Ornis Fennica 78:49–60. 2001

Breeding of the Great Tit and Blue Tit in urban and rural habitats in southern Finland

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Received 28 September 2000, accepted 19 February 2001

Studies at various localities in Europe have shown that nest-box populations of tits in urban habitats produce fewer eggs and fledglings than do birds in rural habitats. The results of the present 7-year study on dense urban and moderately dense rural tit populations also show that the average clutch size was significantly lower in the urban than in the rural populations. The difference was 17% in the Great Tit *Parus major* and 10% in the Blue Tit *P. caeruleus*. The fledgling production of tits calculated per egg laid, per breeding attempt, or per successful nesting was lower in the urban populations than in the rural ones. However, the opposite was true when the young production per habitat area was considered. During the breeding season, the absolute amount of insect food in the environment did not seem to differ considerably between the urban and rural habitats, suggesting that food supply as such did not limit the young production of breeding pairs. The variation in the density and clutch size of tits was also largely determined by other factors than the absolute amount of food. Densities of tits were determined by the environmental conditions in the winter before the breeding season. In the Great Tit, habitat (the degree of urbanisation), population density, and the weather conditions in spring (March and April) affected the clutch size significantly, while fledgling production was affected by late spring weather and Blue Tit density. In the Blue Tit, habitat was the only factor studied having a significant effect on the clutch size. The clutch size, in turn, as well as the weather conditions in May, significantly affected fledgling production. The poor quality of food before the breeding season in urban habitats may be partly responsible for the small clutch size of tits, while the low quantitative share of food due to high densities may be primarily responsible for the low egg and fledgling production of breeding pairs.

1. Introduction

Great Tits (*Parus major*) and Blue Tits (*P. caeruleus*) are common breeders in mixed and deciduous forests in southern Finland (von Haartman et al. 1963–72, Väisänen et al. 1998). The densities of Great Tits are, in general, about double to fourfold compared to those of the smaller Blue Tit (Solonen 1996). In natural and semi-natural forests that mainly offer only old holes of primary hole-nesters (woodpeckers, some other species of tits) for breeding, the general densities of

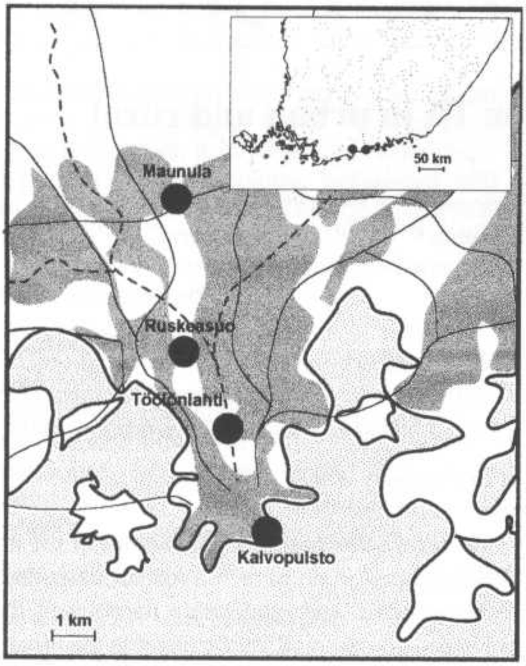

Fig. 1. The location of the urban (eastern) and rural (western) study areas on the southern coast of Finland, and the urban study areas in Helsinki. The coastal line (heavy line), main roads (thin line), and railroads (dashed line) are shown. The shading indicates the most densely built-up areas.

Great Tits and Blue Tits are about 20 and 5 pairs/km^2, respectively. However, in rich deciduous forests and in areas where nesting opportunities have been improved by providing plenty of nest-boxes, the respective densities may reach 80 and 30 pairs/km^2, or even more (Lehikoinen 1983, Solonen 1986, Koskimies 1989). In urban habitats, densities of up to 50 and 14 pairs/km^2 have been recorded in the Great Tit and Blue Tit, respectively (Suhonen & Jokimäki 1988, Väisänen et al. 1998). Numbers of both species have considerably increased during recent decades, largely due to winter feeding at bird tables (Hildén 1990, Väisänen & Solonen 1997, Väisänen et al. 1998).

Great and Blue Tits seem to move into urban areas in winter, probably largely due to improved feeding conditions provided by man, and many of them settle there to breed (van Balen 1980, Lehikoinen 1986, Orell 1989, Hõrak 1993). The density of urban populations may thus grow very much if there is an excess of nest-boxes at their disposal. Studies in various localities in Europe have shown that nest-box populations of tits in urban habitats produce fewer eggs and fledglings than do birds in rural habitats (Perrins 1965, Berressem et al. 1983, Cowie & Hinsley 1987, Hildén & Solonen 1990, Hõrak 1993). However, in spite of small clutch sizes, the fledging success in urban areas has proved still lower than in rural habitats (Hõrak 1993).

