less than 5, FISHER's exact probability test (two-tailed) was preferred (SOKAL & ROHLF 1998); d.f.=1 in every case.

3. Results

3.1. Breeding dispersal

Adult Great Reed Warblers are more likely to return to their breeding sites after a successful breeding season than after an unsuccessful one (Table 1). Differences in summarized results for males and females were significant both for Lake Sebezhskoe and the Courish Spit. It is however more correct to interpret the results separately for each sex because the level of control (probability of capture or control) was different for males and females. Only the difference in the rate of return for males at Lake Sebezhskoe was not significant, but demonstrated the same tendency.

Table 1: Relationship between breeding success and site fidelity. – Beziehung zwischen Bruterfolg und Brutortstreue.

	Number of breeding individuals	Number of returning individuals	%	Statistics
Seebezhskoe l. males+females, successful	79	32	40.5	$\chi^2 = 5.69$; $P < 0.05$
Seebezhskoe l. males+females, unsuccessful	37	6	16.2	
Seebezhskoe l. males, successful	37	21	56.8	n. s.
Seebezhskoe l. males, unsuccessful	15	5	33.3	
Seebezhskoe l. females, successful	42	11	26.2	Fisher's exact test,
Seebezhskoe l. males, unsuccessful	22	1	4.5	$P = 0.045$
Courish Spit. males+females, successful	259	106	40.9	$\chi^2 = 20.33$; $P < 0.001$
Courish Spit. males+females, unsuccessful	49	3	6.1	
Courish Spit. males, successful	133	54	40.6	$\chi^2 = 6.29$; $P < 0.05$
Courish Spit. males, unsuccessful	21	2	9.5	
Courish Spit. females, successful	126	52	41.3	$\chi^2 = 12.8$; $P < 0.001$
Courish Spit. females, unsuccessful	28	1	3.6	

After breeding failure, Great Reed Warblers start to breed again within several days. As a rule, after the second unsuccessful attempt birds disappear from the area. Usually the loss of the second nest occurs in mid-July and it is from about this time onwards that un-ringed adults begin to be caught. It seems that these are birds which have moved after one or more unsuccessful breeding attempts. During the period 1985–88, at the Lake Sebezhskoe control area, 29 such Great Reed Warblers were caught of which 6 returned to breed in this same area the year after the first capture. Later, on the Courish Spit, similar evidence emerged confirming such a scenario.

1) Female XD388747 was caught as an adult at Rybachy on 2.08, 20.08 and 1.09 1998. It did not breed at Rybachy because it is hardly possible that a local individual could avoid capture as late as August. Besides, this year all the locally breeding females (n = 5) were caught and individually marked at the nest. This bird returned to Rybachy in 1999 and nested there (first egg laid on 18.06).

2) Female XD388004 was trapped at the nest in the Museum area on 24.05.97. Its nest containing eggs was predated between 2.06 and 6.06. This bird was then retrapped at Lake Chaika on 9.06 where it bred that same year. It subsequently nested at the Chaika lake in 1998 and 1999. The same phenomenon of a female of this species having time to move after breeding failure and to nest elsewhere was observed in Sweden (BENSCH & HASSELQUIST 1991). Such behaviour however seems to be more characteristic of the Reed Warbler *(Acrocephalus scirpaceus)*.

3) Male 0740287 was trapped as an adult in Ventes Ragas, Lithuania (see Fig.) on 23.05.95. It was highly probable that this bird bred in the vicinity. On 15.07 of the same year this bird was caught in the Museum area. It was in a very intensive and advanced body moult (birds continuing to breed at this stage usually only entering moult or have not moulted at all). This bird is assumed to have moved after an unsuccessful breeding attempt. In the following year, this male returned to breed in the Museum area, its nest being located less than 100 m from where it was caught in the previous year.

4) Female 0740020 in 1995 nested in the Museum area. The first nest with nestlings failed on 24.06 just before fledging. Soon the bird started to build a new nest with the same male. This nest was predated in the period from 12.07 to 19.07. After this failure, the bird was not seen again in the area, but on 24.07 it was caught at Rybachy. This was the last record for this female.

