AVIAN ECOLOGY AND BEHAVIOUR

PROCEEDINGS OF THE BIOLOGICAL STATION
"RYBACHY"

Volume 14 **2008**

Avian Ecol. Behav. 14, 2008: 1-33

Population ecology of the Great Tit *Parus major* in taiga forest on Lake Ladoga coast

Alexander V. Artemyev

Abstract: Artemyev A.V. (2008): Population ecology of the Great Tit *Parus major* in taiga forest on Lake Ladoga coast. Avian Ecol. Behav. 14: 1-33.

Studies done in 1979-1004 in Karelia showed that taiga forests are suboptimal habitats for the Great Tit, where breeding density is low and proportion of yearlings among breeders is high. Laying dates depended on habitat and April air temperatures. Clutch size was not related either to breeding density or to habitat. Yearlings bred earlier than older birds, laid more eggs and raised more fledglings. Age of males influenced timing of breeding but not clutch size. It is assumed that in the study area external factors have a stronger impact on birds than their age, so that age-related variation is lacking or strongly transformed.

On average, 47.8% pairs laid second clutches after a successful first breeding cycle. Breeding density or age composition of pairs did not influence the occurrence of second breeding cycle. Second cycle occurred more often in forest stands with high specific diversity of trees. The mean air temperature in September was positively related to the occurrence of second broods. As many as 77% of nests survived to fledging, and 67.9% of eggs laid produced fledglings. Breeding performance was not related to breeding density, habitat, age composition of the population, or timing of breeding. It was mainly governed by partial nestling loss, proportion of nests lost and mean monthly temperature of May. A breeding pair produced on average 10 fledglings per season. This figure was related to breeding success, occurrence of second clutches, and winter and spring weather.

Low breeding density of Great Tits in the Ladoga area prevented development of density-dependent regulation mechanisms. Therefore, reproductive strategy is aimed at achieving the maximum reproduction rate possible, limited only by the physiological capacity of birds and resources in the environment. Breeding density was practically unrelated to breeding performance in the preceding year. It was governed by immigration rate and survival rate during the non-breeding season. Weather during the critical periods of the annual cycle, i.e. during autumn and spring movements and during winter had a certain impact on breeding density.

Key words: Great Tit, taiga forest, breeding density, reproductive biology, breeding productivity, mechanisms of numbers regulation.

Address: Institute of Biology, Karelian Research Centre, Russian Academy of Sciences, 185610 Petrozavodsk, Russia. E-mail: artem@karelia.ru

Received 26 January 2005/ Received in revised form 13 March 2006/ Accepted 16 March 2006.

1. Introduction

Breeding range of the nominotypical subspecies of the Great Tit includes nearly the whole of Europe and a large part of Asia. It stretches from Turkey to northern Scandinavia, and from the Atlantic to the coast of Sea of Okhotsk (Cramp & Perrins 1993). Living conditions vary broadly across this vast area, therefore the response of different populations to environmental stimuli may differ considerably. Thus, a comparative analysis of ecology and population dynamics in different parts of the range is of interest for the study of both general rules and local specializations. Most detailed studies of the Great Tit biology were done in the birds belonging to the nominotypical subspecies and the subspecies of the British Isles in European deciduous and mixed forests (Kluyver 1951, Lack 1954, Perrins 1965, Cramp & Perrins 1993, Likhachev 2002 etc.). This study analyses in detail population ecology of Great Tits in the taiga forests of European Russia where climate, vegetation and a number of other parameters differ markedly from the core parts of the species' breeding range.

2. Study area, materials and methods

The study was done in 1979-2004 at the Mayachino field station of the Institute of Biology, Karelian Research Centre of Russian Academy of Sciences (60°46´N, 32°48´E). The station is located at the southeast Lake Ladoga coast in Olonets district of Russian Karelia in the subzone of middle taiga. The landscape is rather marshy: forests on dry soil comprise just 8% of the total area, and most forests grow on more or less wet soil. Most widespread are pine forests (65%), spruce forests cover 16% of the total forest area, aspen cover 10%, birch 8% and alder 1%. A strong anthropogenic transformation of habitats caused a significant change in age composition of forests, but their specific composition underwent smaller changes over the last 125-135 years. The reason is that after felling pine forests, there are usually replaced by pine and mixed pine-deciduous young stands, and spruce forests are restored through the stage of deciduous forest (Volkov et al. 1990).

Long but relatively mild winters and cool summers are typical of the study area and the whole region. Snow cover lays for some 125 days, temperatures above the freezing point last on average for 205 days (between 10 April and 1 November), above +5 °C on average 160 days (between 29 April and 6 October). April is rather cool, the long-term mean air temperature at the latitude of Petrozavodsk is just 1.2 °C, i.e. lower than the temperature of the coldest month in southern England, the Netherlands, lowland Switzerland and some other parts of the Great Tit's range (Alisov et al. 1954). Spring weather is unstable due to alternation of air flows from the Atlantic and the Arctic (Agroclimatic Directory 1959, Romanov 1961). As a result, the timing of many phenological events is more variable than in central European Russia (Minin 1992).

The birds bred in standard-sized wooden nest boxes (Blagosklonov 1991). They were set up in forests typical of the area, mainly in mature pine forests and mixed pine and birch forests of varying age, some in mature spruce stands, spruce and pine forests and in black alder stands. The first set of 100 nest boxes was provided in 1979, 200 nest boxes were added in 1980, in subsequent years their number varied between 270 and 400 (Fig. 1). Most nest boxes were set up in lines along roads, compartment lines and reclamation drains, with an interval of 20-100 m, on average 40 m between the nest boxes. Furthermore, three study plots containing 15, 25, and 50 nest boxes with the density of ca. 10 nest boxes per 1 ha were set up. The nest boxes were located in the area of ca. 10 km^2 in a contiguous woodland area 25 km from the small town of Olonets. To estimate breeding density, we included only the area of the close vicinity of nest boxes. We included 100 m stripe along the lines of nest boxes (50 m on each side), and added 100 m to the length of the line (50 m on each end). In the plots of nest boxes, a 50 m stripe outside the outermost lines of nest boxes was included in the area. The overall area varied between 120-170 ha since 1980, on average 145 ha. Numbers of nest boxes available and occupied by Great Tits are given in Tab. 1.

Annually, the fate of each nest was followed, laying dates and clutch size recorded, together with incubation success rate and nestling survival rate. Practically all nestlings were ringed. Adults (87% of females and 84% of males) were captured at nests and ringed when the young were 7-14 days old. Age of adults was identified on the basis of contrast between greater and primary coverts (Svensson 1975, Vinogradova et al. 1976).

In 1979-2004, a total of 159 pairs bred in nest boxes (1 to 18 pairs annually), the fate of 235 nests was followed. Onset of breeding was determined as laying the first egg in the earliest nest. Mean annual dates of beginning of breeding were calculated on the basis of clutches initiated within 30 days after the season's earliest nest, thus mainly excluding repeat and second clutches (following Both et al. 2004). Breeding performance was estimated as the rate of nests surviving until fledging, and as the numbers of fledglings produced from all eggs laid. Embryonic mortality rate (egg loss without predated clutches) and partial loss of nestlings (without nest predation) were calculated separately. The overall incubation success and nestling survival rates accounted for the loss of complete nests. The mean brood size at fledging was calculated on the basis of nests where at least one chick survived to fledging. Breeding productivity was determined as the number of fledglings produced divided by the number of females that had bred. The preliminary results of the study of breeding biology of the Great Tit have been published earlier (Artemyev 1993).

It is usually assumed that fluctuations of bird numbers breeding in nest boxes reflect the population dynamics in the adjacent forest areas. Breeding density of the Great Tit in the study area was very low (Tab. 1) which resulted in small annual sample sizes. Even though the study area and the number of nest boxes available were large, the material could not always be subject of rigorous statistical analysis. Therefore some of the conclusions concerning the factors that influence population dynamics are suggestive and not final.

Weather variables were characterized on the basis of data from Olonets weather station located 25 km to the northeast of the centre of the study area. We used mean monthly and daily air temperatures. It should be emphasized that these figures do not reflect the microclimate in the breeding habitats and just reflect the general weather tendencies in the study area.

The usual methods of variation statistics were used in data analysis (Lakin 1973, Ivanter & Korosov 2003). Pearson correlation and stepwise multiple regression analysis were used for estimating relationships between variables. Percentages were compared by Fisher's exact test.

3. Results and discussion

3.1. Breeding density

Breeding density of Great Tits in the areas where nest boxes were provided varied between 0.76 and 12.61 pairs·km^{-2}, on average 4.2 pairs·km^{-2} (Fig. 1). Great Tits occupied most eagerly nest boxes in mature mixed forests with a considerable proportion (40-70%) of deciduous trees: birch, aspen, alder (Tab. 1). The highest breeding density in the study area was recorded in a mature mixed pine and deciduous forest: during the peak of numbers in 1983 it reached 24.4 pairs·km^{-2} (eight pairs in 94 nest boxes). In pure stands of black alder, young and ripening mixed forests of pines and deciduous trees, and coniferous forests with a small proportion of deciduous trees admixed Great Tits settled less frequently. The least attractive forest types

Table 1. Occupancy of nest boxes and breeding density of Great Tits in different habitats on Lake Ladoga coast in 1979-2003.

Habitats	Number of nest boxes	Area, ha	Number of breeding pairs	Pairs per 100 nest boxes	Breeding density, pairs·km^{-2}
Black alder forest	664	318.8	11	1.66	3.45
Spruce forest	909	636.9	6	0.66	0.94
Spruce and pine forest	542	239.4	9	1.66	3.76
Mixed deciduous and coniferous stands	1991	720.6	54	2.71	7.49
Pine forest	871	563.6	9	1.03	1.60
Pine and deciduous stands	1931	713.6	48	2.49	6.73
Young pine and deciduous stands	348	154.8	6	1.72	3.88
Submature pine and deciduous stands	655	240.1	8	1.22	3.33
Total	7911	3587.8	151	1.91	4.21

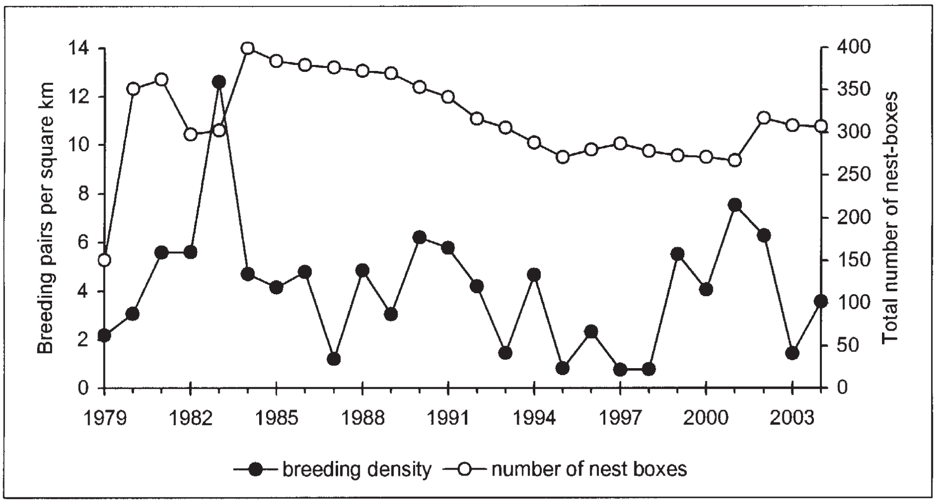

Figure 1. Number of nest boxes available and breeding density of Great Tits in the Ladoga area in 1979-2004.

were practically pure spruce and pine stands, where in the years of low overall density (< 3 pairs·km^{-2}) no Great Tits bred at all.

