The expansion of the Great Reed Warbler Acrocephalus arundinaceus into Finland

PERTTI KOSKIMIES

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All the known records of the Great Reed Warbler in Finland were collected. The oldest one is from 1930 in Helsinki. The mean annual number of birds recorded was 3.6 in the 1950s, 7.5 in the 1960s and 30.2 in the 1970s, with great annual fluctuations, but these figures somewhat exaggerate the increase, since observation activity has intensified. Most records concern singing males; nesting has been confirmed only about 15 times. Until the beginning of the 1970s the range was restricted to the S coast but nowadays it covers the SW coast and SE Finland, too. The reasons for the expansion are supposed to be the amelioration of the climate, the resultant increase of the E European population, and the concurrent development of suitable habitats in N Europe.

Pertti Koskimies, Hallituskatu 21 as. 11, SF-53300 Lappeenranta 30, Finland

Introduction

In recent decades the Acrocephalus species have extended their ranges towards the north and north-west in Europe. In Finland four of the five species are newcomers, which arrived during the 1920s to 1940s. The Great Reed Warbler A. arundinaceus is the rarest of the Finnish species. Its population remained small up to the 1960s (Eriksson 1969) but increased during the 1970s. Inland colonization began at the same time.

Study of the expansion of the Great Reed Warbler into Finland may serve to elucidate some general questions concerning bird dispersal. This species is easily censused due to its special habitat requirements and loud song, so that accurate records can be obtained. The expansion of the Great Reed Warbler is one of the best known in the Finnish avifauna.

Material

All the known records of the Great Reed Warbler in Finland were collected for this study. Eriksson (1969) has listed most of the observations made between the years 1930 and 1967. All the published and many unpublished records made in the period 1968—1979 were collected with the aid of a request inserted in the field ornithologists' journal *Lintumies*. In addition, I studied the atlas maps for the years 1974—79.

Up to the 1960s the Great Reed Warbler was rare in Finland and most of the records were published. In spite of the population increase, the proportion of records published has remained high because of the present thoroughness with which the local ornithological clubs gather bird observations.

Increase in observation activity is a major source of bias, which must be kept in mind when the expansion of the species into Finland is discussed.

Results

The oldest record of the Great Reed Warbler in Finland was made on 25

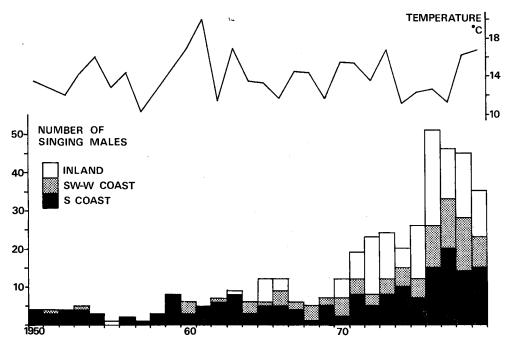


Fig. 1. The number of singing Great Reed Warbler males in Finland in 1950—79 compared with the mean temperature of two warmest five-day periods between 21 May and 9 June in Helsinki (from Ilmatieteen laitos 1950—79).

May 1930 in Vanhankaupunginlahti near Helsinki (Hytönen 1930). During the late 1930s five additional birds were found in the vicinity of Helsinki. In the 1940s the species was observed almost annually in the Helsinki area and in Porvoo, about 50 km east of Helsinki; the westernmost record is from Hanko Peninsula in 1940. There is one separate inland record: in 1941 a male was heard singing in Riistavesi, near Kuopio, about 300 km north of the southern coast.

From 1950 on, the Great Reed Warbler was recorded annually in Finland in increasing numbers. The annual number of birds was 1—8 (mean 3.6) in the 1950s, 5—12 (7.5) in the 1960s and 13—51 (30.2) in the 1970s. The increase was not linear due to great annual fluctuations (Fig. 1).

The geographical distribution of the observations changed, especially from the middle of the 1960s to the early 1970s (Figs. 1 and 2). The species was restricted to the southern coast until the summer of 1965, when numerous birds were seen inland in S and SE Finland. In the following years only a few inland records were reported but an increasing number of birds were sighted along the SW coast near Turku. In the years 1976—78 altogether 143 Great Reed Warbler territories were found in various parts of Finland, mostly on the S and SW coast and in SE Finland (Fig. 2). Singing males were also heard irregularly in southern parts of the W coast, in southern Central Finland. The Häme and northernmost records come from Kuopio in E Finland.