3.2. Natal dispersal

As mentioned above, natal dispersal depends on whether young birds undergo dispersal from the nesting area to any new area or whether they begin autumn migration straight from the natal site. Some young Great Reed Warblers seem to stay in their native area until the start of migration. On the Courish Spit 5 birds were caught not more than a few hundred metres from the nest at the age of 51–57 days. However, some younger individuals can disperse quite far from the birth place. During the period 1993–98 on the Spit, 14 examples of juvenile dispersal were recorded (Table 2). All these birds were hatched in the Museum area and were subsequently retrapped at Rybachy. This movement of about 20 km was in a reverse direction to their autumn migration.

Table 2: Some parameters of young Great Reed Warblers that underwent postjuvenile dispersal/Courish Spit 1993–98. – Einige Parameter für Jungvögel, die nach dem Flüggewerden abwanderten/Kurische Nehrung 1993–98.

Ring No	Date of hatching	Hatching sequence	Nest status	Conditions of growth	Capture (age in days)	Control of siblings	Control in following year	see text
0640151	06.06.93	4th of 5	Unknown	Bad weather	31	–	-	+
0640205	15.06.93	1st of 5	Unknown	Very bad weather. 3 nestl. dead of starvation	58	–	Bred on birth site – 94–95.	+!
0640235	16.06.93	3rd of 5	Unknown	Very bad weather. 3 nestl. (incl. 2nd) dead of starvation	60	–	–	+!
0640514	12.06.94	5th of 5	Polyg.1	Moderation of growth. Bad weather.	45	1st and 3rd – bred on birth site – 98; 4th captured in Rybachy – 96.	–	+!
0640519	11.06.94	5th of 6	Monog.	Bad weather	41	–	–	+
0640581	13.06.94	4th of 6	Polyg.1	Bad weather. 6th dead of starvation.	44–48*	1st – bred on birth site – 95.	–	+!
0740175	22.06.95	5th of 5	Polyg.2	–	45–55*	–	–	+
XD370331	18.07.95	1st of 4	Polyg.2	Late breeding.	55–65*	–	–	?
0740529	14.06.96	1 st of 5	Monog.	–	54–55*	2nd captured on l.Chaica – 97; bred on birth site – 98.	Bred on birth site – 98.	–
0740536	13.06.96	Unknown (4 nestligs)	Monog.	–	54–63*	–	–	?
XD388033	17.06.97	4th of 5	Polyg.2	–	44–47*	2nd – bred on birth site – 98.	–	+
XD388057	17.06.97	2nd of 2	Monog.	–	49	–	–	–
XD388075	29.06.97	3rd of 3	Monog.	Late breeding.	51–56*	–	–	+!
XD435027	14.06.98.	5th of 5	Monog.	Very bad weather; moderation of growth.	48	–	–	+!

* = first and last capture.

Before analyzing possible reasons for dispersal, it is worthwhile mentioning some features of the Great Reed Warbler nesting biology. Firstly, considerable differences in hatching time between the oldest and the youngest nestlings (up to 2.5 days) were observed. Secondly, birds of this species are very sensitive to changes in weather conditions. During bad weather periods (low temperature, persistent rain), decreases in nestling growth and development (runting) are regularly observed in Great Reed Warbler broods. The youngest birds suffer mainly from the lack of food. Such runt nestlings may die of starvation but some do survive. The runting effect is more marked during late breeding and in polygynous nests, especially in the nests of the second and third females. These peculiarities are well known from the literature (DYRCZ 1974) and were observed both in the Pskov Region and on the Courish Spit. On the Spit, cases of growth moderation in Great Reed Warbler broods were especially frequent due to high cyclonic activity in this region.

As can be seen from Table 2, young Great Reed Warblers undergoing postjuvenile dispersal were often the youngest of the brood. Sometimes their nestling period coincided with bad weather that resulted in poor feeding and in some nestlings dying of starvation. The bird with ring 0640235 (see Table 2) should be mentioned separately. This nestling hatched as the 3rd in the brood. The weather was very bad and the whole brood suffered from poor feeding. This bird was very active in the nest and survived despite the fact that three nestlings in the brood including the 2nd, older one died of starvation.