As in other parts of the breeding range (Kluyver 1951, Shcherbakov 1956, Perrins 1965, Zimin 1978, Cramp & Perrins 1993 etc.) Great Tits in the Ladoga area also prefer forests with predominating deciduous trees. An exception is mature black alder stands that are less preferred than mixed forests of birch and pine. The reason is probably the late opening of leaves in black alder and thus low attractiveness of this habitat in early spring.

In northwestern Russia Great Tits prefer to breed in forests located close to their wintering habitats. Therefore the maximum values of breeding density in the Leningrad Region (30-40 pairs·km^{-2}) and in Russian Karelia (28 pairs·km^{-2}) are recorded in mixed forests in the vicinity of towns and villages or in old urban parks (Malchevsky & Pukinsky 1983, Zimin et al. 1993). In this region Great Tits usually do not overwinter in the woods far from human settlements and breed there with a low density (Noskov & Smirnov 1981). Therefore, nest box occupancy rate is 80-90% in optimal habitats in the vicinity of large cities and just 2-10% in the core areas of large forests (Smirnov & Tyurin 1981). In natural forests of Ladoga area breeding density of this species varies between 0.4 and 6.3 pairs·km^{-2} in the most common habitat, different types of pine forest (Volkov et al. 1990). Providing nest boxes in such habitats does not result in increased numbers of breeding Great Tits (Tab. 1). Even though Great Tits readily occupy nest boxes, they breed in natural cavities equally eagerly. Unlike Pied Flycatchers *Ficedula hypoleuca*, whose breeding density is to a great extent governed by the availability of holes and is sharply increased by providing nest boxes, this factor is much less important for population dynamics of the Great Tits. In taiga forests far from villages their breeding density is low and no shortage of breeding cavities exists. Only in young forests providing nest boxes increases Great Tit numbers (Zimin 1978).

3.2. Structure of the breeding population

Age structure of the breeding Great Tit population is biased towards yearlings, older birds comprise 48.4% among males and 24.4% among females (Fig. 2). A similar age ratio is observed on Lake Ladoga coast during the pre-breeding period in March and April when the proportion of yearlings is 53% among males and 72% among females (Noskov & Smirnov 1981). Our data probably reflect the real age ratio in the forests of the Ladoga area. Most Great Tits breeding in nest boxes were immigrants hatched elsewhere and first settling within the study area. Residents earlier recorded in this area made up just 8.3%, and autochthonous birds hatched here just 2.5% of the population (Fig. 3). This differs considerably from the pattern found in sedentary populations of European broad-leaved forests where immigrants make up 20-57% of breeders, and locally hatched birds usually comprise over 25% (Kluyver 1951, Perrins 1965, van Balen et al. 1987, McCleery & Clobert 1990).

3.3. Timing of breeding

In the Ladoga area Great Tits usually start breeding in late April – early May. The season's earliest clutch was started between 22 April (in 1983) and 25 May (1997), on average on 7 May. The whole period of starting new clutches stretches for nearly three months, both due to second broods in a proportion of birds and to replacement clutches (Fig. 4).

Over most of its range, the Great Tits is double-brooded (Likhachev 1961, Cramp & Perrins 1993). In the study area the proportion of pairs laying genuine second clutches varied between 0 and 100%, on average 47.8% (n = 116).

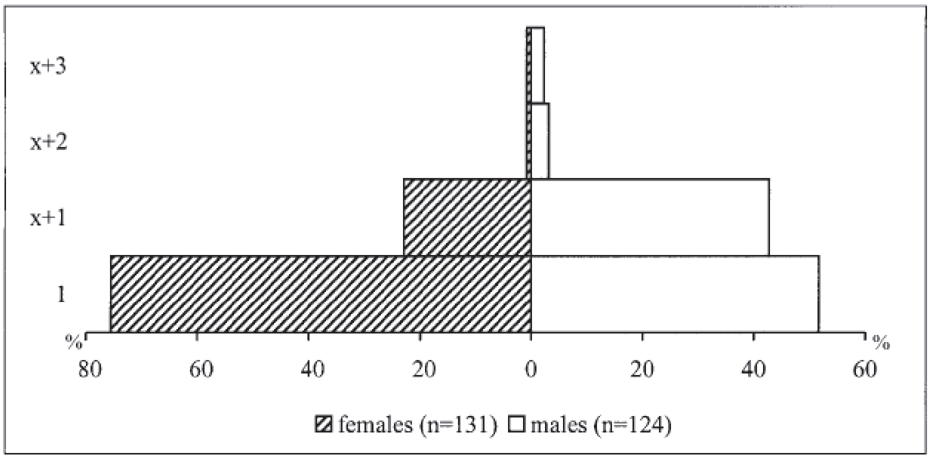

Figure 2. Age structure of breeding Great Tits in the Ladoga area in 1979-2004.

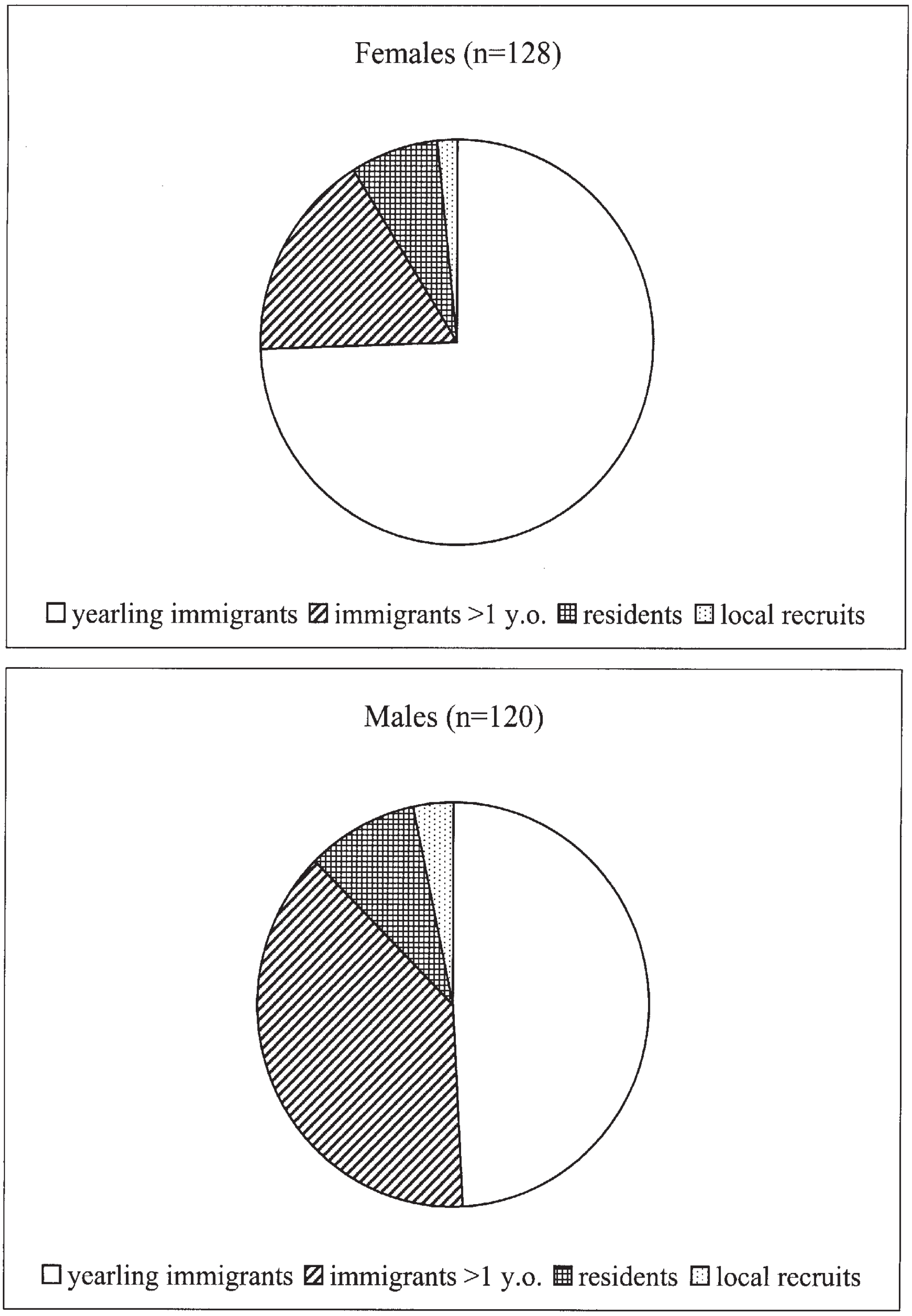

Figure 3. Origin of breeding Great Tits in the Ladoga area in 1981-2004.

The onset of first clutches varies between 22 April and 26 May (mean 8 May, n = 65), of second clutches between 6 June and 15 July (mean 23 June, n = 55). Replacement clutches were recorded between 1 May and 25 July, after loss of first or second clutches. A similar timing of breeding was reported from other sites in southern Karelia: at 61°30´-62°30´N the breeding begins between 20 April and 18 July (Zimin 1978). The mean date of starting clutches initiated within 30 days after the season's earliest one is 10 May (n = 145, 1979-2004).

Timing of breeding of Great Tits in southern Karelia generally follows the Hopkins' rule (Slagsvold 1976, Sanz 1998) which states that phenological events occur later further in the north. At the same time, no longitudinal trend is evident at the latitude of 60°-61°N (Tab. 2), in spite of generally milder climate and higher spring temperatures in the western parts of the range.

In many parts of their range, timing of breeding of Great Tits is largely governed by air temperatures and by the development of spring phenological events (Kluyver 1951, Slagsvold 1976). In the Ladoga area the strongest correlation exists between timing of breeding and the mean temperature of April (Tab. 3), whereas temperatures of other months were unrelated to the timing of reproduction. In spring, most important for plant vegetation at temperate latitudes are effective temperatures, i.e. those exceeding +5°C (Schulz 1981). We therefore tested for a relationship between timing of breeding and the dynamics of temperatures above +5 °C. The closest correlation was revealed between the time of starting the season's earliest clutch and the mean date of the onset of breeding in the population and the date when the cumulative sum of effective temperatures reached 50 °C. However, the interval between these events varied widely between the years. A somewhat weaker correlation was recorded between the aforementioned breeding parameters and the dates when the minimum temperatures showed a sustainable excess over 0 °C and when the cumulative sum of positive temperatures reached 100 °C.

In many birds of temperate and high latitudes the timing of breeding is known to be controlled by an endogenous programme which is triggered by a species-specific threshold change of photoperiod (Gwinner 1996, Dawson et. al. 2001). Great Tits show population-related variation in photoperiodic thresholds of developing reproductive condition, threshold being lower at higher latitudes (Silverin 1995). Photoperiod controls just the possible time window of beginning of breeding. Actual onset of reproduction is fine-tuned by environmental stimuli: phenology of vegetation, dynamics of air temperatures, food availability, social interactions etc. (Perrins 1965, 1996; Zimin 1988, Nager & Noordwijk 1995).