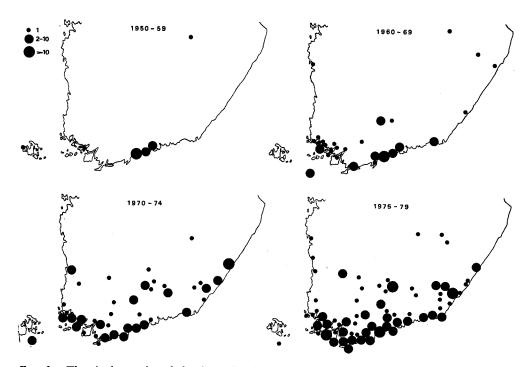


Fig. 2. The singing males of the Great Reed Warbler in Finland in 1950-79.

The areas occupied most regularly in Finland are Vanhankaupunginlahti, Ruskis and Lupinlahti on the S coast, Parainen on the SW coast, and Siikalahti, the eutrophic lakes of Lappeenranta and Vesijärvi in the interior of S Finland (Fig. 2, Table 1, Eriksson 1969, Lammi 1976, Piha 1978, Sojamo 1979). Usually only 1—2 and at most 5—7 males have been singing in a single locality. The mean number of males

per locality increased towards the beginning of the 1960s and, after a drop, again in the 1970s (Table 2). The mean number of times that each locality was occupied increased except on the S coast (Table 3).

The Great Reed Warbler winters in Central and S Africa (v. Haartman et al. 1963—72) and arrives in Finland late in the spring (Fig. 3). It favours extensive reed beds, and only irregular

Table 1. Numbers of singing Great Reed Warbler males in frequently occupied localities in 1965—79.

Locality	1965	66	67	68	69	70	71	72	73	74	75	76	77	78	79
Vanhankaupunginlahti	2	2	1			_				_	2			_	
Vesijärvi Siikalahti	_		_	_	_	_2	1	1 3	_	_	3 1	-6 	4	1	1 2
Lakes of Lappeenranta	-	_	-	_		_	_	4	2		2	6	3	2	2

Table 2. The mean number of singing males per locality in different regions in Finland in 1950—79.

Period	S coast	SW-W coast	Inland	Total
1950—54	1.3	1.0		1.1
1955—59	1.6	_	1.0	1.3
1960-64	1.7	1.0	1.0	1.5
196569	1.1	1.0	1.1	1.1
1970-74	1.0	1.1	1.2	1.2
1975-79	1.3	1.4	1.3	1.3

visitors may stay a couple of days in willow shrubs along shores or ditches (Eriksson 1969, Sojamo 1979).

Most of the records of the Great Reed Warbler concern males, singing in a regular territory some days or weeks. Nesting has been confirmed only about 15 times. However, no systematic effort has been made to study nesting or the proportion of breeding males.

At present, my rough estimate of the breeding population is 10 to 20 pairs, in addition to some 30 to 50 unpaired males.

Discussion

The course of expansion into N Europe. The range of the palaearctic subspecies A. arundinaceus arundinaceus extends from the Atlantic coast in the west to Central Asia in the east.

Finland and Sweden lie along the

northernmost limit of the range, so the expansion has taken place from the south, probably the Baltic states. The Matsalu Bay on the western coast of Estonia is probably an important expansion centre. The Great Reed Warbler has been numerous there ever since the 1870s and has increased in numbers during the last few decades (Kumari 1970). At the beginning of the 1900s the species was found only on the western coast of Estonia but after that it expanded inland (Lepiksaar & Zastrov 1963).

In Sweden there have been more records since the early 1960s, the greatest increase taking place in 1972—76, when the annual numbers rose from 49 to about 150 (Holmbring 1979). Most of the Swedish records come from the south-eastern parts of the country, between the latitudes 59° and 60°N. A fair number of the observations are from southernmost Sweden, too.

In Norway the Great Reed Warbler has been found only six times up to 1970 (Haftorn 1971) but has probably increased in numbers during recent years (Olav Hogstad, in litt.). In Denmark the colonization began early in the 1850s, but since the 1940s the species has retreated southwards and nowadays occurs only in the southern part of the country (Dybbro 1976).

In Germany the population of the Great Reed Warbler has declined during the last few decades (Wink 1974, Rheinwald 1977, Rutschke 1980), ac-

Table 3. The mean number of times (years) that the Finnish localities were occupied in 1950—79. Numbers of localities in parenthesis.

Period	S coast	SW-W coast	S Karelia & Päijät-Häme	Other inland areas	Total		
1950s 1960s 1970s	2.8 (8) 2.3 (13) 2.1 (41)	1.0 (3) 1.1 (15) 1.5 (36)	1.0 (2) 1.9 (38)	1.0 (1) 1.0 (7) 1.3 (28)	2.2 (12) 1.7 (37) 1.7 (133)		

cording to Rutschke (1980) due to destruction of its habitats.

