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Effect of nestling history on adult size and reproduction in the Great Tit

Peeter Hõrak

Hõrak, P., Laboratory of Ecological Zoology, Department of Biology, University of Turku, FIN-20500 Turku, Finland. — Present address: Section of Animal Ecology, Institute of Zoology and Botany, University of Tartu, Vanemuise 21, Tartu EE-2400, Estonia

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I found a heritable variation of about 60% in the tarsus length of Great Tits in two populations, breeding in different (urban and rural) habitats of south-east Estonia. In spite of high heritability, the size of fledglings was also sensitive to growth conditions. Young from broods where nestling mortality occurred developed shorter tarsi compared to broods where all hatchlings fledged. Phenotypic variation in size was also remarkable among breeders. Cohorts of adults, born in poor breeding years had shorter tarsi than those born in normal years. Small females tended to lay small clutches which is consistent with the hypothesis that poor nestling history may have a lasting effect on the condition of breeding females and affect clutch size. I could not establish significant differences between populations in any of the aspects studied.

1. Introduction

Body size of birds is known to have both a heritable and environmental component. Several studies have shown that heritabilities of morphological characters may range up to 60–70% (review in Boag & van Noordwijk 1987). The size of an individual is also known to be affected by environmental conditions experienced during growth (Garnett 1981, van Noordwijk et al. 1988, Boag 1987, Richner et al. 1989, Smith 1993). The relative importance of selection and growth conditions in shaping the traits of the individuals in wild populations is open to discussion. Boag (1987) pointed out that avian ecologists regularly seek for adaptive explanations for size differences of a magnitude that can easily be produced by differences in growth conditions. On the other hand, it has been shown that selection on body size tends to reduce environmental, rather than genetic variation among individuals (van Noordwijk et al. 1988, Lindén 1990, Alatalo et al. 1990). It is not clear therefore to what extent the variation in growth conditions contributes to size differences among individuals in a breeding population.

Recent experimental studies by Haywood & Perrins (1992) and Schluter & Gustafsson (1993) have shown that the conditions experienced by females during the nestling stage can also affect their future clutch size. If both the body size and the clutch size of an individual reflect the conditions experienced during growth, one can expect a positive phenotypic correlation between those traits. Detection of a correlation between body size and clutch size in a population where female size is affected by growth conditions can therefore be considered as indirect evidence for the effect of an individual's ontogeny on its reproduction. Though indirect, this will probably be the only realistic way to gather replicative data about the commonness of this phenomenon because of the difficulties in recapturing a sufficient amount of breeding females which have been measured as nestlings.

In this paper I investigate both the heritable and environmental variation of body size in the Great Tit (*Parus major*). I address the question of whether the tarsus length of a fledgling reflects the conditions experienced during growth (i), whether size differences can be detected among adults born in good and poor breeding years (ii), and whether such condition-dependent breeding traits as clutch size and laying date are related to female size (iii).

Growth, survival and reproduction are sensitive to habitat characteristics. Therefore I conducted my study in two Great Tit populations, facing different conditions for breeding and wintering in rural and urban habitat in south-east Estonia. I expect the phenotypic correlations between individuals' size and reproduction to become apparent especially in the urban population. Due to the favourable wintering conditions in the town, selection against phenotypically small individuals might be less severe in the urban population rather than in the rural population. Energetic constraints on laying are also more likely to occur in the urban population, since the habitat has poor resources for breeding (e.g. Hõrak 1993).

2. Material and methods

2.1. Study area

Data were collected in two main study areas: in Tartu (58°22′N 26°43′E; human population about 120 000) and in rural area of Tõrvandi, 5 km from Tartu in 1987–92. The urban study area in Tartu consisted of two large and two small parks (about 22 ha) and immediate neighbourhoods of streets (total length 9 km). Main tree-species were *Tilia cordata, Acer platanoides, Betula pendula, Querqus robur,* and *Populus suaveolens.* All streets in the urban study area were surrounded by gardens where winter feeding of birds was common.

The rural study area in the vicinity of Tartu contained two mixed woods, 2.5 kilometers apart and surrounded by agricultural land. Dominating tree-species were *Picea abies, Pinus sylvestris, Betula pendula, Corylus avellana* and *Populus tremula.* The total number of nestboxes (in two areas together) varied from 327 to 497 in different years.