If available nest-sites do not limit the population size, density and breeding success are largely determined by food-related factors, including competition and predation (Perrins 1979, Newton 1980, 1998). Breeding success is primarily determined by the food supply, but predation (e.g., Solonen 1979, Jokimäki & Huhta 2000) and weather conditions (e.g., Hildén et al. 1982) may also have considerable direct effects. The local food supply in turn is determined by relatively predictable local habitat factors and annually variable weather factors. The food supply may also affect breeding success indirectly through density-dependent factors (competition, predation).

The high density of many urban tit populations may be a detrimental factor affecting breeding success. In dense populations, the possibility of intra- and inter-specific competition for food increases (Dhondt & Eyckerman 1980, Minot 1981, Minot & Perrins 1986). From an energetics point of view, urban habitats can be expected to offer worse breeding conditions, but better areas for wintering than do rural habitats (see Hõrak 1993).

In this paper, I present results of a seven-year study on the breeding of urban and rural populations of Great Tits and Blue Tits near the southern coast of Finland. To track variations in density, the populations were provided with a superabundance of nest-boxes. Differences in the density, clutch size, and breeding success of each species within the urban habitats, and between the urban and rural populations, are analysed. As pointed out above, from the point of view of breeding tits, urban and rural habitats may differ in many respects other than the direct effects of human activities. Such factors examined in this study include wintering conditions, the density of tits, local food supply, and predation. The main hypotheses were formulated as follows:

1. In areas saturated with nest-boxes, urban tit populations may grow denser than rural ones due to better wintering conditions, as suggested by minor effects of winter temperatures.
2. Urban tits produce fewer eggs and fledglings per pair than do birds in less urban habitats, suggesting that breeding conditions as a whole become worse with an increasing degree of urbanisation of the environment.
3. If the population size is not limited by the availability of nest-sites, breeding success may be affected not only by habitat, weather and predation, but also by competition for food, suggested by negative relationships between breeding success and the population densities.

2. Material and methods

2.1. Study areas and design

The urban and rural study areas were situated near the southern coast of Finland (60°N, 24–25°E), about 20–25 km apart (Fig. 1). In 1987–1988, four nest-box areas were established in urban environments in Helsinki. An old nest-box area in continuous rural habitat in the municipality of Kirkkonummi, established already in 1965 (Hildén, O. 1977, 1978), served as a reference. The density of nest-boxes was set to a level high enough to reveal the local population fluctuations. The urban study areas were situated along a 7.7 km line — an isolated park on the coast and three other areas located along a green belt running through the city of Helsinki northwards (Fig. 1). The outermost urban study area was about 5 km from the nearest rural environments.

Two of the urban study areas (Kaivopuisto, Töölönlahti) were in old managed parks with planted deciduous trees, and closely surrounded by densely built-up areas and intense traffic ('City Centre'; virtually no habitat outside parks). The other two areas (Ruskeasuo, Maunula) were within a fairly large, less managed urban park-forest dominated by natural deciduous and coniferous trees, especially spruce. The surrounding moderately densely populated urban settlement and roadways were situated further away than was the case with the parks of the city area.

In early spring 1987, 275 nest-boxes were placed in the three urban inland study areas, and in 1988, 55 additional boxes were placed in the coastal park (Table 1). To ensure breeding facilities for both species studied, two kinds of nest-boxes were used. In the urban parks, 75% of the boxes had an entrance hole diameter of 32 mm, while in the rest it was 28 mm. In the rural habitats, the respective percentages were 80% and 20%. The larger entrance hole was suitable for the Great Tit, while the smaller Blue Tit could avail of both kinds of boxes.

The nest-boxes were of a standard type and were erected in a standard manner (though with varying orientation) at a height of about 3–4 m above ground and an average distance of 50 m apart (and 25 m from the border of the study area).

Table 1. The study sites in the urban parks of Helsinki and in a rural area of Kirkkonummi: the area (km²) covered by nest-boxes, the distance (km) from the sea coast, and the numbers of nest-boxes inspected in each year.

			Numbers of nest-boxes in each year						
Study site	Km²	Km	1987	1988	1989	1990	1991	1992	1993
Urban parks									
Kaivopuisto	0.14	0.1	–	55	51	51	48	51	46
Töölönlahti	0.30	2.6	135	133	98	109	36	90	75
Ruskeasuo	0.16	5.3	70	70	70	70	70	70	68
Maunula	0.15	7.7	70	68	69	70	68	68	68
Urban, total	0.75		275	326	288	300	222	279	257
Rural area	2.5		260	260	261	250	250	250	250

In the rural reference area, the nest-boxes were located about 100 m from each other. The higher density of nest-boxes in the urban than in the rural areas was due to the expectation of a similar difference in the densities of tits between the habitats. This was suggested by some earlier studies in which the high densities of nest-boxes even in the most productive rural and suburban habitats did not increase the tit populations to levels as high as in urban areas (Solonen 1986, 1991, 1992, Hildén, M. 1988). In relation to the potential densities of tits, all the study areas can therefore be regarded as having been saturated with nest-boxes.