In the Soviet Union the northern limit lies along the 57th parallel of latitude and has moved northwards in this century. About 30 years ago the Great Reed Warbler was still extremely rare in the Leningrad Region (Dement'ev & Gladkov 1968).

The first occupants of Finland were found in a restricted area around Helsinki. This would indicate that they came from Estonia, across the Gulf of Finland. This assumption is supported by the fact that up to the 1940s the numerous bird watchers did observe the species in the Karelian Isthmus or around Lake Ladoga, or even in the highly eutrophic lake Ayräpäänjärvi (Koskimies 1979). Except for one record in 1965, the Great Reed Warbler has been found in SE Finland only for the last 10 years, the same period in which inland localities have been colonized in other parts of S Finland.

Even for an expansive bird species, the Gulf of Finland could be a barrier to dispersal, which would explain the time lag between the colonization of Estonia and Finland. While colonization progressed in the Baltic, increasing numbers of birds reached Finland and a permanent breeding population was probably established on the southern coast in the late 1950s and early 1960s (see Eriksson 1969). The breeders presumably returned to the localities inhabited the previous year, while the juveniles dispersed more widely and occupied new localities inland and on the SW coast. In Germany most of the breeding adults and nearly one third of the nestlings return to the same area in successive years (Beier 1981), but near the border of the range the sitefidelity may be smaller.

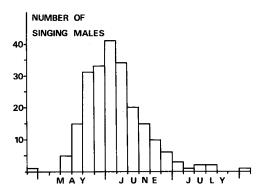


Fig. 3. The onset of the singing period of the Great Reed Warbler in Finland in 1968 -79.

Significance of the intensified observation activity. Although the date recorded for the first occurrence of the Great Reed Warbler in Finland is probably fairly accurate, the real date of the population increase is more obscure. Bird-watching became creasingly popular during the 1960s and 1970s, and this has obviously had some influence on the number of records. Hence, the sharp rise in the mean numbers of observations made in successive decades is without doubt exaggerated. On the other hand, the powerful song of the species makes it easy to observe. The song period of the breeding males is short, however (Kluyver 1955, Beier 1981), but so far they probably form only a minor proportion of the Finnish population.

Although no definite trend can be demonstrated in the number of males in Vanhankaupunginlahti, Vesijärvi, Siikalahti or the lakes of Lappeenranta (Table 1), it seems to be beyond dispute that many previously unoccupied localities have been colonized during the last 10 or 15 years, especially on the SW coast and in SE Finland. In particular, the striking increase in the number of birds in 1976—78 must

be real in view of the comparable and fairly accurate observations made in many eutrophic lakes during the 1970s.

Influence of the climatic change. In the late 1800s the climate of N Europe began to get warmer. The rise in temperature, especially in May-June, culminated in the 1930s, since when the mean temperature has slightly decreased (Heino 1978). During 1966-70 and especially 1971-75 the springs and summers were again warmer than in the normal period 1931—60. According to Kalela (1949), the climate has became more arid in the inner parts of Europe and wetter in W Europe. The Great Reed Warbler is said to prefer a warm, arid and continental climate (Holmbring 1979), which could explain why the population in E Europe has increased while that in the western parts has decreased.

In Sweden influxes of the warblers have occurred in connection with the arrival of warm air masses from the south and south-east in spring (Holmbring 1979). Thus, in warm springs more birds should migrate to the northern parts of the range than in cold ones. However, the present material does not support this idea, because the number of observations and the mean temperature during the migration time do not correlate even in the 1970s, when the most reliable material was obtained (Fig. 1). On the other hand, in warm springs relatively more females may migrate to Finland, which would decrease the proportion of singing and easily observed males. In Blyth's Reed Warbler A. dumetorum, the proportion of breeding males varies from year to year (Koskimies 1980).

The breeding success of the Great Reed Warbler is favoured by a warm climate (Dyrcz 1974, Beier 1981). The slower growth rate of the young and their greater susceptibility to cold and rainy weather compared with the young of the Reed Warbler A. scirpaceus could explain why, in N Europe, the Reed Warbler extends farther north than the Great Reed Warbler.

Creation of suitable new habitats. One important reason for the expansion of the Great Reed Warbler into Finland seems to be the recent creation of suitable habitats. The reed beds along the coast and lakes have extended due to water pollution, cessation of cattle grazing and lowering of the water level in many lakes (v. Haartman 1973, 1978). Previously, the reeds growing at a depth of 0.5—1 m were destroyed by cattle but after the beginning of this century grazing in shore meadows decreased and almost ceased in the 1950s, after which the reeds recovered rapidly (Kalliola 1973).

