

Brief reports

Low fledging success of urban Great Tits

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Introduction

Breeding conditions for birds in urban habitats are different from those of surrounding rural areas, and therefore, the phenomenon of urbanization provides an opportunity for testing the adaptive potentials in birds (Tomiałojć 1985).

Studies from different parts of Europe have shown that clutch-sizes of the urban Great Tit *Parus major* populations are smaller than those of rural populations (Perrins 1965, Berressem et al. 1983, Cowie & Hinsley 1987, Hildén & Solonen 1990). Sparsely vegetated urban areas are probably less suitable breeding habitats for Great Tits than are rural woodlands, and therefore, one might conclude that smaller clutch-sizes indicate an adaptation to the poor breeding habitat. However, these studies reveal a general tendency that, in spite of small clutch sizes, the fledging success in urban areas was still lower than in rural woodlands. There might be three possible explanations for this phenomenon: (i) for urban Great Tits, it is not disadvantageous to lay larger clutches than can be reared, (ii) urban females lay excessively large clutches because they are in a relatively good condition at the onset of laying but overestimate the feeding conditions during the nestling period, and (iii) there is a

perpetual influx of genotypes for the laying of large clutches.

In the following, I summarize the available data on clutch-sizes and fledging success in urban and rural Great Tit populations, and discuss the arguments of different possible explanations for lower fledging success in urban populations.

Breeding success in the urban habitats

Extensive population studies in Western and Northern Europe have demonstrated that Great Tits, breeding in urban and suburban habitats lay fewer eggs and raise fewer and lighter nestlings than those breeding in rural woodlands (Perrins 1965, Berressem et al. 1983, Cowie & Hinsley 1987, Hildén & Solonen 1990). Interestingly, results of all the above-mentioned studies and those of the analogous project in Estonia (P. Hõrak, in prep.) reveal also the similar pattern of lower fledging success in urban populations (Table 1). A low fledging success (number of young fledged per egg) indicates that average clutch sizes in urban habitats (though generally low) match parental rearing ability less exactly than clutch-sizes in rural populations. Therefore, one might expect a better correspondence of

clutch sizes to parental ability to feed nestlings, if the urban Great Tits would lay still fewer eggs than they do and still be able to rear the same number of fledglings.

Why are the clutches of urban Great Tits not smaller?

The phenomenon can be explained by the following hypotheses:

- i) Excessively large clutches of urban tits are not disadvantageous: Brood reduction reduces the number of young to the level that parents can feed and nestling quality is not influenced by their initial number.
- ii) Poor assessment of the quality of the breeding habitat: Urban females are in relatively better condition during the period of egg formation and laying, than are females in rural habitats (possibly due to access to supplementary food and warmer mesoclimate in towns). In this case, the birds wrongly use the good food supply as a cue about the feeding conditions during the nestling period and so lay excessively large clutches.
- iii) Perpetual influx of genotypes for the laying of large clutches (immigration of Great Tits to towns from richer habitats, where laying of large clutches is favoured).

These explanations are not mutually exclusive and may well act together.

The first hypothesis assumes a lack of selection against excessively large clutches. Yet, this is in contradiction with the results from brood manipulation experiments, where increasing brood size causes decrease of weight and/or survival of the entire brood (Pettifor et al. 1988, Smith et al. 1989, Lindén 1990). Thus, it is likely that the Great Tit does not benefit from brood reduction. Therefore, having small clutches in circumstances when the birds have difficulties in raising young, is more likely to enable the parents to raise heavy young (Perrins 1990). Accordingly, laying clutches not corresponding to food resources at the period of rearing the young is disadvantageous, and the clutch-sizes of studied urban populations can be regarded as non-adaptive.

The second hypothesis alone may not be sufficient to explain why natural selection has not reduced the average clutch-size in towns to a level closer to parental rearing ability. It raises the question of why a wrong assessment of habitat quality is not eliminated during the process of selection. Great Tits have lived in urban habitats for many generations and one might expect the spread of alleles which select for a better assessment of breeding habitat quality. On the other hand, supplementary feeding of birds on a large

Table 1. Clutch size and fledgling success of Great Tits in urban and rural habitats. * = % of fledged young (of hatched), ** = clutches failed due to predation excluded. Source: 1 – Perrins 1965, 2 – Schmidt & Einloft-Achenbach 1983, 3 – Cowie & Hinsley 1987, 4 – Hildén & Solonen 1990, 5 – Hórák in prep.

Urban population (years studied)	Mean clutch-size (N)	% of fledglings per egg	Rural population (years studied)	Mean clutch-size (N)	% of fledglings per egg	Source
Gardens in Oxford (1958–61)	7.6 (83)	56*	Marley wood, Oxfordshire (mixed; 1958–62)	8.7 (285)	89*	1
Parks in Frankfurt on Main (1980–82)	7.6 (289)	31	Woodlands near Schlüchtern (deciduous; 1980–82)	9.2 (356)	68	2
Suburban gardens in Cyncoed (Cardiff) (1983)	7.4 (24)	58	Wytham wood, Oxfordshire (mixed; 1983)	9.0 (347)	88	3
Parks in Helsinki (1987–89)	8.2 (233)	51	Rural habitat in Kirkonummi (1987–89)	9.6 (143)	65	4
Parks and avenues in Tartu (Estonia) (1987–91)	8.8 (332)	60**	Woodlands in Tartu District (mixed; 1987–91)	11.1 (228)	75**	5

scale may not be a very old phenomenon. Therefore, I can not totally exclude this possibility.

The third hypothesis does go some way to explain the apparent anomaly, since it shows how the excessively high clutch-sizes in towns can be maintained.