Impact of temperature on the timing of breeding in birds is well-known, but there is still no agreement whether it acts directly on physiology and the development of reproductive state, or on energy budget through development of vegetation and food availability. Van Balen (1973) showed that temperatures acts indirectly and tits react on the timing of hatching and abundance of small caterpillars. Recently Meijer et al. (1999) confirmed in their experiments with Starlings *Sturnus vulgaris* the suggestion of Kluyver (1951) that temperature acts directly on the time of laying. Nager (1990) suggested that this factor acts on birds both directly and indirectly. The response may be population-specific. In the Netherlands and Britain tem-

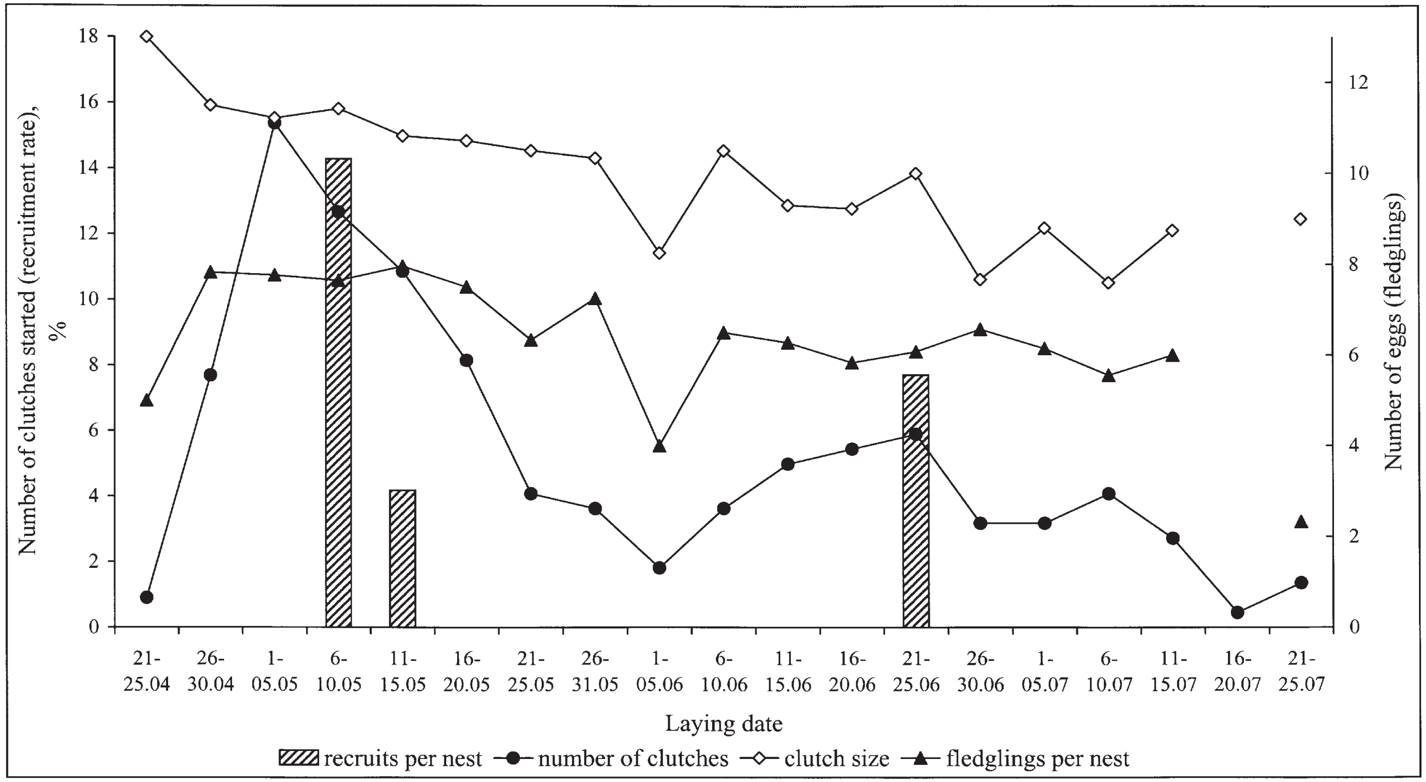

Figure 4. Influence of timing of breeding on clutch size, brood size, and number of recruits in the Great Tit in the Ladoga area in 1979-2004.

Table 2. Main breeding parameters of Great Tits at different European sites at 60°-61°N.

Study site and years	Coordinates and altitude a.s.l.	First and early clutches		Proportion of 2nd clutches, %	Source
		Mean starting date (1 = 1 May)	Mean size, eggs		
Norway, Sørkedal 1968-1974	60°N, 11°E; 200 m	11.7 (35)*	–	–	Slagsvold 1976
Sweden,Tärnsjö 1952-1963, 1972-1974	60°19´N, 16°56´E; 200 m	–	8.2 (400)*	18.5	Johansson 1974
Finland, Lemsjöholm 1953-1967	60°30´N, 22°E; 50 m	10.7 (225)	9.9 (225)	20.2	Haartman 1969
Russia, Karelia, Mayachino 1979-2003	60°46´N, 32°48´E; 20 m	10.1 (141)	11.1 (122)	47.8	This study

Note. * – Number of nests is given in parenthesis.

Table 3. Relationships between timing of breeding in Great Tits and some spring weather parameters in the Ladoga area in 1980-2002.

Weather variable	Onset of the season's earliest clutch	Mean date of clutch onset
Mean temperature of March	r = -0.16, n.s.	r = -0.12, n.s
April	r = -0.62, p < 0.01	r = -0.69, p < 0.001
last 10-day period of April	r = -0.57, p < 0.01	r = -0.7, p < 0.001
Date of reaching the sum of effective temperatures		
(> 0 °C) 50°	r = 0.71, p < 0.001	r = 0.84, p < 0.001
100°	r = 0.59, p < 0.01	r = 0.67, p < 0.01
Date when the minimum temperature becomes		
> 0 °C	r = 0.64, p < 0.01	r = 0.63, p < 0.01

peratures two months before the onset of laying influenced the time of breeding, in Switzerland and Germany – temperatures 1.5 months before laying, in Scandinavia and Karelia important were the temperatures during the preceding month (Kluyver 1951, van Balen 1973, Perrins 1965, Haartman 1969, Slagsvold 1976, Nager 1990, Winkel & Hudde 1997, our data). Everywhere the breeding started after a short period of warm weather, but the thresholds were different: they decreased from the southwest towards the northeast (Slagsvold 1975a, 1975b, 1976; Veistola et al. 1995).

Even at the same site the thresholds may differ between the years, so that in severe and unstable climates it is not possible to determine the temperature that permits to start breeding in a population (Likhachev 1961, 2002; Zimin 1988, our data).

In the Ladoga area the mean daily temperature on the day of onset of the season's earliest clutch varied between 2.2 °C and 14.3 °C, on average 9.0 °C. The determinant date, a parameter suggested by Kluyver (1951) as the time of onset of rapid oocyte development in most females (four days before the population's mean date of clutch beginning), varied between 27 April and 21 May in our study area (on average – 7 May). On this day, weather temperature was on average 8.7 °C. This value however could not be treated as threshold, as it varied from 0.4 °C to 14 °C between the years. The date when the cumulative sum of effective temperatures reached 50 °C practically coincided with the determinant date and varied between 23 April and 19 May, on average 7 May. Even though time lag between these events could reached up to nine days in sme years, this phenological parameter influenced the population under study most significantly.

No significant long-term trend in the time of breeding was revealed in Karelia. Global warming which has a significantly impact on the timing of breeding in Western Europe (Crick et al. 1997, McCleery & Perrins 1998, Both et al. 2004), has not yet shown its influence on Great Tits in the Ladoga area. In our region it is winter which got significantly milder over the last 50 year, and March temperatures increased (Nazarova & Filatov 2004), whereas April and May temperatures which influence spring phenology most strongly, have undergone small changes. Across 1980-2002, the mean April temperature showed a positive trend ($r = 0.35$) which however was not significant, whereas May temperatures showed an opposite trend over the same period ($r = -0.28$), also not significant. The time of breeding did not show a significant trend across this period, either ($r = -0.21$, n.s.). A similar pattern has been reported from the Moscow area and from northern Finland, where, unlike more western parts of the range, the pre-breeding period of Great Tits did not get significantly warmer during the recent decades, either (Visser et al. 2003).

Timing of breeding of Great Tits in different habitats in the Ladoga area was rather similar, so our data show no significant forest type related difference (Tab. 4). However, birds breeding in practically pure conifers (spruce and pine forests pooled) started egg-laying on average seven days later than their conspecifics breeding in mixed and deciduous woods ($F = 6.5$, $p < 0.05$). In spring, conifer stands are less well insolated, snow melts here later, soils warms up slower and the development of vegetation is delayed. In other south Karelian sites Zimin (1978) found significant difference only between mature deciduous forests and young mixed pine-deciduous stands. It is worth noting that habitat-related variation in the time of breeding is not always pronounced in other parts of the range, either. In central Europe earlier breeding was recorded in urban parks as compared with forests in the country (Cramp & Perrins 1993). In England Great Tits breed earlier in gardens than in forests and parks, but no difference between coniferous and deciduous forests was reported (Lack 1966). A similar pattern was reported by Klyuver (1951) from the Netherlands, but another study did find a difference between oak and pine forests (van Balen 1973). In the Mediterranean Great Tits start to breed earlier in seasonal

Table 4. Main parameters of the first breeding cycle and the occurrence of second clutches in relation to habitat in the Ladoga area in 1979-2004.

Habitat	Onset of clutch ± SE (1 = 1 May)	n	Clutch size ± SE	Brood size ± SE	Number of successful clutches	Occurrence of second clutches, %
Black alder forest	9.8 ± 2.1	10	10.9 ± 0.7	8.8 ± 0.5	8	25.0
Spruce forest	14 ± 3.7	5	11.0 ± 0.6	8.5 ± 0.5	4	50.0
Spruce and pine forest	6 ± 4.5	6	11.6 ± 0.2	11.2 ± 0.2	5	20.0
Mixed deciduous and coniferous stands	9.4 ± 1.3	50	11.1 ± 0.2	9.4 ± 0.3	39	46.2
Pine forest	16.4 ± 3.1	9	10.9 ± 0.5	8.9 ± 0.5	7	42.9
Pine and deciduous stands	7.7 ± 1.2	46	11.0 ± 0.2	8.9 ± 0.4	42	54.8
Young pine and deciduous stands	10.3 ± 3.8	6	10.7 ± 0.4	9.2 ± 0.4	5	80.0
Submature pine and deciduous stands	8.8 ± 1.5	8	11.5 ± 0.4	9.5 ± 0.9	6	50.0

oak woods than in evergreen forests (Blondel et al. 1987). Such habitat-related difference is usually obvious between contrasting habitat types and is enhanced by local factors, as artificial illumination in towns, proving additional food in gardens or local phenology and the dynamics of food availability in natural habitats.

In the Ladoga area, female Great Tits show no strong age-related variation in the time of egg-laying (Tab. 5). As many other passerines of boreal forests (Zimin 1988), Great Tits of different age start breeding nearly simultaneously, so that the bulk of the population breed during a narrow time window. The tendency of old females to breed earlier than one-year-old females is not supported by the data from Karelia and Finland. Moreover, an opposite trend exists: yearling females are the first to start laying eggs (Haartman 1969, Zimin 1988, our data). The difference between dates of commencing egg-laying by yearlings and older birds in the Ladoga area and southern Finland (Lemsjöholm) was on average one day, but it was not significant due to small sample sizes. In Western Europe older females normally start breeding earlier than one-year-old birds, time lag being larger further south. It was 4.2 days in Switzerland (Nager & Noordwijk 1995), in the Netherlands it was 2.1 days and recorded not annually (Kluyver 1951), in southern England ca. 1 day (Perrins 1965), and in southern Sweden and in Poland the difference was only recorded in some years (Cichon & Linden 1995).

Table 5. Age of partners and the main parameters of the first breeding cycle.

Age		n	Onset of clutch		Clutch size		Brood size	
female	male		range	Mean* ± SE	range	Mean ± SE	range	Mean ± SE
1 year	all	87	25.04-01.06	08.90 ± 0.92	7-13	11.19 ± 0.14	4-13	9.42 ± 0.21**
x + n	all	29	22.04-29.05	09.97 ± 1.58	6-15	10.86 ± 0.33	4-11	8.33 ± 0.39**
all	1 year	58	27.04-01.06	10.45 ± 1.07**	6-15	10.91 ± 0.21	4-12	9.09 ± 0.26
all	x + n	56	25.04-29.05	08.11 ± 1.16	7-13	11.15 ± 0.17	4-13	9.22 ± 0.28
1 year	1 year	43	28.04-01.06	10.44 ± 1.26	7-13	11.07 ± 0.19	4-12	9.41 ± 0.28
1 year	x + n	40	25.04-27.05	06.95 ± 1.37**	7-13	11.33 ± 0.22	4-13	9.43 ± 0.33
x + n	1 year	13	27.04-28.05	11.15 ± 2.27	6-15	10.54 ± 0.64	4-12	8.08 ± 0.62
x + n	x + n	12	02.05-22.05	09.92 ± 2.12	8-11	10.58 ± 0.26	6-11	8.55 ± 0.56

Notes. * 1 = 1 May; ** – Significantly different values.