As it is mentioned above, some nests were under regular, close surveillance. In such nests all the cases of poor development conditions were directly observed and the sign "+!" in the last column of Table 2 indicates these cases. The sign "+" means that retarded nestling growth and development was highly possible (but not observed) because of bad weather, hatching sequence or the status of a nest. The question mark indicates that the development conditions may have been bad or good and "minus" means that they were presumably good, but still unknown. Table 2 shows that in most cases young Great Reed Warblers before postjuvenile dispersal had difficulties (lack of food) during the nestling period.

4. Discussion

4.1. Breeding dispersal

Despite a restricted body of evidence, the mechanism of breeding success-dependent dispersal in this species seems to be clear. After one or several (usually two) unsuccessful attempts to breed, Great Reed Warblers start to disperse in order to find a new suitable site (or sites). In the following year, such birds return to one of these subsequent sites. It may be beneficial for these birds because of the presumed success in the new site. This behaviour can be very important for this species which exploits a fragmented habitat. It is possible for birds to find places for future breeding in the summer before autumn migration and thus save time searching the following spring.

Some birds do not move from the breeding sites after unsuccessful nesting. Among 5 males returning to the breeding site at Lake Sebezhskoe after breeding failure (see Table 1) two were caught in the control area in the second half of July in unsuccessful years. It may be supposed that breeding-site fidelity depends primarily on the presence or absence of movements after unsuccessful reproduction but not on the breeding success itself (FEDOROV 1996). It is highly significant that these two birds nested successfully at this site for several (2 and 4) seasons previously, because both were registered on the study area as adults in 1983, the first year of research. Such behaviour should also be considered as beneficial because several successful seasons indicate that the site is good enough. It can be better to return there even after an unsuccessful year rather than to search for a new place. It is also well known (e.g. JACOBER & STAUBER 1989) that old birds, accustomed to returning to the breeding sites over several seasons, are more faithful to them.

Unfortunately, there have been only few studies devoted to this kind of problem in the Great Reed Warbler. SPRINGER (1960) mentioned that nonbreeding Great Reed Warblers might start to ap-

pear in the study area from mid-July, which reflects closely the case observed at Lake Sebezhskoe. He also wrote of one male, which did not breed in the area and was ringed only on 27.09, returning to the site in the following year.

Breeding dispersal of this species has been also investigated in Sweden (BENSCH & HASSELQUIST 1991). No significant differences between successful and unsuccessful breeding birds have been reported from the point of view of their returning to the study area. These results are a bit surprising – but can be easily explained. The study area in this study was very isolated. It was quite a long distance to the nearest reeds. That is why possibilities for dispersal outside the area after breeding failure were limited. But it was shown that successful breeding birds were more likely to return to their nesting marsh inside the study area. This investigation also gave two very impressive examples of long-distance breeding dispersal in the Great Reed Warbler after unsuccessful reproduction.

4.2. Natal dispersal

Different factors may affect natal dispersal. Several authors have supposed that the tendency to disperse is at least partially determined by genetic, inheritable features (e.g. FISHER 1955, HOWARD 1960, JOHNSTON 1961, SOKOLOV 1991). The purpose of this paper has been to show that there is a relationship between dispersal and conditions affecting each nestling's development. Unfortunately, the amount of data seems to be insufficient to prove a clear link. However, the collected data allows the proposition that in young birds the tendency to disperse is affected by difficulties (poor feeding) prior to fledging.

With the help of this hypothesis it is possible to explain some poorly understood phenomena. For example, many studies (e.g. KLUYVER 1951, PERRINS 1965) have shown that birds from early broods are more likely to be found breeding in the study area in subsequent years. KLUYVER (1971) termed this survival "local survival" in order to stress that disappearing birds could either have died or emigrated. It is likely that birds from late broods had poorer feeding conditions in their nests. Probably, they were more inclined to disperse because of these difficulties (which does not mean of course that such birds do not suffer a higher mortality rate). It is also known that Reed Warblers from large broods were more prone to emigrate from natal sites than birds from small broods (BIBBY 1978). These differences in behaviour may be also explained by differences in feeding conditions which should be better in small broods.