There were only a few suitable nest-sites other than nest-boxes available for tits in the study areas. The tits seemed to use mainly the nest-boxes, but each year a considerable proportion of the boxes were also left unoccupied. Thus, the densities of tits were calculated on the basis of occupied nest-boxes. In any case, the differences, if they existed, were insignificant and concerned mainly the rural study area where the holes of woodpeckers might have attracted some pairs to places where they could breed undetected.

The number of nest-boxes remained relatively stable throughout the seven-year study period of 1987–1993 (Table 1). This was due to the attempts made to compensate for nest-box losses, but there was still some decline in nest-box numbers in some areas. In some years, a small fraction of the boxes were also left uninspected. Because of various differences in the study design between the urban and rural areas, the present study should be considered as a simple comparison between habitats rather than as a strictly designed experiment.

2.2. Breeding success and food availability

Each year, the fieldwork included the inspecting of nest-boxes to find out the number of boxes occupied by each species, the onset of laying, clutch size, hatching success, and the number of young fledged. Fledging success was ascertained by ringing the nestlings and searching the nests after the breeding season for possible dead nestlings and signs of failure of total broods. By the last visit, old nests were also removed to keep the parasite load of the nest-boxes at a minimum. In the present study, only the first clutches laid before the end of May were considered.

For studying local variation in the relative availability of food, each study area was examined using plastic funnels (diameter 440 mm) by sampling pellets of moth caterpillars falling from trees (Gibb 1950, van Balen 1973, Eeva et al. 1997). Due to limited resources, however, this was done only in 1992. In total, 50 funnels were fastened to trunks of various tree species approximately in the proportion to their frequency in each study area. The sampling was done during six consecutive periods of about a week, covering the nesting season of the tits. Between 38 and 46 samples per period were suitable for analysis. For the whole study period, the young production of tits per habitat area was used as an indirect measure of the general availability of food. This was based on the assumption that, in the present case, predation and/or other factors should have a relatively minor effect on the young production.

2.3. Statistical procedures

General statistical procedures followed the standard methods (Sokal & Rohlf 1981, Fowler & Cohen 1986). P-values higher than 0.05 were considered non-significant. In cases of skewed distributions, non-parametric methods or log- or arcsin-transformed data were used. Before the tests for differences between means, the similarity between two variances was checked with an F-test. For comparing the means of large samples, a z-test (Fowler & Cohen 1986) was used. Repeated measures analyses of variance (Glantz 1997) and forward stepwise multiple regression analyses were performed by SigmaStat statistical software (P-to-enter 0.054, P-to-remove 0.057). Variables studied in the analyses that might affect the breeding of the Great Tit and Blue Tit can be characterised as follows:

The monthly mean temperatures in Helsinki, Kaisaniemi (in the immediate vicinity of the study area of Töölönlahti) (data from the Finnish Meteorological Institute 1987–1993) in January–March, March–May, and May–June were related to density, clutch size, and fledgling production, respectively.

Habitats (or localities) were characterised by a decreasing marine effect (the increasing distance from the sea coast; Table 1), that, to some extent, corresponded to the decreasing degree of urbanisation (intensity of built-up areas and traffic) in the immediate vicinity of the study areas (Fig. 1). In 1992, habitats were also characterised by the local food supply, based on moth caterpillar pellet samples.

It is supposed that the competition for food increases with increasing population densities, as the number of potential interactions between pairs or individuals per area increases. The amount of food available per pair diminishes due to the decreasing territory size. Accordingly, densities of tits were considered as rough indicators of potential competition.

The effects of starvation were measured by the percentage of total broods lost to starvation. The suggested starvation of nestlings was based on a visual inspection of dead nestlings. It was also suggested by the lower mean weight of urban nestlings (Hildén & Solonen 1990).

The strength of local predation was measured as the percentage of nests of both species lost to predation. Predation was indicated indirectly by lost eggs and nestlings, destroyed nests, and some characteristic signs of predators (such as those of the Great Spotted Woodpecker *Dendrocopos major*).

3. Results

3.1. Population density

Tits rapidly occupied the urban nest-box areas established, and after the first or second year their numbers remained relatively stable (Table 2). The development of the rural Great Tit population was largely similar to the urban ones (significantly so with Ruskeasuo, $r_s = 0.79$, $P < 0.05$, $n = 7$, and Kaivopuisto, $r_s = 1.00$, $P < 0.05$, $n = 6$). The urban Blue Tits first increased, but numbers levelled off already in the third year, while the rural Blue Tits showed a consistent increasing trend ($r_s = 1.00$, $P < 0.01$, $n = 7$). There was a significant positive correlation ($r = 0.65$, $P < 0.001$, $df = 31$) between the annual local densities of the two species.