In our study site the time of breeding was also significantly related to the age of the male: pairs with one-year-old males usually bred 1-4 days later than pairs where the male was older (Tab. 5). Even though the tendency existed in all combinations of partners, a significant difference was only recorded between the groups 'old male – yearling female' vs. 'yearling male – female of any age' ($t = 2.01$ $p < 0.05$). Age-related variation in the timing of breeding, quite obvious in more southern parts of the Great Tit's breeding range (Perrins & McCleery 1985, Glutz von Blotzheim & Bauer 1993), is less pronounced in the Ladoga area due to extrinsic factors, mainly the unstable weather in spring.

Timing of breeding of Great Tits is known to be fine-tuned to fit the period of maximum abundance of food for nestlings, but it also depends on food availability for the female during egg-laying (Lack 1954, 1966; Perrins 1965). Breeding is also influenced by territory quality and the male's individual characteristics: his sexual activity which stimulates the development of the female's reproductive system, and courtship feeding rate which provides additional energy during egg-laying. Old males normally occupy territories of higher quality and start their sexual activity earlier than yearlings. It is not improbable that during cold and unstable spring weather in the Ladoga area, females have difficulties with keeping a positive energy balance during egg-laying. Therefore, age of the male partner, his quality and the ability to occupy a good territory may seriously influence the onset of breeding. In the southern Netherlands, where climate is mild and springs are warm, the age of the male partner does not influence the time of breeding (Kluyver, 1951). The same was recorded in southern England in 1947-1964 (Perrins 1965), but later the impact of male age of breeding was detected (Perrins & McCleery 1985). In southern Sweden and in Poland a similar relationship was also recorded in some years (Cichon & Linden 1995).

The fact that at our latitudes older females breed somewhat later than yearlings might suggest that the former can better predict the time of maximum abundance of food for their nestlings. As spring and early summer are unstable in the taiga zone, early breeding is not always most productive (Zimin 1988). It has been reported that with growing age, the birds can adjust the time of their breeding, as more experience allows better predictions of caterpillar peak (Nager & Noordwijk 1995). It cannot be ruled out that yearling females start breeding as early as made possible by their physiology and food availability, whereas older females start egg-laying when it is optimal for their future offspring.

3.4. Clutch size

Reduction of clutch size along the breeding season, reported from many parts of the Great Tit's range, has been believed to be a general rule for this species (Kluyver 1951, Perrins 1965, Klomp 1970, Crick et al. 1993 etc.). However, in some habitats clutch size increased from the beginning to the middle or to the end of the season. Its trend, like in some other avian species, depends on the environment and on population characteristics (van Balen 1973, Cramp & Perrins 1993, Dhondt et al. 2002).

In Karelia the full clutch size of Great Tits decreased along the season (Fig. 4). The relationship is described by the linear regression: $y = 11.51 - 0.043\ x$ ($R^2 = 33.5\%$), with y for the number of eggs laid, and x for the date of laying the first egg (1 is 1 May). The size of clutches started in April and May was less dependent on the calendar date ($r = -0.28$, $p < 0.001$), than the size of late clutches laid in June and July ($r = -0.46$, $p < 0.001$). The reason for this could be unstable weather and foraging conditions in the beginning of the breeding season.

Double-brooded pairs have 7-12 eggs in their first nests (on average 11.2 ± 0.1, n = 61) and 6-12 eggs in second nests (on average 9.3 ± 0.3, n = 41). Early clutches of single-brooded pairs contained 6-15, on average 11.0 ± 0.2 eggs (n = 64), replacement clutches – 1-14, on average 9.6 ± 0.5 eggs (n = 23). Annual variation of the mean clutch size in early and late nests was related to the laying date of the season's earliest clutch ($r = 0.43$, $p < 0.05$), but not to the population's mean date of starting breeding ($r = 0.32$, n.s.).

No habitat-related variation in clutch size was revealed for first and early clutches in the Ladoga area: clutch size was somewhat different in different types of forest, but insignificantly so (Tab. 4). Unlike western and southern Europe where habitat-related variation in clutch size is pronounced (Kluyver 1951, Perrins 1965, van Balen 1973, Blondel et al. 1987, Beldal et al. 1998), in the north it is weaker and may be absent (Haartman 1969). Such a difference in Karelia existed only between optimal and marginal habitats: mature deciduous forests vs. young mixed pined and deciduous stands (Zimin 1978). In Finland the difference was only considerable in the suburbs of Oulu where different types of forest strongly differ in specific composition of trees and breeding density of Great Tits (Orell & Ojanen 1983a).

Habitat-related breeding density did not influence clutch size in first and early nests of Great Tits in the Ladoga area ($r = 0.01$, n.s.). The mean clutch size was directly related to the numbers of Great Tits in the area under study ($r = 0.42$, $p < 0.05$). Clutch size is not reduced with increasing breeding density either in southern Finland or in Russian Karelia (Haartman 1969, 1971; Zimin 1988). The reason is that in boreal forests the breeding density of the Great Tits remains below the critical level when density-dependent mechanisms of population regulation start to act, including the reduction of clutch size. In the Netherlands these mechanisms are switched on when breeding density exceeds the threshold of 40 pairs·km^{-2} (Kluyver 1951). In our region this density is never reached even in optimal habitats (Zimin et al. 1993).

In western European populations adult females lay larger clutches than yearlings (Kluyver 1951, Perrins 1965, Lack 1966). The same tendency was reported from southern Finland, however the difference is smaller and not significant here (Haartman 1969). In the Ladoga area one-year-old females laid slightly more eggs than adult ones with similar time of laying. Even the difference in clutch size was not significant, it became significant in brood size. The age of the male did not influence the size of clutch or brood at all (Tab. 5). Annual variation of the age composition of breeders had no impact on clutch size, as it did not depend on the proportion of males and females older than one year (r = 0.31 and r = -0.01, n.s.). Apparently, in northern regions other factors are much more important than the age of parents, and they override age-related variation. In the framework of clutch size optimization hypothesis (Perrins & Moss 1975, Pettifor et al. 1988, Godfray et al. 1991) it can be assumed that adult females are better able to predict the future food availability and lay clutches optimal for the current season, whereas yearling females lay the largest clutches possible.

3.5. Factors that influence the occurrence of second clutches

In southern Karelia one of the most variable demographic parameters of Great Tits, both across years and across study areas, is the proportion of genuine second clutches in the population. At our study site in the Ladoga area it varied between 0 and 100%, on average 47.8% (n = 116).

A general tendency of decreasing proportion of second clutches is recorded towards the north (Sanz 1998). However, latitudinal trends may be concealed by other factors, as habitat, breeding density, age structure of the population etc. For instance, no such trend is observed in the sector between 28°E and 41°E, and the occurrence of second broods is considerably reduced only in the Arctic (Tab. 6). In Scandinavia at the latitude of our study site the proportion of second clutches is higher in more eastern populations. This may be due to local conditions, in particular to the prevailing habitats (Tab. 2).

One of the most important factors for the occurrence of second clutches is the specific composition of trees in the forest. In western Europe Great Tits are double-brooded more often in coniferous and evergreen forests than in deciduous woods (Cramp & Perrins 1993). The proportion of second clutches is lower in deciduous forests than in mixed stands, and in mixed stands it is lower than in conifers (Kluyver 1951, Perrins 1965, Lack 1966). In Kivach Nature Reserve in Karelia in mature forests with prevailing coniferous trees ca. 18% of Great Tits make the second breeding attempt, in mixed pine and deciduous woods of Onego area this proportion is 55.8% (Zimin 1978), in mature small-leaved forests of Trans-Onego area – ca. 82% (Khokhlova 1976).

In the Ladoga area Great Tits were most often double-brooded in forests with mixed and variable specific composition (Tab. 4). The frequency of second clutches is

Table 6. Occurrence of second clutches in Great Tits at different latitudes between 28°E and 41°E.

Study site	Coordinates	Occurrence of second clutches, %	Source
Murmansk Region, Lapland Nature Reserve	67°54´N, 32°50´E	singular	Semenov-Tien-Shansky & Gilyazov 1991
Murmansk Region, Kandalaksha Nature Reserve	67°00´N, 32°20´E	singular	Bianchi & Shutova 1978
Karelia, Onego area	61°30´N, 34°58´E	55.8	Zimin 1978
Karelia, Mayachino	60°46´N, 32°48´E	47.8	This study
Suburbs of St. Petersburg	59°55´N, 30°30´E	27.6	Smirnov & Tyurin 1981
Moscow Region, Prioksko-Terrasny Nature Reserve	54°50´N, 37°40´E	63.4	Likhachev 2002
Ryazan Region, Oka Nature Reserve	54°46´N, 40°45´E	28.1	Numerov 1987
Ukraine, Zhitomir Region	50°15´N, 28°40´E	37.0	Yaremchenko & Bolotnikov 1988

the highest in the forests of different age with equal proportions of pines and birches, somewhat lower in mixed woods with prevailing deciduous trees and nearly pure pine stands and at minimum in practivally pure black alder and spruce forests, and in spruce and pine forests with a small proportion of deciduous trees. Generally, 57% of Great Tits ($n = 53$) started second clutches in diverse forests stands with a considerable proportion of both conifers and deciduous trees, as opposed by just 24% of pairs ($n = 17$) in largely uniform stands (black alder, spruce, spruce and pine, $F = 6.2$; $p < 0.05$). The only exception were pure pine forests that showed average frequency of double-brooded Great Tits in spite of their pure composition.

In western European population the occurrence of second clutches is significantly dependent on breeding density (Kluyver 1951, etc.). No such pattern was observed in our study area. In spite of a large range of variation of breeding density across habitats, no relationship existed between this parameter and the frequency of second clutches ($r = -0.1$, n.s.), even in years when breeding density was above the long-term mean.

Participation in the second breeding cycle is known to be age-dependent: older birds do it more frequently than yearlings (Kluyver 1951, Perrins 1965, Lack 1966). The same tendency was recorded in the Ladoga area, but no clear relationship between the occurrence of second broods and age was revealed. Annual variation of the proportion of adults among breeders were directly related to the proportion of second clutches, but relationship was only marginally significant ($r = 0.39$, $p = 0.06$). Pairs that made second breeding attempts more often included old birds than single-brooded pairs: in the former ones, 57% of males were older than one year ($n = 64$), in the latter ones, 42% (n = 60). The corresponding figures for females were 28% and 23%. The difference was, however, not significant. In the region studied the frequency of second clutches is apparently influenced by many extrinsic factors, so that age-dependence is here less pronounced than in western and southern Europe where living conditions are more stable.

The occurrence of second broods was not influenced either by the population's timing of breeding ($r = -0.14$, n.s.), or by spring weather which governs this timing to a great extent. It is worth noting that in years with large first and early clutches frequency of second broods increased ($r = 0.57$, $p < 0.05$). It suggests that both clutch size and frequency of second broods were related to food availability during spring.