Gene flow hypothesis

Gene flow between habitats of different qualities has been claimed to be responsible for nonadaptive clutch-sizes in Great Tits by Hamann et al. (1989) and Dhondt et al. (1990). The mechanism was first suggested by Perrins & Moss (1975) and developed further by Perrins in 1990. These authors claim that if the most productive brood size differs between habitats, then dispersal of individuals may lead to a situation where the optimal clutch-size of Great Tits is smaller than the modal one in favourable habitats (woodlands) and larger than the modal in less favourable habitats (gardens).

Nevertheless, it can hardly be directly demonstrated in a bird species that the average clutch size of a population is affected by gene influx. In the case of Great Tits, however, there is a reason to expect immigration into urban areas, if one assumes that the bulk of the population breeds in the productive rural habitats.

Role of wintering conditions

Considering the possibility of immigration into urban habitat, it is also relevant to examine the role of conditions during the nonbreeding period.

The wintering period is critical for the survival of temperate zone passerines. There is evidence from different parts of Europe that fluctuations in Great Tit numbers can be attributed to the effects of low ambient temperatures and food availability. Berndt & Frantzen (1964), Dhondt (1971), von Haartmann (1973), van Balen (1980), Källander (1981), Bejer & Rudemo (1984), (but Krebs 1971, Schmidt & Wolf 1985) have demonstrated the effect of beech crop and/or the extent of winter feeding by humans on Great Tit populations.

The latter suggests that for the Great Tits, human settlements are probably more suitable for wintering than rural woodlands. Urban mesoclimate is warmer than in rural surroundings (Haggard 1990) and supplementary food resources (winter feeding, food remnants) for birds are available. In the northernmost parts of its range, the Great Tit has been found to depend predominantly on food near human habitations in winter (Hildén & Koskimies 1969). One might, therefore, expect an extra reason for immigration of rural birds into urban habitats, if one is to assume that Great Tits move from breeding grounds to more suitable wintering areas and settle there to breed. The published evidence suggests that the latter might really be the case:

- i) In some areas most of the Great Tits leave the breeding grounds, at least temporarily, when conditions in winter are unfavourable (Drent 1979, van Balen 1980, Lehtikoinen 1986). It has also been reported that the density of Great Tits in human settlements increases markedly during the wintering period (Vilbaste 1976).
- ii) Breeding densities of Great Tits are higher near areas with winter feeding (Hansson 1986, Orell 1989, Eeva et al. 1989). It has been stated that juvenile Great Tits establish territories at any time during the autumn and winter as soon as an opportunity is offered (Drent pers. comm. in Klomp 1980) and, therefore, it is probable that a certain amount of the wintering birds of rural origin settle to breed in towns.

Finally, there is evidence for immigration to urban areas from two studies: Perrins & Moss (1975) reported a large amount of interchange of Great Tits between gardens in Oxford and woodland areas, and Berressem et al. (1983) showed that the maintenance of local Great Tit populations in parks and cemeteries of Frankfurt depended on immigrants from small urban woods.

Conclusions

Data from different parts of Great Tits' range indicate that breeding conditions in urban areas are worse than in rural woodlands, whilst the

former is evidently a more suitable habitat for wintering. The published evidence suggests that birds originating from the rich breeding habitats may use urban areas for wintering, and (since the early establishing of breeding territories is important) also settle to breed there. Therefore, it is likely that good wintering conditions play a role in attracting birds to breed in suboptimal habitats.

The clutch size of the Great Tit is known to have a heritable component (van Noordwijk et al. 1981), and because of this, one may conclude that immigrants from productive rural breeding habitats are genetically determined to lay larger clutches than might be suitable in urban areas.

Therefore the example of urban Great Tit populations seems to serve as an illustration for the hypothesis of prevention of local adaptations by gene flow.

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Selostus: Kaupunkilaistalitiaisten keho pesimämenestys

Useissa tutkimuksissa on havaittu, että kaupungeissa pesivillä talitiaisilla on pienempi pesyekoko ja huonompi poikastuotto kuin maaseudun asukeilla (Taulukko 1). Tutkijoita on askarruttanut miksi talitiaisen pesyeet eivät ole kaupungeissa vielä pienempiä eli eikö talitiainen ole vielä sopeutunut kaupunkilaiselämään. Ilmiötä on pyritty selittämään seuraavilla hypoteeseilla: (1) Suurista pesyeistä ei ole erikoisempaa haittaakaan, koska ylimääräiset poikaset kuolevat pesään. (2) Munintakaudella kaupunkien talitiaisnaaraat ovat hyvässä kunnossa syötyään talven lintulautojen antimia. Hyvä muninta-aikainen ravinto ei kuitenkaan ennusta hyvää poikasaikaista ravintoa, jolloin osa poikasista menehtyy. (3) Kaupunkeihin muuttaa jatkuvasti maaseudulta lintuja, jotka ovat sopeutuneet munimaan suuria pesyeitä, joita ne eivät kuitenkaan pysty huoltamaan. On huomattava, että hypoteesit eivät ole toisensa pois sulkevia.

Kirjoittaja päättelee, että kaupungit ovat edullisia talvehtimisympäristöjä, jotka houkut-

televat jatkuvasti uusia lintuja ympäröivältä maaseudulta. Maaseudun talitiaiset ovat sopeutuneet munimaan suuria pesyeitä, koska kuoriutuville poikasille riittää runsaasti ravintoa. Geenivirta maaseudulta kaupunkiin estää kaupunkipopulaatioiden paikallisen sopeutumisen huonoon poikasaikaiseen ravintotilanteeseen.

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