At present, lack of suitable habitats cannot severely restrict the increase of the population, because the number of males per locality is low and many suitable reed beds are still empty. Hence, the inland colonization cannot be merely a consequence of filling of all the coastal localities. Besides, the Great Reed Warbler is a semicolonial species, at least in Central Europe (Dyrcz 1977, Beier 1981).

Annual fluctuations and reasons for expansions. Great annual fluctuations are typical of an expansive species at the northernmost limit of its range. Both the fluctuations in observation activity and changes in the habitats have been too gradual to cause the sharp annual variations recorded in the numbers of Great Reed Warblers in Finland, e.g. in the 1970s. Nor do the spring temperatures correlate with the fluctuations.

In Germany, in the central parts of

the species' range, marked annual fluctuations in numbers and breeding success have been observed (Beier 1981). Since the nestlings are susceptible to rainy and cold weather (Dyrcz 1974, Beier 1981), the total production of the warbler population can vary annually over the large areas, which may be reflected in the numbers in the following spring.

The wintering success in tropical Africa may cause population fluctuations uncorrelated with the controlling environmental factors in the breeding range. Because of its high site-fidelity and rather special habitat requirements in the wintering grounds (De Roo & Deheegher 1969), the wintering success of the Great Reed Warbler may alter if the habitats change, e.g. due to man. Changes increasing the winter survival of birds over a long period can affect the total breeding population (cf. Ulfstrand 1978:111), provided there are no other selection pressures damping this increase. The colonization of reed beds in N Europe by many bird species during the last hundred years indicates that the bird communities of these productive habitats were still capable of increase (e.g. Järvinen & Ülfstrand 1980). Interspecific competition with the Reed Warbler, an earlier colonizer of the same reed beds, does not prevent the Great Reed Warbler expanding its range, because the two closely related species have different microhabitats (Beier 1981), food and feeding habits (Bussmann 1979).

To conclude, the expansion of the Great Reed Warbler can be explained by changes in climate, habitats, breeding success and wintering success. Both the climatic amelioration and creation of new habitats started somewhat earlier than the expansion. In most cases not a single factor but a complex of reasons regulates the range of bird

species and size of populations. Although agreeing with the modern view that bird populations are chiefly affected by changes in their habitats caused by man (e.g. Ahlén 1977, v. Haartman 1973, 1978, Järvinen & Ulfstrand 1980, Hildén & Hyytiä 1981), I feel that at least in the case of the Great Reed Warbler the influence of the climatic amelioration must be stressed. In E Europe increased continentality of the climate (Kalela 1949) could raise the breeding success and cause overpopulation in the central parts of the range. Population pressure towards the periphery, and successful breeding there due to the rise in temperature and decline in precipitation would cause the species to expand further north. The rate of expansion was presumably regulated by the availability of suitable habitats and nestling production: the Reed Warbler, with a substantially higher reproductive rate and greater tolerance of cold and rainy weather (Beier 1981), has expanded faster and further north than the Great Reed Warbler.

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Selostus: Rastaskerttusen esiintyminen Suomessa

Rastaskerttunen tavattiin Suomessa ensi kerran Helsingissä 1930. 1940-luvulla laji havaittiin lähes vuosittain Helsingin ja Porvoon seudulla. 1950-luvulta havaintoja on vuodessa 1—8 (keskimäärin 3.6), 1960-luvulta 5—12 (7.5) ja 1970-luvulta 13—51 (30.2) laulavasta koiraasta. Samanaikainen havainnoinnin tehostuminen selittää vain osittain havaintomäärien kasvun. Pesiminen on varmistettu maassamme vain viitisentoista kertaa. Vuosittaiset kannanvaihtelut ovat huomattavia eivätkä näytä olevan suorassa riippuvuussuhteessa kevätmuuton aikaisiin lämpötiloihin (kuva 1) vaan johtuvat ehkä pesimätuloksen vaihtelusta.

1960-luvun puolivälistä alkaen rastaskerttusia

on etelärannikon lisäksi tavattu enenevässä määrin myös lounaisrannikolla ja sisämaassa (kuva 1). 1970-luvun havainnoista 35 % on etelärannikolta, 24 % lounaisrannikolta ja 41 % sisä-maasta, lähinnä Etelä-Karjalasta ja Päijät-Hämeestä (kuva 2).

Rastaskerttusen ekspansion syynä lienee kannan vahvistuminen Itä-Euroopassa pesimätuloksen parannuttua ilmaston mantereistumisen myötä sekä samanaikainen Pohjois-Euroopan ilmaston lämpeneminen ja ruoikoiden laajeneminen vesistöjen rehevöitymisen, laidunnuksen lopettamisen ja vedenpinnan laskujen ansiosta.

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