2.2. Tarsus length

Tarsus length is correlated with many multivariate measures of size and suits therefore well for estimating the overall body size of birds (Rising & Somers 1989). In Great Tits, the tarsus attains its full size about 12 days after hatching (Gebhardt-Henrich & van Noordwijk 1991) and remains constant throughout life.

Tarsus lengths of adult Great Tits were measured since 1990, but since the birds were individually marked, it was also possible to gather data about size of individuals born since 1987 and still alive in 1990. Measurements of adults were taken in the breeding period (nestlings 7–16 days old), during night inspections of nestboxes during the winter, and (for the rural population only) by winter trapping using feeders baited with sunflower seeds. Since 1991 tarsus length of nestlings was measured at 14–16 days of age.

Tarsi were measured to the nearest 0.1 mm with a sliding caliper, bending the birds' toes back (see Svensson (1992)). All measurements were recorded by the same person. For individuals which were measured repeatedly, the average of tarsus length measurements was used in analyses. Repeatability (Lessells & Boag 1987) for tarsus length was 0.71 for 193 birds captured more than once (472 captures).

Heritabilities for tarsus length were estimated from mid-offspring — single parent and mid-offspring — midparent regressions (Falconer 1989).

2.3. Breeding parameters

Breeding parameters (clutch size, laying date, number of dead and fledged young) were recorded by regular checking of the nestboxes in the breeding period. Adults were sexed and aged using plumage characteristics as described by Svensson (1992). In order to eliminate the year effect in calculations with pooled data, clutch size and laying date were standardized by expressing individual values relative to the annual mean of the population (see van Noordwijk et al. 1981). In all analyses only data from the first clutches were used. Statistical analyses were performed using SYSTAT (Wilkinson 1987). All significance levels are for two-tailed tests.

3. Results

3.1. Heritability of tarsus length

All three heritability estimates for tarsus length were significantly different from zero for the urban population (Table 1). In the rural population only the female — mid-offspring regression was statistically significant. Heritability estimate from female — mid-offspring regression (0.57) in the rural population was probably reliable since I found no evidence for assortative mating in respect to tarsus length (correlation between tarsus length of female and male partners: $r = 0.13$, $P = 0.57$, $n = 22$). Lack of significance was probably not only due to small sample size, because also the correlation between tarsus length of partners in the sample of all measured rural birds was not significant ($r = -0.10$, $P = 0.45$, $n = 57$).

Positive assortative mating was observed in the urban population ($r = 0.20$, $P = 0.019$, $n = 142$). Assortative mating may affect heritability estimates from a single parent but not midparent values (Falconer 1989). This could be a reason why the female — mid-offspring regression gave a higher heritability estimate (0.71) than the midparent — mid-offspring regression (0.63). After correcting for assortative mating the heritability estimate from female — mid-offspring data was 0.56, which is similar to the estimate for the rural population.

Table 1. Heritabilities of tarsus length (with standard errors). Regression coefficients of single parents and their SE are doubled. Data are pooled over three years.

Population	Female	Male	Midparent
Urban	0.71 (0.24) 0.56* N=99 P=0.005	0.43 (0.12) 0.34* N=74 P<0.001	0.63 (0.14) N=74 P<0.001
Rural	0.57 (0.21) N=46 P=0.012	0.38 (0.54) N=22 P=0.492	0.40 (0.30) N=22 P=0.191

* Corrected for assortative mating: $h^2 = 2b/(1+r)$; (Falconer 1989).

3.2. Tarsus length in different populations

Data for comparison of populations were available for 1992 and 1993 (normal breeding years) only. Average tarsus length of fledglings was 19.6 ± 0.5 (SD) mm for the rural and 19.5 ± 0.6 mm for the urban population. The difference was not significant ($F_{1,128} = 0.23$, $P = 0.63$). Nor did the tarsus lengths of adult birds differ between populations (Females: $F_{1,285} = 2.27$, $P = 0.13$, Males: $F_{1,180} = 0.11$, $P = 0.74$).

3.3. Nest conditions and tarsus length

In testing for the effect of growth conditions on fledgling tarsus length I proceeded from data of nestling mortality. I assumed that growth conditions for young are good if parents can fledge all their hatchlings, and that these conditions are poor in the case when at least one of the hatchlings dies in the nest. Since the heritability estimates for tarsus length were similar for both populations, I pooled all available data over three years and both populations.