It is necessary to add that the described behaviour (to disperse after poor feeding conditions in the nest) should be considered as highly beneficial. Suffering from a lack of food indicates that the site is not rich enough in insects. It is highly probable that birds surviving despite problems experienced during nestling development will face the same problem of the lack of food for their own nestlings in the following year assuming they return to the same site. That is why dispersal after a difficult nestling period can be a useful strategy because birds may find habitats of a higher quality.

Unfortunately, the reed beds at Rybachy were not suitable for Great Reed Warblers. It may be a reason why not a single dispersed juvenile (see Table 2) returned to this place in the following year. It is not helpful that juvenile dispersal was controlled on the Courish Spit in a single direction only. As a result, the available data gave us a picture which is somewhat incomplete. In order to check a proposed hypothesis it is essential to continue investigation of this kind in different places and in various species. The possible physiological mechanism of feeding-dependent dispersal already described might also be a subject for future studies.

In conclusion it is necessary to remark that in spite of much research being done in the field of avian dispersal (e.g. BERNDT & STERNBERG 1968, GREENWOOD & HARVEY 1982, BAUER 1987, BAKER 1993, WEATHERHEAD & FORBES 1994, CLARK et al. 1997, PARADIS et al. 1998) these phenomena are still poorly understood. Much data has been collected on hole-nesting species (GREENWOOD 1980). Birds inhabiting fragmented habitats (the Great Reed Warbler is a good example) can be also very useful subjects for this kind of investigation.

Zusammenfassung

Über den Einfluß brutzeitlicher „Erfahrungen" auf die Dismigration juveniler und adulter Drosselrohrsänger *(Acrocephalus arundinaceus)*.

In Untersuchungsgebieten südlich von Pskov und auf der Kurischen Nehrung/Ostseeküste wurde die Dismigration juveniler und adulter Drosselrohrsänger *(Acrocephalus arundinaceus)* erfaßt. Wie auch von anderen Arten bekannt, kehrten adulte Vögel nach erfolgreicher Reproduktion häufiger an den Brutort zurück als nach einem Brut-Mißerfolg. Altvögel verlassen nach mehreren (meist zwei) mißglückten Brutversuchen die Nestregion. Im nächsten Jahr kehren sie nicht nach hier zurück, sondern dorthin, wo sie im Vorjahr anschließend hingewandert waren. Bei Jungvögeln konnten Beziehungen zwischen Dismigration und „Nestlingserfahrung" festgestellt werden.