On average, 60% of the urban and 40% of the rural nest-boxes were occupied by Great and Blue Tits (cf. Tables 1 and 2). As expected, there was no correlation between the density of nest-boxes and the total combined density of tits (urban data; $r = 0.36$, $P > 0.05$, $df = 24$). Urban Blue Tit and Great Tit average densities were respectively threefold and sevenfold that of the rural ones (Table 2). Within the urban study areas, the average density of Great Tits increased with decreasing

Table 2. Population developments in urban (Helsinki) and rural (Kirkkonummi) Great Tits *Parus major* and Blue Tits *P. caeruleus* studied in 1987–1993 (number of pairs), and their average densities (pairs/km^2 ± SD). Incomplete pair numbers (in parentheses) were not included. Populations were arranged on the basis of a decreasing degree of urbanisation.

Populations	1987	1988	1989	1990	1991	1992	1993	Pairs/km^2
Parus major								
Urban sites								
Kaivopuisto	–	12	21	17	13	16	18	116 ± 24
Töölönlahti	22	46	55	56	(17)	34	34	137 ± 45
Ruskeasuo	14	28	33	36	33	30	37	188 ± 49
Maunula	18	27	31	37	40	41	38	221 ± 56
Urban, total	(54)	113	140	146	(103)	121	127	173 ± 18
Rural	36	48	64	61	56	60	63	25 ± 5
Parus caeruleus								
Urban sites								
Kaivopuisto	–	4	11	12	8	6	10	61 ± 22
Töölönlahti	5	13	18	10	(–)	12	14	40 ± 15
Ruskeasuo	2	5	9	9	10	12	9	50 ± 21
Maunula	2	6	8	10	7	7	8	46 ± 17
Urban, total	(9)	28	46	41	(25)	37	41	52 ± 9
Rural	12	32	37	43	47	49	55	16 ± 6

urbanisation (corresponding the increasing distance from the sea coast) from 116 to 221 pairs/km², while for Blue Tits there was no such trend. The Great Tit densities of the more urban areas (Kaivopuisto, Töölönlahti) were significantly lower than those of the less urban ones (Ruskeasuo, Maunula) (one way repeated measures analysis of variance, $F_{3,16} = 15.2$, $P < 0.001$; Tukey test, $P < 0.05$). The highest local densities recorded in each species were 273 pairs/km² for Great Tits (Maunula in 1992) and 86 pairs/km² for Blue Tits (Kaivopuisto in 1990).

There were significant positive relationships between temperatures in late winter (February,

Table 3. Relationships (r_s) between the mean temperatures (°C) of the winter months (January–March; source: Finnish Meteorological Institute) and the densities of urban and rural tit populations in the following breeding season in 1987–1993. The significance of the relationships is indicated as follows: * = P < 0.05, ** = P < 0.01.

Locality	Species	January	February	March	n
Kaivopuisto	*P. major*	0.55	0.66	0.66	6
	P. caeruleus	–0.09	0.71	0.71	6
Töölönlahti	*P. major*	0.24	0.81	0.75	6
	P. caeruleus	0.90 *	0.26	0.49	6
Ruskeasuo	*P. major*	0.33	0.58	0.52	7
	P. caeruleus	0.43	0.37	0.59	7
Maunula	*P. major*	0.36	0.29	0.43	7
	P. caeruleus	0.35	0.85 **	0.78 *	7
Urban, total	*P. major*	0.09	0.61	0.75 *	7
	P. caeruleus	0.51	0.79 *	0.86 **	7
Rural	*P. major*	0.51	0.79 *	0.86 **	7
	P. caeruleus	0.45	0.32	0.32	7

Table 4. Clutch sizes of the Great Tit and Blue Tit in urban parks of Helsinki and in rural habitats of Kirkkonummi in 1987–1993. Populations were arranged on the basis of a decreasing degree of urbanisation.

Population	Clutch size			
	Mean	± SD	Range	n
Parus major				
Urban sites				
Kaivopuisto	7.84	1.53	4–11	51
Töölönlahti	7.72	1.34	4–11	124
Ruskeasuo	8.01	1.47	4–11	135
Maunula	8.12	1.39	4–12	144
Urban, total	7.94	1.42	4–12	454
Rural	9.60	1.31	6–13	342
Parus caeruleus				
Urban sites				
Kaivopuisto	10.07	1.47	6–12	46
Töölönlahti	10.18	1.63	6–15	61
Ruskeasuo	10.16	1.38	5–13	51
Maunula	10.43	1.36	6–14	46
Urban, total	10.21	1.47	5–15	204
Rural	11.32	1.46	7–16	248

Table 5. Brood sizes (fledgling production per breeding attempt) in the Great Tit and Blue Tit in urban parks of Helsinki and in rural habitats of Kirkkonummi in 1987–1993. Suc. = the number of successful nestings (at least one young fledged).