Winter weather conditions also had a certain impact on the proportion of second clutches. In the Ladoga area the occurrences of second broods was usually higher after mild winters. A similar tendency was reported from the Moscow region (Likhachev 1961). Our data suggest a marginally significant relationship between the proportion of second clutches and the cumulative sum of mean monthly temperatures of December, January, and February ($r = 0.35$, $p = 0.09$) and a significant relationship with the mean temperature of February ($r = 0.41$, $p < 0.05$). In February, Great Tits start to develop their reproductive system and it may be assumed that this process is influenced by the weather. It has been shown experimentally that physiological development of reproductive system in northern tits is not influenced by low temperatures and is accelerated by high temperatures (Silverin 1995). Therefore, during warm years the birds are ready for breeding earlier than in cold ones, thus timing of breeding is shifted. Our data support this, but in the Ladoga area only April temperatures influence the time of breeding (Tab. 3), not March or February temperatures ($r = -0.1$, n.s.). Air temperatures remain low during the latter months and probably do not reach the threshold necessary to trigger reproductive system development. Moreover, just a fraction of local Great Tits spends winter in the study area, and most birds move to winter habitats, sometimes covering hundreds of kilometers, where weather conditions may be very different (Dobrynina 1991, Noskov & Rezvyi 1995).

It is more likely that winter temperatures influence frequency of second clutches indirectly, through food availability. Winter weather is known to have a serious impact on insect abundance (Viktorov 1967, Vorontsov 1975). Food availability is an important factor which influences frequency of second clutches (Tinbergen 1987). Low winter temperatures may reduce survival rates of wintering invertebrates and thus reduce their abundance in spring. Therefore, after cold winters fewer Great Tits are double-brooded. This is indirectly supported by the fact that nestling survival rates in first and early nests are inversely proportional to the sum of mean monthly temperatures of December, January, and February ($r = -0.44$, $p < 0.05$).

In the Ladoga area the distance between the first and the second nest of the same pair was on average 228 m (range = 0-1350 m, n = 55). This value is somewhat larger than in other parts of the range (Jezerskas 1961, Likhachev 1961, Glutz von Blotzheim & Bauer 1993), maybe due to low breeding density and the lack of competition for territories. Some pairs moved long distances from one habitat to another one, probably because of habitat-related dynamics of food availability.

Interval between laying the first egg in the first and the second clutch varied between 33 and 63 days, on average 46 days (n = 55). Interval between hatching in the first nest and start of egg-laying in the second one was one average 22 days (range = 12-38). The latter parameter is believed to better reflect the time lag between breeding attempts (Tinbergen 1987). Time of starting the first clutch did not influence it ($r = 0.10$, n.s.), but the impacts on clutch size ($r = 0.50$, $p < 0.001$), hatching date ($r = 0.30$, $p < 0.05$), and first brood size ($r = 0.35$, $p < 0.01$) were significant. This interval was most strongly related to the time of starting the second clutch ($r = 0.75$, $p < 0.001$). A direct relationship between the time lag between breeding attempts and first clutch size has been reported from field experiments (Smith et al. 1987, Tinbergen 1987). An increased interval during late breeding hints to deterioration of food availability in late summer. Apart from food abundance and availability, an important factor shaping this interval is probably the physiological condition of the female, i.e. its readiness to produce a new clutch.

3.6. Success rate and productivity of breeding

In the Ladoga area 77.1% of Great Tit nests survived to fledging (n = 236). Nest survival rate did not depend on time of breeding, as losses of first and early clutches and broods were 22.1% (n = 145), on second and replacement clutches 24.2% (n = 91). A significant proportion of nests were abandoned after inspection or captures of females on clutches or nestlings (Tab. 7). A proportion of losses (22.2%) is due to predation, mainly by the Stoat *Mustela erminea*, Least Weasel *Mustela nivalis*, and Greater Spotted Woodpecker *Dendrocopos major*. Almost one-quarter of lost nests were abandoned for unknown reasons, mainly during egg-laying. A proportion of losses is due to disturbance by humans camping near nest boxes. In spite of a high density of Pied Flycatchers, only singular cases of interspecies competition for nest boxes were recorded in the Ladoga area, even though such cases are not unusual in other places (Likhachev 1954, Slagsvold 1975c, Haartman 1990). We recorded just one case when a clutch of a Great Tit perished, because a female Pied Flycatcher covered it by nest material.

The overall breeding success rate, i.e. the proportion of fledglings produced from eggs laid, was 67.9% (n = 2295). It varied between 34% in 1994 and 100% in 1995. No significant relationship between this parameter and breeding density was recorded ($r = -0.27$, n.s.). Breeding success rate was related to the partial loss rate in first and early nests ($r = -0.71$, $p < 0.01$), proportion of lost nests ($r = -0.68$, $p < 0.01$) and mean monthly temperature of May ($r = 0.43$, $p < 0.05$). Winter weather seems to play a role, too: marginally significant relationships exist with the mean monthly temperature of January ($r = 0.39$, $p=0.06$) and cumulative sum of mean monthly temperatures of December, January, and February ($r = 0.37$, $p = 0.07$). The causes and rates of egg and nestling losses in first and second clutches were similar (Tab. 8). Overall incubation success rate was 81.6%, nestling survival rate was 83.2% (n = 1873).

A total of 13.8% of eggs perish in abandoned and predated nests, the proportion being higher in second clutches, than the first ones ($F=15.3$, $p < 0.01$). Embry-

Table 7. Causes of nest loss in Great Tits in 1979-2004.

Causes of nest loss	First and early nests		Second and late nests		Total	
	clutches	broods	clutches	broods	n	%
Abandoned after capture of the female	6	4	5	2	17	31.48
Abandoned after inspection	4				4	7.41
Destroyed by humans	1		3		4	7.41
Predated by Stoat or Least Weasel	2		3		5	9.26
by Marten or Mink		1			1	1.85
by Hooded Crow	1				1	1.85
by Greater Spotted Woodpecker		2	1		3	5.56
by Sparrowhawk				1	1	1.85
Predator not identified	1				1	1.85
Abandoned for a reason unknown	7	2	4	1	14	25.93
because of a Pied Flycatcher	1				1	1.85
because of ants			1		1	1.85
Eggs not fertilised			1		1	1.85
Total	23	9	18	4	54	100

onic mortality rates did not differ between early and late clutches, being 4.6% of the pooled number of eggs laid. The highest proportion of nestling losses (10.1%) was due to partial mortality during feeding; 6.7% of nestlings hatched died in predated and abandoned nests. Small habitat-related variation in breeding success rate was due to stochastic causes, mainly to human-induced mortality.

In successful nests (predated and abandoned nests excluded) embryonic mortality rate was 4.9% of all eggs survived to hatching ($n = 2157$). Partial mortality rate of nestlings was 10.8% of all hatched ($n = 1748$). These rates did not depend on age composition of pairs, were similar in different habitats and roughly the same during first, repeat and second breeding attempts (Tab. 9). Only among first clutches a significant difference existed: in forest with dominating spruce partial losses of eggs and nestlings were lower than in black alder stands ($F = 4.5$, $p < 0.05$) and mixed pine/deciduous forests ($F = 5.3$, $p < 0.05$).

Breeding performance of Great Tits is dependent on a large array of factors and varies within Europe from 42% to 86% (Kluyver 1951, Lack 1966, Bianchi & Shutova 1978, Orell & Ojanen 1983b, Payevsky 1985, Numerov 1987, Yaremchenko & Bolotnikov 1988, Semenov-Tien-Shansky & Gilyazov 1991, Glutz von Blotzheim & Bauer 1993, Likhachev 2002 etc.). The lowest rates are reported from marginal habitats, e.g. urban parks and orchards with poor specific composition, or boreal forests; the

Table 8. Survival rates of Great Tit offspring during incubation and rearing the young in 1979-2004.

Parameter	First and early nests		Second and late nests	
	n	% of eggs laid	n	% of eggs laid
Eggs laid	1520	100	775	100
Egg loss				
Clutch abandoned	128	8.4	92	11.9
Clutch predated	50	3.3	46	5.9
Partial loss of eggs	77	5.1	29	3.7
unfertilised	26	1.7	10	1.3
embryo perished	43	2.9	12	1.5
eggs broken	2	0.1	2	0.3
reason not identified	6	0.4	5	0.6
Nestlings hatched	1265	83.2	608	78.5
Nestling loss				
Nest abandoned	61	4.0	20	2.6
Nest predated	37	2.4	7	0.9
Partial loss of nestlings	127	8.4	62	8.0
aged 1-7 days	105	6.9	53	6.8
>7 days	22	1.5	9	1.2
Nestlings fledged	1040	68.4	519	67.0

highest rates are known from mature broad-leaved forests with high food availability. A similar range of variation is known to occur between habitats in southern Karelia, from 50% in young mixed deciduous and pine stands to 86% in mature deciduous forests (Zimin 1978). The study population shows a high breeding performance rate and does not differ in this respect from populations in southern Finland, central European Russia and mixed forests in the Netherlands (Kluyver 1951, Haartman 1969, Dekhuijzen & Schuijl 1996, Likhachev 2002). In boreal forests of the Ladoga area Great Tits find favourable breeding conditions, with optimal period for feeding their young is longer here than in other parts of the range. This is suggested by relatively high and stable breeding success rate during both breeding cycles, whereas in the centre and in the north of the range breeding performance considerably decreases towards the end of the breeding season (Lack 1966, van Balen 1973, Orell & Ojanen 1983b, Numerov 1987).

Productivity of clutches of varying size is similar during the first breeding cycle, it is significantly lower only in clutches containing > 12 eggs (Tab. 10). In second and replacement nests small clutches produce relatively more fledglings, but the dif-

Table 9. Partial losses of eggs and nestlings in Great Tit nests in relation to habitats in the Ladoga area in 1979-2004.

Habitats	First and early nests		Second and late nests	
	Eggs laid	Fledglings, %	Eggs laid	Fledglings, %
Black alder forest	87	80.5	13	69.2
Spruce and spruce + pine forests (70-80% spruce or spruce + pine)	91	91.2	60	88.3
Mixed deciduous and coniferous stands	414	86.2	183	88.0
Pine forest	72	86.1	34	79.4
Pine and deciduous stands	433	82.2	209	83.7
Young pine and deciduous stands	55	83.6	37	81.1
Submature pine and deciduous stands	68	83.8	9	88.9

ference is significant only between the clutches of seven and 12 eggs ($F = 4.7$, $p < 0.05$). It is commonly believed that in tits clutches slightly larger than population mean are most productive (Lack 1966), but this tendency is not always obvious, probably due to variation of many factors governing this parameter (Kluyver 1951, our data).

The overall productivity of reproduction across the whole study period was 10.1 fledglings per breeding pairs per season, varying between 3.5 in 1994 and 15.1 in 1981. This parameter was directly related to occurrence of second broods ($r = 0.67$, $p < 0.01$) and breeding performance ($r = 0.62$, $p < 0.01$). Apart from this, productivity of reproduction depended on the weather during previous winter and spring: cumulative sum of December, January, and February ($r = 0.48$, $p < 0.05$), mean temperature of February ($r = 0.43$, $p < 0.05$) and May ($r = 0.41$, $p < 0.05$). Time of onset of breeding and breeding density did not influence productivity of reproduction ($r = -0.18$ and $r = -0.02$, respectively, n.s.). Multiple regression analysis yielded the equation $y = 0.08 + 0.67 \cdot x_1 + 0.62 \cdot x_2$ with a high predictive power ($R^2 = 82.4$). We used normalized values, with y standing for the number of fledglings per breeding pair, x_1 for the number of fledglings per egg laid and x_2 for the occurrence of second clutches. ANOVA showed that the most important predictor was production of fledglings per egg (48.5% of variance), less important was frequency of second breeding attempts (33.8%).

The population under study shows a typical r-strategy (Pianka 1978) which is optimal in unstable environments (Naumov & Nikolsky 1962). Reproduction rate

Table 10. Productivity of clutches of varying size in the Ladoga area in 1979-2004.