References

Baker, R. R. (1993): The function of post-fledging exploration: a pilot study of three species of passerines ringed in Britain. Ornis Scand. 24: 71–79. * Bauer, H. G. (1987): Geburtsortstreue und Streuungsverhalten junger Singvögel. Vogelwarte 34: 15–32. * Bensch, S., & D. Hasselquist (1991): Territory infidelity in the polygynous Great Reed Warbler *Acrocephalus arundinaceus:* the effect of variation in territory attractiveness. J.Anim.Ecol. 60:857–871. * Berndt, R., & H. Sternberg (1968): Terms, studies and experiments on the problems of bird dispersion. Ibis 110: 256–269. * Berndt, R., & W. Winkel (1979): Verfrachtungs-Experimente zur Frage der Geburtsortsprägung beim Trauerschnäpper *(Ficedula hypoleuca)*. J. Ornithol. 120: 41–53. * Bibby, C. J. (1978): Some breeding statistics of Reed and Sedge Warblers. Bird Study 25: 207–222. * Clarke, A. L., B.-E. Sæther & E. Røskaft (1997): Sex biases in avian dispersal: a reappraisal. Oikos 79: 429–438. * Darley, J. A., D. M. Scott & N. K. Taylor (1977): Effects of Age, Sex and Breeding Success on Site Fidelity of Grey Catbirds. Bird Banding 48: 145–151. * Dyrcz, A. (1974): Factors affecting the growth rate of nestling Great Reed Warblers at Milicz, Poland. Ibis 116: 330–339. * Fedorov, V. A. (1988): Data on the breeding biology of Great Reed Warblers in the South of Pskov region. Abstracts XII Eastern Baltic Orn. Conf. (Vilnius): 227–228 (in russ.). * Idem (1996): On the system of spatial distribution of individuals in some *Acrocephalus* species. Russ. J. Ornithol. Express-issue 1: 8–12 (in russ.). * Fisher, J. (1955): The Dispersal Mechanism of some Birds. Acta XI Congr. Intern. Ornithol. (Basel, Stuttgart): 437–442. * Freer, V. M. (1979): Factors Affecting Site Tenacity in New York Bank Swallows. Bird Banding 50: 349–357. * Gratto, C. L., R. I. G. Morrison & F. Cooke (1985): Philopatry, Site Tenacity and Mate Fidelity in the Semipalmated Sandpiper. Auk 102: 16–24. * Greenwood, P. J. (1980): Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28: 1140–1162. * Greenwood, P. J., & P. H. Harvey (1982): The natal and breeding dispersal of birds. Ann. Rev. Ecol. Syst. 13: 1–21. * Haartman, L. von (1949): Der Trauerfliegenschnäpper. I. Ortstreue und Rassenbildung. Acta Zool. Fenn. 56: 1–104. * Howard, W. E. (1960): Innate and Environmental Dispersal of Individual Vertebrates. Amer. Midl. Nat. 63: 152–161. * Hötker, H. (1982): Studies of Meadow Pipit *Anthus pratensis* Dispersal. Ringing & Migration 4: 45–50. * Jakober, H., & W. Stauber (1989): Beeinflussen Bruterfolg und Alter die Ortstreue des Neuntöters *(Lanius collurio)*? Vogelwarte 35: 32–36. * Johnston, R. F. (1956): Population Structure in Salt Marsh Song Sparrows. Part I. Environment and Annual Cycle. Condor 58: 24–44. * Idem (1961): Population movements of birds. Condor 63:386–389. * Kluijver, H. N. (1935): Waarnemingen over de levenswijze van de Spreeuw *(Sturnus v. vulgaris)* met behulp van geringde individuen. Ardea 24: 133–166. * Kluyver, H. N. (1951): The population ecology of the Great Tit, *Parus m. major* L. Ardea 39: 1–135. * Idem (1971): Regulation of numbers in populations of Great Tits *(Parus m. major)*. Proc. Adv. Study Inst. Dynamics Numbers Popul. (Oosterbeek 1970): 507–523. * Löhrl, H. (1959): Zur Frage des Zeitpunktes einer Prägung auf die Heimatregion beim Halsbandschnäpper *(Ficedula albicollis)*. J. Ornithol. 100: 132–140. * Oring, L. W., & D. B. Lank (1982): Sexual selection, arrival times, philopatry and site fidelity in the polyandrous Spotted Sandpiper. Behav. Ecol. Sociobiol. 10: 185–191. * Paradis, E., S. R. Baillie, W. J. Sutherland. & R. D. Gregory (1998): Patterns of natal and breeding dispersal in birds. J. Anim. Ecol. 67: 518–536. * Perrins, C. M. (1965): Population fluctuations and clutch-size in the Great Tit *Parus major* L. J. Anim. Ecol. 34: 601–647. * Shields, W. M. (1984): Factors Affecting Nest and Site Fidelity in Adirondack Barn Swallows *(Hirundo rustica)*. Auk 101: 780–789. * Sokal, R. R., & F. J. Rohlf (1998): Biometry (3rd edition). Freeman & Co, New York: 887 p. * Sokolov, L. V. (1976): Time of the formation of connections with place of future nesting in some birds of passage on the Kurshsky Spit. Zool. Zhurnal 55: 395–401 (in russ.). * Idem (1991): Philopatry and dispersal of birds. USSR Acad. Scien., Leningrad: 233 p. (in russ.). * Springer, H. (1960): Studien an Rohrsängern. Anz. Ornithol. Ges. Bayern 5: 389–433. * Weatherhead, P. J., & M. R. L. Forbes (1994): Natal philopatry in passerine birds: genetic or ecological influences? Behav. Ecol. 5: 426–433.