Population	Brood size				
	Mean	± SD	Range	n	Suc.
Parus major					
Urban sites					
Kaivopuisto	3.63	2.75	0–9	70	54
Töölönlahti	3.92	2.62	0–9	210	163
Ruskeasuo	3.47	2.60	0–8	186	139
Maunula	4.52	2.74	0–10	210	171
Urban, total	3.95	2.69	0–10	676	527
Rural	5.03	3.78	0–12	240	175
Parus caeruleus					
Urban sites					
Kaivopuisto	5.11	3.68	0–12	46	34
Töölönlahti	4.89	3.61	0–12	61	46
Ruskeasuo	4.89	3.69	0–11	46	33
Maunula	6.25	4.12	0–13	40	30
Urban, total	5.22	3.77	0–13	193	143
Rural	6.47	4.66	0–13	158	114

March) and the density in the total sample of urban tits of both species, though in the four subpopulations the relationships largely disappeared (Table 3). There were, however, no significant relationships when the first year of study (when the winter was exceptionally cold) was excluded. In the rural populations, significant relationships between temperatures and densities were found only in the Great Tit.

3.2. Breeding success

In urban Great Tits, the average clutch size was highest in the first year of study, while in the other tit populations there was no difference. The difference was significant, however, only in the data of Ruskeasuo and in 1987 vs. 1990, 1992 and 1993 (one way analysis of variance, $F_{6,128} = 3.98$, $P < 0.001$; Tukey test, $P < 0.05$). The average clutch size was significantly lower in the urban than in the rural populations of the Great Tit ($z = 17.06$, $P < 0.001$, $n = 796$) and Blue Tit ($z = 8.01$, $P < 0.001$, $n = 452$) (Table 4).

The variances of the brood size differed significantly between the urban and rural habitats both in the Great Tit ($F_{175,527} = 1.97$, $P < 0.01$) and Blue Tit ($F_{114,143} = 1.53$, $P < 0.05$). The average fledgling production per breeding attempt was lower in the urban than in the rural populations (Table 5). The proportions of successful nests (at least one young fledged) did not differ significantly between the urban and rural populations, totalling 78.0% vs. 72.9% in the Great Tit ($\chi^2_1 = 2.27$, $P > 0.05$) and 74.1% vs. 72.2% in the Blue Tit ($\chi^2_1 = 0.08$, $P > 0.05$).

On average, half or slightly more than half of the eggs laid produced fledglings (Table 6). The proportion of fledglings produced per eggs laid was somewhat, though not significantly, higher in the rural than the urban populations of tits (one way analysis of variance, $F_{2,28} = 0.055$, $P > 0.05$, and $F_{2,29} = 0.402$, $P > 0.05$, for the Great Tit and Blue Tit, respectively). Although the breeding success of tits calculated per eggs laid, per breeding attempt, or per successful nesting was more or less higher in the rural populations than in the urban ones, the opposite was true when the young produced per habitat area was considered. On average, the fledgling production per square kilometre of the urban Great Tits was 5.4-fold and that of the Blue Tits 2.7-fold that of the rural populations. There were significant differences only in the Great Tit (one way repeated measures analysis of variance, $F_{4,15} = 17.4$, $P < 0.001$): the rural population differed from those of urban areas other than Kaivopuisto, while the population of Maunula differed significantly from those of all other areas (Tukey test, $P < 0.05$). The breeding success of tits seemed to have no significant effect on the density of the populations in the following year (relationship between the fledgling production of the preceding year and the annual change in the population density in 1988–1993; $r = 0.13$ and $r = -0.09$, for the Great Tit and Blue Tit, respectively, $P > 0.05$, $df = 25$).

3.3. Factors affecting breeding success

Stepwise multiple regression analyses of the factors proposed to affect the clutch size of tits showed that the distance from the most urban area (decreasing degree of urbanisation) was significant for both Great Tit (regression coefficient $b = 0.073$, $P < 0.001$, $r^2 = 0.65$) and Blue Tit ($b =$

Table 6. Average annual breeding success of the Great Tit and Blue Tit in urban parks of Helsinki and in rural habitats of Kirkkonummi in 1987–1993: the number of fledglings, A. per egg laid, B. per breeding attempt, C. per successful nesting, and D. per ha.

Population	A	B	C	D	n
Parus major					
Urban sites					
Kaivopuisto	0.46	3.63	4.71	4.19	6
Töölönlahti	0.51	3.92	5.05	5.38	6
Ruskeasuo	0.43	3.47	4.64	6.54	7
Maunula	0.56	4.52	5.55	9.99	7
Urban, total	0.50	3.95	5.07	6.81	26
Rural	0.52	5.03	6.90	1.25	6
Parus caeruleus					
Urban sites					
Kaivopuisto	0.51	5.11	6.91	3.10	6
Töölönlahti	0.48	4.89	6.48	1.96	6
Ruskeasuo	0.48	4.89	6.82	2.45	7
Maunula	0.60	6.25	8.33	2.86	7
Urban, total	0.51	5.22	7.05	2.69	26
Rural	0.57	6.47	8.97	1.00	6