Number of eggs	First and early nests				Second and repeat nests			
	n	Eggs laid	Fledglings	Fledglings per egg	n	Eggs laid	Fledglings	Fledglings per egg
1	–	–	–	–	1	1	0	0
5	–	–	–	–	1	5	4	0.8
6	1	6	4	0.67	4	24	23	0.96
7	3	21	21	1	10	70	58	0.83
8	2	16	15	0.94	15	120	89	0.74
9	9	81	56	0.69	11	99	68	0.69
10	22	220	175	0.80	15	150	108	0.72
11	48	528	391	0.74	13	143	109	0.76
12	26	312	232	0.74	7	84	57	0.68
13	17	221	125	0.57	–	–	–	–
14	1	14	0	0	1	14	0	0
15	1	15	7	0.47	–	–	–	–

is high and probably close to the species-specific maximum. At many sites within the breeding range productivity of reproduction is lower than the in Ladoga area, and only on Vlieland (the Netherlands) and in Prioksko-Terrasny Nature Reserve (central Russia) is reaches 11.0 and 11.2 fledglings per breeding pair (Kluyver 1966, Cramp & Perrins 1993, Glutz von Blotzheim & Bauer 1993, Likhachev 2002).

Few birds return to breed to the natal area in the Ladoga area, so it is difficult to estimate the relative importance of first and second broods in local recruitment. Of the 1511 nestlings ringed in 1979-2003, only six were found breeding in the study area (0.4%). These were nestlings from first and second broods of average size laid in average season (Fig. 4).

3.7. Mortality rates of adults and juveniles

Estimates of adult mortality rate on the basis of ratio of yearlings among breeders are on average 51.6% among males and 75.6% among females. Estimates based on capture-recapture methods are hampered by very low recapture rates. Of 127 males captured at nests in 1979-2003, only 14 (11%) were recaptured in subsequent years, of 132 females 8 (6%) were recaptured. If recapture rate in nest boxes is taken into account, return rate of males is estimated at 13.2%, of females at 7%. Low return rates are also typical for other central Russian sites (Likhachev 1961).

Mortality rate of young birds since fledging until the next breeding season, calculated after Payevsky (1985) for a relatively stable population is 87.3%.

Mortality rate of adults varies among study sites between 40-60%, in males it is usually by 3-8% lower than in females (Payevsky 1985, Cramp & Perrins 1993, Glutz von Blotzheim & Bauer 1993 etc.). In northern populations adult survival rates are rather high, e.g. in the vicinity of Oulu at 65°N 52% of males and 48% of females survive to next breeding (Orell & Ojanen 1979). High estimate of female mortality in our calculations is probably due to a methodological bias. The assumption that all adults replaced by yearlings have died does not account for emigration. Boreal forests far from human settlements are suboptimal or buffer habitats for Great Tits (Klyuver & Tinbergen 1953), mainly because of their low suitability for wintering (Noskov & Smirnov 1981). High proportion of yearling females in such habitats may be due to movement in better habitats later in life. Males are more faithful to their breeding sites, so that most survivors return to the site of their first breeding. It may be hypothesized that females are less site-faithful, so when during second winter their social status improves they try to remain to breed in optimal habitats in the vicinity of human settlements where they spent the winter. Therefore many of them do not return to breed to the forest and are replaced by yearlings. This assumption is indirectly supported by age composition of urban Great Tit populations in north-eastern Europe: in the suburbs of St. Petersburg yearlings comprise ca. 50% of breeders, in Tartu and suburbs of Helsinki 44-45% (Smirnov & Noskov 1975, Järvinen & Pryl 1989, Hõrak & Lebreton 1998).

Overestimated mortality rates of females cause overestimated survival rates of yearlings. In reality, the mortality rate of adult females in the Ladoga area probably does not exceed 55-60%, and the mortality rate during the first year of life is some 89%. Survival rate of juveniles during the first year varies in European Great Tits between 11-31%, usually it is around 15-20% (Kluyver 1951, Bulmer & Perrins 1973, Orell & Ojanen 1979, van Balen et al. 1987 etc.). Mortality rate of juveniles in the Ladoga area is among the highest values reported only from two sites: a dense breeding population on Vlieland in Holland and in Oka Nature Reserve in central Russia (Kluyver 1966, Numerov 1987). This might be due to unstable and severe wintering conditions in the study area and to increased migratory distance.

3.8. Regulation of Great Tit populations in the forests of Ladoga area

As shown in the preceding chapters, in the Ladoga area breeding density shows no great influence on main breeding parameters of Great Tits. In a number of western European populations with high breeding densities, density-dependent regulation mechanisms are more obvious and influence clutch size, frequency of second broods, breeding performance and productivity (Lack 1954, 1966; Kluyver 1951, Perrins 1965, Krebs 1970, Klomp 1980). None of this kind is observed in our study population, apparently because breeding density here does not reach threshold values when the aforementioned mechanisms start to act. Reproduction rate in Great Tits starts to decrease when breeding density exceeds 4 pairs per 10 ha (Klyuver 1951). In our study area, breeding density in optimal habitats remained below 2.5 pairs per 10 ha even in peak years. Great Tits pairs bred at a large distance from each other and often kept only acoustic contacts, and sometimes were ‘not aware’ of the presence of neighbours. In England in a wood near Oxford the mean distance between nests of neighbouring pairs was 40-50 m (Krebs 1971), whereas in the Ladoga area this distance varied between 60 and 2800 m, on average 730 ± 50 m (n = 97). In some years only singular pairs bred in 3-6 km long nest box lines. Even though some Great Tits bred in natural cavities in the vicinity of nest boxes, distance between the nests was large. Under such low breeding densities the population's reproductive strategy was aimed at reproduction at maximum possible rate. The overall breeding productivity was practically unrelated to composition and density of the breeding population and varied mainly due to extrinsic factors that governed breeding performance and frequency of second clutches. An important factor was the weather during winter and early spring which probably acted indirectly through food availability.

Number of breeding pairs and main breeding parameters of the current season were practically unrelated to breeding density in the consequent season (Tab. 11). The main factors governing population dynamics was survival rate during the non-breeding season and immigration rate. Breeding population was annually practically completely replaced by immigrants. Residents and autochthonous birds comprised a fraction of population (< 11%) and had a negligible impact on its dynamics. This is confirmed by formal calculations. Population dynamics of the study population was reasonably well described by the linear regression $y = 0.02 + 0.82 \cdot x_1 + 0.19 \cdot x_2$ ($R^2 = 90.3$), with x_1 for breeding density of immigrants and x_2 for breeding density of residents and autochthonous birds (normalized values used in the equation). ANOVA showed that breeding density of immigrants predicted 88.1% of variance, and the second parameter explained just 2.1%.

Breeding density was also influenced by the weather during the preceding winter: this parameters was marginally significantly related to the mean monthly temperature of December ($r = 0.39$, $p = 0.06$). In our study area Great Tits usually did not overwinter in the woods where nest boxes were set up. However, in 1980-1992, two or three feeding tables were operated in this area in December – March, and some birds remained there in winter. Therefore, the impact of winter temperatures was analysed separately for this period and for 1993-2003, when no feeding tables were set up. In 1980-1992, breeding density was directly related to the mean temperature of December ($r = 0.67$, $p < 0.05$) and probably to the temperature of January ($r = 0.46$, $p = 0.11$). In 1993-2003, the relationships were not significant ($r = 0.15$ и $r = -0.04$, respectively), probably because most birds spend winter elsewhere under different temperature regimes.

Survival rates are known to be influenced not only by weather and feeding conditions, but also by autumn numbers: winter cold spells have a stronger effect on dense populations (Kluyver, 1951). In our study area autumn density (the sum of fledged young and adult breeders) was on average 46.2 $\text{birds} \cdot \text{km}^{-2}$. In the years when autumn density was above this value, weather conditions in autumn and winter had a stronger effect on the future number of breeding pairs. In such seasons, breeding density was directly related to November temperatures ($r = 0.69$, $p < 0.05$), but not to December ($r = 0.35$, n.s.) and January ($r = 0.22$, n.s.) temperatures. In the years with low autumn density, breeding density in the subsequent years was inversely related to November temperatures ($r = -0.5$, $p < 0.05$), and temperatures in December and January had no effect ($r = 0.27$, $r = 0.17$, respectively, n.s.).

Table 11. Correlations between Great Tit breeding density and demographic parameters of the current and previous breeding seasons and weather variables.

Parameter	r	p	n
Breeding density of immigrants	0.94*	< 0.001	25
Breeding density of residents and autochthonous birds	0.73*	< 0.001	25
Proportion of yearlings among breeders	0.15	n.s.	25
Return rate of birds hatches in the previous year	0.19	n.s.	25
Age of nest boxes	-0.25	n.s.	25
Date when the minimum temperature becomes >0°C	0.45*	< 0.05	23
Date of reaching the sum of effective temperatures 50°	-0.42*	< 0.05	23
Mean monthly temperature of January	0.19	n.s.	23
February	-0.10	n.s.	23
March	0.02	n.s.	23
April	0.49*	< 0.05	23
May	0.10	n.s.	23
Previous season:			
breeding density	0.21	n.s.	25
mean size of the first clutch	0.26	n.s.	25
breeding success rate	-0.07	n.s.	25
occurrence of second clutches	0.29	n.s.	20
breeding performance (fledglings per pairs)	0.15	n.s.	25
autumn population density (adults + fledged young · km^{-2})	0.27	n.s.	25
Mean monthly temperature of November (previous year)	0.16	n.s.	24
December (previous year)	0.39	0.06	24

Note. * – Significant values.

Spring weather, primarily mean April temperatures, were directly related to the dynamics of Great Tit numbers (Tab. 11). They could have influenced survival rates during gaining territories and increased social conflicts. It also cannot be ruled out that the weather influenced habitat distribution of birds: cold temperatures in spring could delay leaving winter habitats and stimulate breeding in optimal habitats instead of colonizing the suboptimal ones.

Population dynamics of the Great Tits, along with many other bird species, is influenced by a wide array of factors, both intrinsic, e.g. density-dependent breeding productivity, mortality rates of juveniles and adults, emigration and immigration, and extrinsic, e.g. foraging conditions, weather etc. A complex interaction of these factors can differently influence the numbers of different populations and hamper the creation of a global model (Kluyver 1951, Lack 1954, 1966; Wynne-Edwards 1962, Naumov 1963, Haartman 1971, Payevsky 1985 etc.). The study of a sedentary Great Tit population in southern England in a wood near Oxford showed that the main cause of annual variation of breeding numbers was survival rate of yearlings (Lack 1964, 1966; Perrins 1965). It was practically unrelated to winter weather and showed a clear correlation only to beach mast crops, even though most mortality events occurs during the first months of life before this food became essential. A possible explanation was that good beach mast crops could be related to the crops of other tree species, favourbale weather and high insect abundance. The dynamics of breeding population was to a smaller extent related to adult survival rates, and density-dependent breeding productivity, emigration and immigration had no effect at all. Krebs (1970) confirmed the main results of Lack (1964, 1966) and Perrins (1965) and concluded that winter mortality of yearlings and adults, weakly related to density and territorial structure, was the key factor governing the dynamics of the population under study. Later Klomp (1980), without arguing against this viewpoint, showed that in Marley Wood near Oxford density-dependent breeding productivity played an important role in stabilizing titmice numbers. Lack (1964, 1966) and Perrins (1965) assumed that the impact of weather on dynamics of this population was insignificant and only evident in abnormally cold winters 1946/47 and 1966/67 when snow cover remained for a long time. However when their data were reanalyzed taking into account a number of weather variables, breeding density appeared to be related to winter and early spring air temperatures: mean temperatures of February (Krebs 1970), of the period between late January and mid April, and most strongly of the period 11-30 March (Slagsvold 1975d). In other parts of Britain November temperatures appeared to influence population dynamics of Great Tits (O'Connor 1980). A detailed analysis of longer time series of the Oxford population showed that its dynamics was related to winter and early spring temperatures, to beach mast crops, and to breeding density in the preceding year (Lebreton 1990).