Tarsi of the young from the broods where nestling mortality occurred were on average 0.4 mm shorter than those from the broods where all hatchlings fledged (19.3 ± 0.5 mm ($n = 33$) vs. 19.7 ± 0.5 mm ($n = 50$); $t = -3.69$, $P < 0.001$, t-test on brood means with pooled data). Heritabilities of tarsus length were similar for both groups (Fig. 1).

Fledgling tarsus length was significantly affected by the year of birth (Table 2). Average tarsus length for a poor breeding year (1991) was 18.4 ± 0.8 mm ($n = 18$), which is about one mm shorter than the average for normal breeding years: 19.3 ± 0.6 mm ($n = 43$) for 1992 and 19.6 ± 0.5 mm ($n = 87$) for 1993 respectively; means ± SD presented, data pooled over two popu-

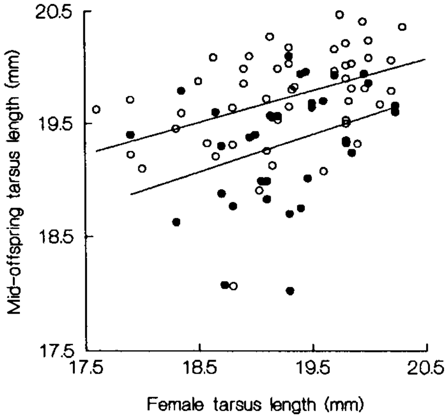

Fig. 1. Plot of mid-offspring tarsus length vs. female tarsus length. Filled symbols represent broods where at least one nestling died in the nest. Data are pooled over three years and two populations. Female tarsus is used instead of midparent tarsus because of larger sample size. Slopes for the lines: y=14.30+0.28 (±0.09)x, P = 0.002, n = 50, (upper line, no nestling mortality) and y=12.93+0.33(±0.16)x, P = 0.048, n = 33 (lower line, broods with nestling mortality).

lations). Nevertheless, an effect of adverse nest conditions (indicated by the occurrence of nestling mortality) on fledgling size was also apparent within individual years, as the nestling mortality term was significant in the model that includes year term (Table 2).

3.3. Effect of the year of birth on adult tarsus length

As the growth conditions affected nestling tarsus length, I tested for the presence of the same pattern among adults, comparing the size of birds born in good and poor years.

Adult size varied remarkably with the year of birth. Variation was parallel for both females and males and for urban and rural population (Fig. 2). There were two years (1987 and 1991) in the study period which were evidently poor for the breeding of Great Tits, as indicated by the low number of fledged young per pair (Fig. 2). Females born in 1991 were significantly smaller than those, born in the 1988–1990 and 1992 (all $P < 0.05$ in pairwise comparisons by t-test, data pooled over both populations). The same was true for males with the exception of comparison of 1990 vs. 1991. Birds born in 1987 also tended to be small (Fig. 2), but the data were too few for statistical comparison.

Table 2. Factors affecting fledgling tarsus length. $R^2 = 0.37$. Female tarsus length is used instead of midparent tarsus length because of larger sample size. (Dependent variable: Brood's average fledgling tarsus length).

Source of variation	df	Sum of squares	F value	P
Nestling mortality	1	2.73	15.10	<0.001
Year	2	1.46	4.02	0.022
Population	1	0.43	2.37	0.128
Female tarsus	1	1.98	10.86	0.001
Error	76	13.76		

3.5. Female size and reproduction

A significant relationship between clutch size of a female and its tarsus length in an individual year was revealed in 1990 (Fig. 3). In the urban population, two four-egg clutches had a profound effect on the regression.

The relationship was weak but significant for the urban population (and nearly significant for the rural population) when data were pooled over four years and calculated for the standardized clutch size (Fig. 3). Fig. 3 indicates also that the positive correlation between a female's tarsus length and her clutch size was mostly due to very small females laying small clutches.

An ANCOVA did not reveal that the relationship between female tarsus length and clutch size was significantly different for either of the populations (nonsignificant population*tarsus interaction; Table 3).

Laying date was negatively correlated with tarsus length of the female only in the urban population in 1992 (Fig. 4). I tested whether this effect could have been caused by the later onset of laying of yearlings (which were small as they were born in the poor 1991 year) by calculating correlations for yearlings and older breeders separately. The correlation was still significant for yearlings ($r = -0.52$, $P = 0.045$, $n = 15$) but not for older breeders ($r = -0.15$, $P = 0.422$, $n = 31$).