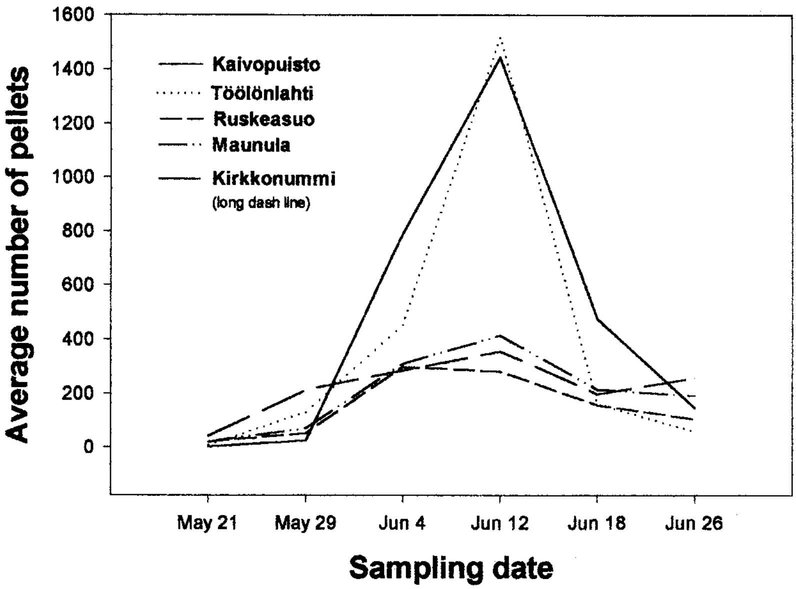

Fig. 2. The average number of moth caterpillar pellets in the samples collected in each study area and period in 1992. The sampling funnels were fastened to trunks of trees about a week before the first sampling date.

0.065, $P < 0.001$, $r^2 = 0.46$). In the Great Tit, an additional positive contribution was due to the mean temperature in April ($b = 0.22$, $P < 0.001$, $r^2 = 0.039$), and negative contributions were due to the species' breeding pair density ($b = -0.003$, $P < 0.01$, $r^2 = 0.076$), and the mean temperature in March ($b = -0.12$, $P < 0.01$, $r^2 = 0.075$). In the Great Tit, the total explained variation (R^2) was 83.8% ($F_{4,28} = 36.2$, $P < 0.001$) while in the Blue Tit it was 45.6% ($F_{1,31} = 26.0$, $P < 0.001$).

The variation in the fledgling production per breeding attempt was explained by the mean temperature in May in both Great and Blue Tits ($b = 0.69$, $P < 0.01$, $r^2 = 0.26$, and $b = 0.99$, $P < 0.001$, $r^2 = 0.40$, respectively) as well as by the density of breeding Blue Tits in the Great Tit ($b = -0.039$, $P < 0.001$, $r^2 = 0.27$), and by the clutch size in the Blue Tit ($b = 1.32$, $P < 0.01$, $r^2 = 0.14$). The total contribution of the two significant variables (R^2) was 52.6% ($F_{2,29} = 16.1$, $P < 0.001$) in the Great Tit and 53.7% ($F_{2,29} = 16.8$, $P < 0.001$) in the Blue Tit.

At least during the breeding season of 1992, the absolute amount of insect food in the environment did not seem to differ considerably between the urban and rural habitats (Kruskal-Wallis analysis of variance; $H_4 = 1.10$, $P > 0.05$), but there was marked variation between samples (Fig. 2). Significant positive relationships between the local food abundance (indicated by the moth caterpillar pellet samples) and the breeding parameters studied could be found in two cases: between the food samples of the period before 21 May and the average clutch size of the Blue Tit ($r_s = 0.99$, $P < 0.01$, $n = 6$), and between the food samples of the period before 18 June and the average fledgling production of the Great Tit ($r_s = 0.90$, $P < 0.05$, $n = 6$).

Starvation of nestlings seemed to be the main cause for the losses of total broods. The proportions of broods lost by starvation of nestlings did not differ between the urban and rural populations of the Great Tit (15.9% vs. 12.1%, respectively; $\chi^2_1 = 1.82$, ns), while in the Blue Tit the losses were significantly heavier in rural (22.8%) than in urban (14.0%) habitats ($\chi^2_1 = 3.99$, $P < 0.05$). The annual predation rates on tit nests were variable, totalling 1.4% in the urban and 9.3% in the rural habitats, the difference being highly significant ($\chi^2_1 = 44.0$, $P < 0.001$).

4. Discussion

4.1. Densities

The densities of Great Tits in the present study (up to 273 pairs/km^2) were much higher than reported earlier in Finland (up to 90 pairs/km^2; Väisänen et al. 1988), while those of the Blue Tit (up to 86 pairs/km^2) did not reach the highest values recorded in small areas of preferred habitat in the south-western part of the country (70–200 pairs/km^2; Lehikoinen 1983). However, the densities recorded in small plots of a few hectares are not quite comparable with those of larger areas (e.g., Solonen 1996). The fact that 40–60% of the boxes studied were left unoccupied strongly suggests that the differences in bird densities between urban and rural habitats were not due to the different density of nest-boxes. Also in accordance with this assumption, in some of the less urban areas saturated with nest-box densities comparable with those in the parks of Helsinki, the densities of the Great Tit were 64–95 pairs/km^2 and those of the Blue Tit 16–24 pairs/km^2 (Solonen 1986, 1991, 1992). These figures are, in general, higher compared to those of the rural populations of Kirkkonummi but considerably lower than those of the urban populations of Helsinki.