Survival rate during the non-breeding season was a key factor for population dynamics of Great Tits in the Netherlands and Belgium, but here it was more clearly related to breeding density and winter weather. Important factors were breeding productivity, spatial behaviour, emigration and immigration which were related to both breeding density and foraging conditions (Kluyver 1951, 1966; Kluyver & Tinbergen 1953, Klomp 1980, van Balen 1980, van Balen et al. 1987, Dhondt 2001).

In southwestern Finland population dynamics of Great Tits was clearly influenced only by winter weather (Haartman 1971). In more severe conditions of Moscow Region the relationshop between breeding density and weather was less pronounced, because a significant proportion of birds spent their winter outside the breeding area (Likhachev 1961, 2002).

Thus, in different parts of the range different arrays of factors influence population dynamics of Great Tits due to local conditions, so that it is not always possible to identify the key factors. Naumov (1963) warned against attempts to identify such factors as this was too simplistic in his opinion. Composition and dynamics of local breeding populations suggest that boreal forests of the Ladoga area are suboptimal or buffer habitats for the Great Tit. Breeding density here is low and strongly varies between the years. Reproductive strategy of the population is aimed at maximum reproduction rate, limited by the physiological capacity and environmental resources, but the resulting breeding productivity does not influence the future breeding density. Dynamics of numbers is mainly governed by immigrants. The existing data do not make it possible to identify origin of these birds: they may originate from adjacent forest plots or from rather distant areas.

A certain role in determining breeding density is played by the weather, but its action is modified by a number of other factors. Mild November temperatures positively influence future breeding density under high autumn numbers, and negatively influence it when numbers are low. This might be a result of a combined action of the weather and spatial behaviour on survival rates. Warm weather in late autumn stimulates birds to remain in the study area and probably causes their increased mortality during winter. When population density is low, most birds may remain here, and when it is high just a proportion remains due to competition forcing others to emigrate to other habitats where they can find more suitable conditions and survive the winter.

Cold weather in winter, mainly in December, influences breeding density, but its action was also mediated by spatial issues. In years when a proportion of birds remained to spend winter in the breeding area, this relationship was pronounced, and in years when the birds overwintered elsewhere it was not.

In the Ladoga area, like in southern England (Slagsvold 1975d, Lebreton 1990), a great role in the population dynamics of Great Tits was played by April temperatures. They could govern the distribution of birds across optimal and marginal habitats, or their mortality rates during this period.

Our data make it possible to conclude that the dynamics of local population was influenced by different, often interrelated factors. It is difficult to identify the key one(s), which could be immigration rate, survival rate during the non-breeding period, autumn numbers and spatial behaviour.

4. Conclusions

Boreal forests of the Ladoga area are a suboptimal habitat for Great Tits, as shown by their low breeding density (ca. 4 pairs·km^{-2}) and a considerably increased proportion of yearlings in the breeding population. As in other parts of their range, Great Tits prefer mature stands with prevailing or at least a large proportion of deciduous trees. However, pure black alder stands are avoided, probably due to the late vegetation of this tree species. Closed coniferous forests are less attractive, as snow melts later there, causing belated phenological development, also shown by later onset of breeding. Occurrence of second broods is also habitat-related: a higher proportion of birds lay second clutches in the preferred forest types, probably due to habitat-related foraging opportunities.

Onset of egg-laying was related to habitat and air temperatures in April, especially to the date of reaching the cumulative sum of temperatures 50 °C which practically coincides with the determinant date when oocystes start their rapid development in most females (Kluyver 1951). However neither this nor any other analysed temperature variable can be called a threshold one due to their wide annual variation.

Clutch size was not related either to breeding density or to habitat. It decreased linearly with the season, on average by 0.043 eggs per day. Unlike more southern sites, in the Ladoga area yearling females started breeding on average one day earlier and laid slightly more eggs than older birds. This variation was not statistically significant, but resulted in a significant difference in brood size (larger in yearlings). Male age was positively related to the time of breeding but unrelated to clutch size. Lack of significant age-related variation in the time of egg-laying and clutch size in female Great Tits is typical for this region (Haartman 1969, Zimin 1988). The reason must be that at these latitudes unstable environmental conditions play a great role and mask age-related variation in reproduction variables.

In the Ladoga area 47.8% of pairs that successfully raised their first brood, made a second breeding attempt. Occurrence of second broods was not related to breeding density or age of parents. In forests with diverse composition of stands more Great Tits were double-brooded. Winter weather, i.e. mean monthly temperature of February was positively related to the proportion of second broods, probably acting through foraging conditions and winter survival of invertebrate prey. Time lag between the breeding cycles was similar to the values reported from other parts of the range. Mean distance between the nests of the same pair was larger than elsewhere (ca. 230 m), probably due to prey depletion in the breeding territory along the season and lack of competition for territories.

Breeding success rate in the Ladoga area was rather high: 77% of nests survive until fledging, and 67.9% of laid eggs produce fledglings. In spite of considerable annual variation, it was not related to breeding density, habitat, age composition of the population or timing of breeding. The main factor that governed variation in nest survival rate was partial mortality in first and early broods, proportion of lost nests and mean monthly temperature of May. Proportion of nests completely lost varied due to stochastic factors, and partial mortality of nestlings was clearly related to the weather during preceding winter: the sum of mean monthly temperatures of December, January, and February. Winter and spring weather apparently influenced winter survival and summer abundance of the Great Tit's invertebrate prey. The overall breeding productivity varied between the years and was on average 10 fledglings per breeding pair per season. It was governed by breeding performance and occurrence of second broods and to a smaller extent by winter and spring weather.

Rough estimates of annual mortality rates suggest the values of 52% in adult males, 50-60% in adult females and ca. 89% during the first year of life.

Low breeding density of Great Tits in the Ladoga area prevented the action of density-dependent regulation mechanisms. Therefore, the population's reproductive strategy is aimed at reaching the maximum physiologically possible reproduction rate, limited only by the available resources.

Local population dynamics was practically unrelated to breeding productivity during the preceding season. It was mainly governed by immigration rate, immigrants making up 89% of breeders, and by survival rate during the non-breeding period. Weather conditions during the critical periods of the annual cycle, i.e. during autumn and spring re-distribution across the area and during winter, also played a certain role in determining population dynamics. The effect of the weather was modified by population density and spatial behaviour of the birds.

Acknowledgements

During the whole of my work I always enjoyed support and assistance of my colleagues V.B. Zimin, N.V. Lapshin, and T.Yu. Khokhlova. At the final stages, the study was partly supported by Netherlands' Organisation for Scientific Research.

References

Agroclimatic Directory for Karelian ASSR. 1959. Gidrometeoizdat, Leningrad (in Russian).

Alisov, B.P., Berlin, I.A. & Mikhel, V.M. 1954. A course of climatology. Part 3. Climates of the world. Gidrometeoizdat, Leningrad (in Russian).

Artemyev, A.V. 1993. Breeding biology of the Great Tit *Parus major* on southeast coast of Lake Ladoga. Russ. J. Ornithol. 2: 201-207 (in Russian with English summary).

van Balen, J.H. 1973. A comparative study of the breeding ecology of the Great Tit (*Parus major*) in different habitats. Ardea 61: 1-93.

van Balen, J.H., van Noordwijk, A.J. & Visser, M.E. 1987. Lifetime reproductive success and recruitment in two Great Tit populations. Ardea 75: 1-11.

Beldal, E.J., Barba, E., Gil-Delgado, J.A., Iglesias, D.J., Lorez, G.M. & Monros, J.S. 1998. Laying date and clutch size of Great Tit (*Parus major*) in the Mediterranean region: a comparison of four habitat types. J. Ornithol. 139: 269-276.

Bianchi, V.V. & Shutova, E.V. 1978. To ecology of the Great Tit in Murmansk Region. Bull. Moscow Soc. Natur. Biology series 83 (2): 63-70 (in Russian).

Blagosklonov, K.N. 1991. Breeding and attracting of birds to orchards and parks. Moscow Univ. Press, Moscow (in Russian).

Blondel, J., Clamens, A., Cramm, P., Gaubert, H. & Isenmann, P. 1987. Population studies on tits in the Mediterranean region. Ardea 75: 21-34.

Both, C., Artemyev, A.V., Blaauw, B., Cowie, R.J., Dekhuijzen, A.J., Eeva, T., Enemar, A., Gustaffson, L., Ivankina, E.V., Järvinen, A., Metcalfe, N.B., Nyholm, N.E.I., Potti, J., Ravussin, P.-A., Sanz, J.J., Silverin, B., Slater, F.M., Sokolov, L.V., Török, J., Winkel, W., Wright, J., Zang, H. & Visser, M.E. 2004. Large-scale geographical variation confirms that climate change causes birds to lay earlier. Proc. R. Soc. Lond. B 271: 1657-1662.

Bulmer, M.G. & Perrins, C.M. 1973. Mortality in the Great Tit *Parus major*. Ibis 115: 277-281.

Cichon, M. & Linden, M. 1995. The timing of breeding and offspring size in Great Tits *Parus major*. Ibis 137: 364-370.

Cramp, S. & Perrins, C.M., 1993. Flycatchers to Shrikes. The Birds of the Western Palearctic. Vol. VII. Oxford University press. 577 p.

Crick, H.Q.P., Dudley, C., Glue, D.E. & Thomson, D.L. 1997. UK birds are laying eggs earlier. Nature 388: 526.

Dawson, A., King, V.M., Bentley, G.E. & Ball, G. 2001. Photoperiodic Control of Seasonality in Birds. J. Biol. Rhythms 16: 365-380.

Dekhuijzen, H.M. & Schuijl, G.P.J. 1996. Changes in breeding success of Great Tit *Parus major* and Pied Flycatcher *Ficedula hypoleuca* on the Veluwe and the Gooi, 1973-92. Limosa 69: 165-174.

Dementiev, G.P. 1940. Birds. Handbook of Zoology. Vol. VI. Publ. Academy of Sciences of USSR, Moscow – Leningrad (in Russian).

Dobrynina, I.N. 1991. Preliminary results of ringing of Great Tits (*Parus major*) in the north-western USSR. In: Bird ringing and marking results 1985. Nauka Press, Moscow: 68-75 (in Russian).

Dhondt, A.A. 2001. Trade-offs between reproduction and survival in tits. Ardea 89: 155-166.

Dhondt, A.A., Kast, T.L. & Allen, P.E. 2002. Geographical differences in seasonal clutch size variation in multi-brooded bird species. Ibis 144: 646-651.

Glutz von Blotzheim, U.N. & Bauer, K.M. 1993. Muscicapidae – Paridae. Handbuch der Vögel Mitteleuropas. Bd.13. Teil 1. Wiesbaden, Aula-Verlag.

Godfray, H.C.J., Partridge, L. & Harvey, E.H. 1991. Clutch size. Annual Rev. Ecology Syst. 22: 409-429.

Gwinner, E. 1996. Circannual clocks in avian reproduction and migration. Ibis 138: 47-63.

von Haartman, L. 1969. The Nesting Habits of Finnish birds. 1. Passeriformes. Commentationes Biologicae Soc. Sci. Fenn. 32: 1-187.

von Haartman, L. 1971. Population dynamics. In: Farner, D.S. & King, J.R. (eds.). Avian biology. Vol. 1. Academic Press, London: 391-459.

von Haartman, L. 1990. Breeding time of the Pied Flycatcher *Ficedula hypoleuca*. Population biology in passerine birds. NATO ASI Series. G 21. Springer, Berlin: 1-16.

Hõrak, P. & Lebreton, J.-D. 1998. Survival of adult Great Tits in relation to sex and habitat: a comparison of urban and rural populations. Ibis 140: 205-209.

Ivanter, E.V. & Korosov, A.V. 2003. An Introduction to Quantitative Biology. Petrozavodsk State Univ. Press, Petrozavodsk (in Russian).