The incomplete occupation of nest-boxes in the present study also suggests that the density of holes did not limit the densities of the tits. The positive correlation between population densities suggests that the species concerned had no need to compete for nest-sites. Especially at the highest densities, inter-specific competition for nesting holes and food might occur (Dhondt & Eyckerman 1980, Minot 1981, Minot & Perrins 1986). If the population sizes were not limited by the amount of nest-sites, they probably were largely determined by the availability of food, especially before the breeding season (see, e.g., van Balen 1980, Orell 1989).

The lower densities of tits at the beginning of the study might have been partly due to the earlier lack of nest-boxes in the study areas, and partly due to the exceptionally hard winter of 1986/1987 (cf. Väisänen & Solonen 1997). Also the two preceding winters were harder than average. Because the population changes both in new urban and old rural nest-box areas were largely similar, however, it can be concluded that nest-box areas were occupied in relation to the prevailing population size at the beginning of the study. The increase of the rural Blue Tit population coincided with the general increase in the Finnish population of the species (Väisänen & Solonen 1997). In general, fluctuations in tit numbers can be attributed to the effects of low ambient temperatures and food availability in winter (von Haartman 1973, van Balen 1980, Källander 1981).

The present results suggest that in Great Tits the effects of wintering conditions might be less in urban than in rural habitats, while in Blue Tits the situation may be the opposite (Table 3). In urban habitats, due to the high densities of wintering populations and strictly localised food sources (feeding sites) also the effect of inter-specific competition might be harmful for the smaller species. In contrast, in rural habitats Blue Tits may survive better than Great Tits due to additional food resources (such as reed-beds) that are not used by Great Tits. Compared to their urban conspecifics, rural Blue Tits may benefit from the lower densities of tits (less competition for food) as well.

4.2. Clutch size

Urban Great and Blue Tit populations laid fewer eggs than their rural counterparts, suggesting that breeding conditions for tits were less good in urban areas. This is in accordance with earlier findings (Perrins 1965, Berressem et al. 1983, Cowie & Hinsley 1987, Hildén & Solonen 1990, Hõrak 1993). The difference in the clutch size between urban and rural populations might be due to the amount of suitable food available for each pair before and during egg-laying. The poor quality of food before the breeding season in urban habitats (Hildén & Solonen 1990) may also account for the small clutch size of tits.

The high clutch size of the urban Great Tits in the first year of the study may be explained by the minor competition for food resources due to the lower population densities in that year. Their clutch size seemed to be affected negatively largely by the high densities due to good wintering conditions. The mean temperature in March was probably reflected in the clutch size via its indirect effect on density, while the mean temperature in April indicated the quality of feeding conditions before the egg-laying.

In addition to the feeding conditions during the breeding season, the small clutch size of the urban tits may be due to the small body size of the birds. This is suggested by the fact that the urban Great Tits of the present study commonly used nest-boxes with the small entrance hole designed for the Blue Tit. Great Tits immigrating to urban areas may be on average smaller-sized than the birds occupying rural habitats (Lehikoinen 1986). Tits of urban origin may be small due to their inferior feeding conditions and slower weight gain during the nestling period (Hildén & Solonen 1990).

4.3. Breeding success

The clutch size of the tits was 9.8–17.3% smaller, but the fledgling success as much as 19.3–21.5% smaller in the urban compared to the rural areas studied. However, the results on the food supply indicate that there were only minor differences in the general availability of food between habitats. The urban tit populations produced 3.8–10.5% fewer fledglings per egg, but about 3 to 5-fold as many fledglings per area than did birds in the less urban habitats. This also suggests that the general availability of food was not lower in the urban than in the rural habitats. The amount of food available per breeding pair, however, might be lower for the urban compared to rural tits.

Urbanisation as such did not seem to have pronounced direct effects on the fledgling production of tits. The indirect negative effects of urban habitats seemed to be largely due to high densities and lowered clutch size. In various studies, tits in urban habitats have been shown to produce fewer fledglings per breeding attempt than do birds in rural habitats (Perrins 1965, Berressem et al. 1983, Cowie & Hinsley 1987, Hildén & Solonen 1990, Hõrak 1993). In both species, the breeding performance has been shown to decline with decreasing woodland area (Hinsley et al. 1999).

In the present study, the main difference in the annual fledgling production between the habitats resulted from the difference in bird density. Accordingly, the high densities of the urban tit populations apparently have a detrimental effect on their breeding success. This effect is probably reinforced by the presence of other insectivores using similar food resources. Interference from other insectivores, especially Pied Flycatchers *Ficedula hypoleuca* that also use similar nest-sites, was, however, higher in less urban habitats (Hildén & Solonen 1990). This was emphasised in years when, and in areas where the initiation of the breeding of tits was later than usual and there was more temporal overlap in the breeding seasons of the species. Possible inter-specific competitors for food included ants (Aho et al. 1999) which were especially abundant at Ruskeasuo and where they may be partly responsible for the lower breeding success of tits than in the neighbouring areas.

Urban habitats were preferred by tits, probably because they offer good wintering conditions by providing food and artificial roosting holes that later may also be used for breeding. However, these facilities might attract birds to breed in otherwise deficient conditions or in such densities that are detrimental because of intense competition for food (as suggested by the low breeding success). Similarly, in some species, luxuriant habitats with abundant supplies of food and nest sites may be a kind of ecological trap due to heavy predation (Solonen 1979; cf. also Gates & Gysel 1978).

Important factors affecting losses of nestlings in the present study seemed to be starvation and (in rural habitats) predation (cf. Jokimäki & Huhta 2000). However, the possible role of some other causes of death, e.g. diseases, parasites, and pollution, could not be excluded. The breeding success might be affected not only by the amount but also by the quality of food available for each pair of birds. This, in turn, may be affected by the level of pollution in the environment (Eeva et al. 1997, Solonen et al. 1999). Poor quality of food is probably reflected in the quality of eggs and young produced. For a more precise control of the effects of food supply, food sampling should be extended to better cover the individual territories of tits and the years of study. In addition to samples of potential food resources, the quality and quantity of food used by tits needs study (cf. Naef-Daenzer et al. 2000).

Acknowledgements: This study was originally planned and conducted together with Olavi Hildén, who fell ill and died soon after the field work period. Responsibility for the presentation of the results was therefore left to the author. Olavi Hildén was the indispensable *primus motor* of the study. The field study was conducted in collaboration between the University of Helsinki and the Parks Department of the City of Helsinki. The field work was done by Solveig Bergholm (1987–89), Jan-Peter Bäckman

(1991–93), Kaarlo Hildén (1989–92), Martti Hildén (1989), Olavi Hildén (1987–93), Paavo Inkinen (1987–89), Juha Laaksonen (1990–93), Jukka T. Lehtonen (1990–91), Olli Mustonen (1992; food samples), Pekka Paaer (1990), Christina von Pfaler (1987), Aulikki Tervonen (1987) and Rauno Yrjölä (1987). The Directorate of Helsinki City supported the final phases of the study financially. Jon C. Gering, Martti Hildén, Jukka Jokimäki, Jukka Suhonen, Juha Tiainen, Risto A. Väisänen and some anonymous referees read a draft of the manuscript and made valuable suggestions. Pekka Routasuo provided Fig. 1, and Marcus Walsh checked the English.

Selostus: **Tali- ja sinitiaisen pesimätulos eteläsuomalaisessa kaupunki- ja maaseutuympäristössä**

Eri puolilla Eurooppaa tehdyissä tutkimuksissa on todettu, että pöntöissä pesivät tiaiset tuottavat kaupunkiympäristöissä vähemmän munia ja poikasia kuin maaseudulla. Seitsemänvuotisessa tutkimuksessa Helsingissä ja Kirkkonummella tali- ja sinitiaisen pesyekoko oli vastaavasti kaupungin puistoissa merkitsevästi pienempi kuin maalla. Myös tiaisten poikastuotto munittua munaa, aloitettua pesintää ja onnistunutta pesintää kohti laskettuna oli pienempi kaupungissa kuin maaseutuympäristössä. Kuitenkin pinta-alaa kohti laskettuna tulos oli päinvastainen. Pesimäaikaan linnuille sopivan hyönteisravinnon määrässä ei ollut huomattavia eroja eri ympäristöjen välillä, mikä viittaa siihen, ettei ympäristön tuottaman ravinnon määrällä sinänsä olisi ratkaisevaa vaikutusta lintuparien tuottamien poikasten määrään. Muut tekijät kuin pesimäympäristön ravinnon runsaus vaikuttivat tärkeämmiltä myös tiaisten pesimätiheyden ja pesyekoon vaihtelujen ohjaajina. Pesimäkannan tiheyteen vaikuttivat ennen kaikkea ympäristöolosuhteet pesintäajan edellä eli talven ankaruus. Talitiaisella pesimäympäristön etäisyys keskikaupungista, kannantiheys (lajinsisäinen kilpailu) ja alkukevään sääolot näyttivät vaikuttavan pesyekokoon, ja loppukevään säät sekä sinitiaisen tiheys (lajienvälinen kilpailu) poikastuottoon. Sinitiaisella pesimäympäristö (etäisyys kaikkein kaupunkimaisimmilta alueilta) oli tutkituista tekijöistä ainoa, joka näytti vaikuttavan pesyekokoon. Pesyekoko ja loppukevään lämpötilat taas selittivät poikastuoton vaihteluja. Kaupunkiympäristöissä pesinnän edellä käytettävissä oleva ravinto saattaa olla heikkolaatuista, millä voi olla vaikutusta kaupunkitiaisten pieneen pesyekokoon. Kaupungeissa pesivien tiaisparien alhaiseen poikastuottoon taas saattaa olla syynä suuresta tiheydestä ja kilpailusta johtuva ravinnon määrällinen niukkuus.

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