Järvinen, A. & Pryl, M. 1989. Egg dimensions of the Great Tit *Parus major* in southern Finland. Ornis Fennica 66: 69-74.

Jezerskas, L.I. 1961. On biology of hole-nesting birds of tits (Paridae) and flycatchers (Muscicapidae) families in Lithuanian SSR. In: Spuris, Z.D. (ed.) Ecology and migration of birds in the Baltic (Proc. 4th Baltic Orn. Conf.). Publishing House of Latvian Academy of Sciences, Riga: 115-122 (in Russian).

Johansson, H. 1974. Kullstorlek och häckningsframgång hos vissa holkhäckande smafåglar i centrala Sverige 1972-1974 (1952-1963). Fauna och flora 69: 212-218.

Klomp, H. 1980. Fluctuations and stability in Great Tit populations. Ardea 68: 205-224.

Kluyver, H.N. 1951. The population ecology of the Great Tit *Parus m. major* L. Ardea 39: 1-135.

Kluyver, H.N. 1966. Regulation of a bird population. Ostrich. Suppl. 6: 389-396.

Kluyver, H.N. & Tinbergen L. 1953. Territory and the regulation of density in titmice. Arch Neerl. Zool. 10: 265-289.

Krebs, J.R. 1970. Regulation of numbers in the Great Tit (Aves: Passeriformes). J. Zoology (London) 162: 317-333.

Krebs, J.R. 1971. Territory and breeding density in the Great Tit *Parus major*. Ecology 52: 2-22.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.

Lack, D. 1964. A long-term study of the great tits (*Parus major*). J. Anim. Ecol. 50: 375-386.

Lack, D. 1966. Population studies of birds. Clarendon Press, Oxford.

Lakin, G.F. 1973. Biometrics. Vysshaya Shkola, Moscow.

Leberton, J.-D. 1990. Modelling density dependence, environmental variability, and demographic stochasticity from population counts: an example using Wytham Wood Great Tits. In: Population biology of passerine birds. NATO ASI Series. G 21. Springer, Berlin: 89-102.

Likhachev, G.N. 1954. On the relationships between the Great Tit and Pied Flycatcher when occupying nest boxes. In: Attraction and Acclimatization of Useful Insectivorous Birds to Forest Plantations in the Steppe and Forest Steppe. Selkhozgiz, Moscow (in Russian).

Likhachev, G.N. 1961. Materials on biology of birds breeding in next boxes. Proc. Prioksko-Terrrasny Nature Reserve 4: 82-146 (in Russian).

Likhachev, G.N. 2002. Breeding and numbers of Great Tits (*Parus major*) in southern Moscow Region. Siberian Ecol. Journal 6: 757-773 (in Russian).

Malchevsky, A.S. & Pukinsky, Yu.B. 1983. The Birds of Leningrad Region and Adjacent Areas. Vol. 2. Passerines. Leningrad Univ. Press, Leningrad (in Russian).

McCleery, R.H. & Clobert, J. 1990. Differences in recruitment of young by immigrant and resident Great Tits in Wytham Wood. In: Population biology of passerine birds. NATO ASI Series. G 21. Springer, Berlin: 423-439.

McCleery, R.H. & Perrins, C.M. 1998. Temperature and egg-laying trends. Nature 391: 30-31.

Meijer, T., Nienaber, U., Lancer, U. & Trillmich, F. 1999. Temperature and timing of egg-laying of european starlings. Condor 101: 124-132.

Minin, A.A. 1992. Spatiotemporal variation of dates of some phenological events in birds in the Russian plain. Bull. Moscow Soc. Natur. Dept. Biology 97 (5): 28-34 (in Russian).

Nager, R. 1990. On the effects of small scale variation in temperature and food availability on laying date and egg size in Great Tits (*Parus major*). In: Population biology of passerine birds. NATO ASI Series. G 21. Springer, Berlin: 187-197.

Nager, R.G. & van Noordwijk, A.J. 1995. Proximate and ultimate aspects of phenotypic plasticity in timing of great tit breeding in a heterogeneous environment. Am. Nat. 146: 454-474.

Naumov, N.P. 1963. Animal Ecology. Vysshaya Shkola, Moscow (in Russian).

Naumov, N.P. & Nikolsky, G.V. 1962. On some general patterns in animal population dynamics. Zool. zhurn. 41: 1132-1141 (in Russian).

Nazarova, L.E. & Filatov, N.N. 2004. Climate variation on the basis of meteorological observations. In: Climate of Karelia: fluctuations and impact on water objects and basins. Publ. Karelian Research Centre of RAS, Petrozavodsk: 12-34 (in Russian).

Noskov, G.A. & Rezvyi, S.P. (eds.). 1995. Atlas of bird migration according to ringing and recovery data for Leningrad region. Proc. St. Petersburg Soc. Natur. 85. St.Petersburg: 1-232.

Noskov, G.A. & Smirnov, O.P. 1981. Territorial behaviour and migration of the Great Tit (*Parus m. major* L.). Proc. Biol. Res. Inst. of Leningrad State University 32: 100-130 (in Russian).

Numerov, A.D. 1987. Population ecology of the Great Tit in Oka nature reserve. Ornithologia (Moscow) 22: 3-21 (in Russian).

O'Connor, R.J. 1980. Pattern and process in Great Tit (*Parus major*) populations in Britain. Ardea 68: 165-183.

Orell, M. & Ojanen, M. 1979. Mortality rates of the Great Tit, *Parus major*, in a northern population. Ardea 67: 130-133.

Orell, M. & Ojanen, M. 1983a. Effect of habitat, date of laying and density on clutch size of the Great Tit *Parus major* in northern Finland. Holarctic Ecol. 6: 413-423.

Orell, M. & Ojanen, M. 1983b. Breeding success and population dynamics in a northern great tit *Parus major* population. Ann. Zool. Fennici 20: 77-98.

Payevsky, V.A. 1985. Demography of Birds. Nauka Press, Leningrad (in Russian).

Perrins, C.M. 1965. Population fluctuations and clutch-size in the Great Tit, *Parus major* L. J. Anim. Ecol. 34: 601-647.

Perrins, C.M. 1996. Eggs, egg formation and the timing of breeding. Ibis 138: 2-15.

Perrins, C.M. & McCleery, R.H. 1985. The effect of age and pair bond on the breeding success of Great Tit *Parus major*. Ibis 127: 306-315.

Perrins, C.M. & Moss, D. 1975. Reproductive rates in the Great Tit. J. Anim. Ecol. 44: 695-706.

Pettifor, R.A., Perrins, C.M. & McCleery, R.H. 1988. Individual optimization of clutch size in Great Tits. Nature 336: 160-162.

Pianka, E. R. 1978. Evolutionary Ecology. Second Edition. Harper and Row, New York.

Romanov, A.A. 1961. On climate of Karelia. State Publishers of Karelian ASSR, Petrozavodsk (in Russian).

Sanz, J.J. 1998. Effects of geographic location and habitat on breeding parameters of Great Tits. Auk 115: 1034-1051.

Schulz, G.E. 1981. General Phenology. Nauka Press, Leningrad (in Russian).

Shcherbakov, I.D. 1956. Requirements of Pied Flycatchers and Great Tits concerning breeding habitat and nest box. In: Ways and methods of using the birds against insect pests. Moscow: 81-93 (in Russian).

Semenov-Tien-Shansky, O.I. & Gilyazov, A.S. 1991. The Birds of Lapland. Nauka Press, Moscow (in Russian).

Silverin, B. 1995. Reproductive Adaptations to Breeding in the North. Amer. Zoologist. 35: 191-202.

Slagsvold, T. 1975a. Breeding time of birds in relation to latitude. Norw. J. Zool. 23: 213-218.

Slagsvold, T. 1975b. Hypotheses on breeding time and clutch-size in birds. Norw. J. Zool. 23: 219-222.

Slagsvold, T. 1975c. Competition between the Great Tit *Parus major* and the Pied Flycatcher *Ficedula hypoleuca* in the breeding season. Ornis Scand. 6: 179-190.

Slagsvold, T. 1975d. Critical period for regulation of Great Tit (*Parus major* L.) and Blue Tit (*Parus caeruleus* L.) populations. Norw. J. Zool. 23: 67-88.

Slagsvold, T. 1976. Annual and geographical variation in the time of breeding in the Great Tit *Parus major* and the Pied Flycatcher *Ficedula hypoleuca* in relation to environmental phenology and spring temperature. Ornis Scand. 7: 127-145.

Smirnov, O.P. & Noskov, G.A. 1975. Structure of Great Tit population in Leningrad Region. Ekologiya 6: 79-83 (in Russian).

Smirnov, O.P. & Tyurin, V.M. 1981. To breeding biology of the Great Tit in Leningrad Region. Ornithologia (Moscow) 16: 185-188 (in Russian).

Smith, H.G., Källander, H. & Nilsson, J-A. 1987. Effects of experimentally altered brood size on frequency and timing of second clutches in the Great Tit. Auk 104: 700-706.

Svensson, L. 1975. Identification Guide to European Passerines. Naturhist. Riksmuseet, Stockholm.

Tinbergen, J.M. 1987. Costs of reproduction in the Great Tit: intraseasonal costs associated with brood size. Ardea 75: 111-122.

Veistola, S., Lehikoinen, E. & Iso-Iivari, L. 1995. Breeding biology of the Great Tit *Parus major* in a marginal population in northernmost Finland. Ardea 83: 419-420.

Viktorov G.A. 1967. Problems of insect dynamics of numbers: the Sunn Pest case. Nauka Press, Moscow (in Russian).

Vinogradova, N.V., Dolnik, V.R., Yefremov, V.D. & Payevsky, V.A. 1976. Identification of Sex and Age in Passerine Birds of the USSR. Nauka Press, Moscow (in Russian).

Visser, M.E., Adriaensen, F., van Balen, J.H., Blondel, J., Dhondt, A.A., van Dongen, S., du Feu, C., Ivankina, E.V., Kerimov, A.B., de Laet, J., Matthysen, E., McCleery, R., Orell, M. & Thomson, D.L. 2003. Variable responses to large-climate change in European *Parus* populations. Proc. Royal Soc. Lond. B 270: 367-372.

Volkov, A.D., Gromtsev, A.N., Erukov, G.V., Karavaev, V.N., Kolomytsev, V.A., Kurhinen, Y.P., Lak, G.Z., Pyzhin, A.F., Sazonov, S.V. & Shelekhov, A.M. 1995. Ecosystems of western middle taiga (structure and dynamics). Karelia Press, Petrozavodsk (in Russian).

Vorontsov, A.I. 1975. Forest entomology. Vysshaya Shkola, Moscow (in Russian).

Winkel, W. & Hudde, H. 1997. Long-term trends in reproductive traits of tits (*Parus major, P. caeruleus*) and Pied Flycatcher (*Ficedula hypoleuca*). J. Avian Biol. 28: 187-190.

Wynne-Edwards, V.C. 1962. Animal Dispersion in Relation to Social Behaviour. Edinburgh, London.

Yaremchenko, O.A. & Bolotnikov, A.M. 1988. Breeding biology of the Great Tit. Ornithologia (Moscow) 23: 81-93 (in Russian).

Zimin, V.B. 1978. Materials on breeding of the Great Tit (*Parus major* L.) in Karelia. In: Ivanter E.V. (ed.) Fauna and Ecology of Birds and Mammals in the Taiga Zone of Northwest USSR. Publ. Karelian Branch of Soviet Acad. Sci., Petrozavodsk: 17-31 (in Russian).

Zimin, V.B. 1988. Ecology of Passerine Birds of Northwest USSR. Nauka Press, Leningrad (in Russian).

Zimin, V.B., Sazonov, S.V., Lapshin, N.V., Hokhlova, T.Y., Artemyev, A.V., Annenkov, V.G. and Yakovleva, M.V. 1993. Bird fauna of Karelia. Publ. Karelian Research Centre, Petrozavodsk (in Russian).