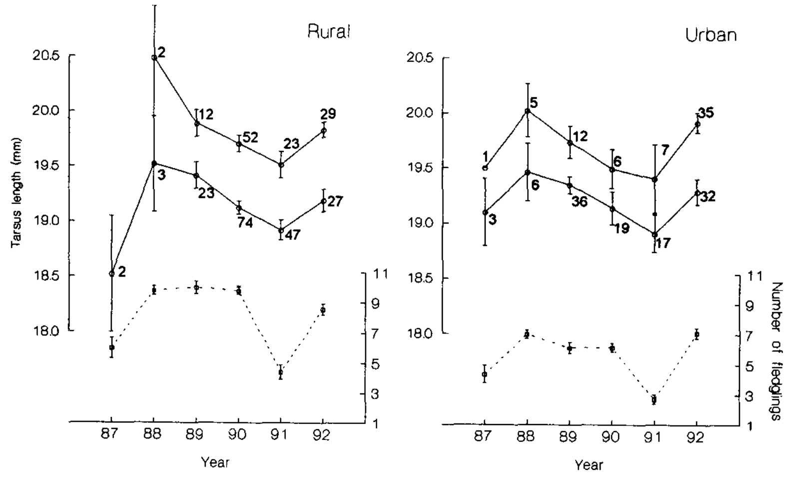

Fig. 2. Tarsus length (mean ± SE) of adult Great Tits plotted against the year of birth (lines, upper = males, lower = females). Data for individuals which were trapped at least three months after leaving the nest. Breeding conditions of a given year (dotted lines) are indicated by the average number of young fledged per pair (predated nests are excluded from the calculation). 1987 and 1991 are considered to be poor years because of low breeding success.

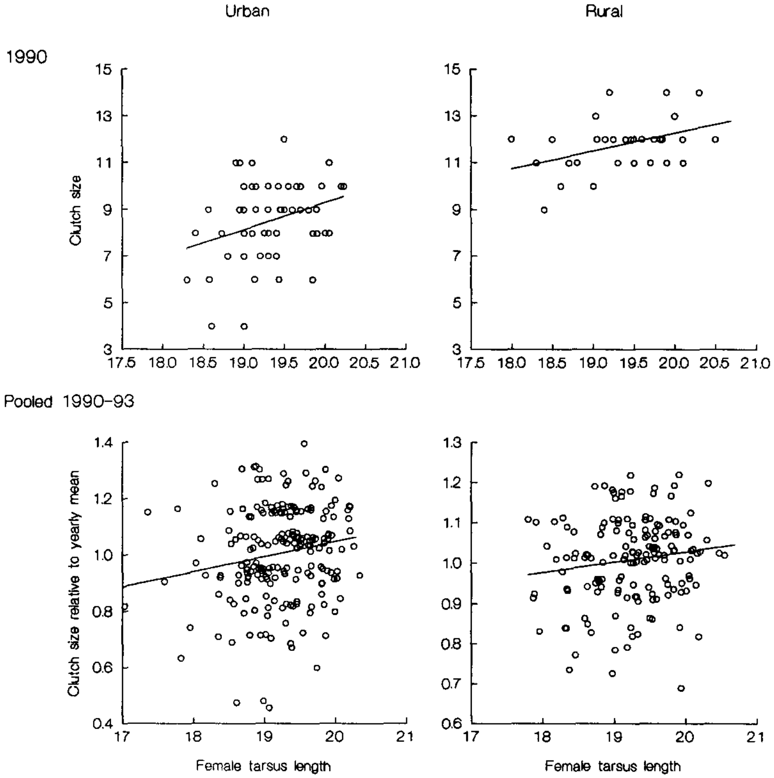

Fig. 3. Relationship between clutch size and female tarsus length in the urban (left) and rural (right) population. Upper: data for 1990; slopes for the lines: y=−13.67+1.15(±0.45)x, P = 0.014, n = 59, (urban) and y=−3.01+0.76(±0.29)x, P = 0.012, n = 34 (rural). Lower: Pooled data from 1990–93. Data points are jittered in order to decrease the overlap. Clutch size is standardized by expressing the individual values in relation to the yearly mean of population. Slopes for the lines: y=0.01+0.05 (±0.02)x, P = 0.016, n = 204 (urban) and y=0.52+ 0.03(±0.01)x, P = 0.076, n = 156 (rural).

4. Discussion

4.1. Variation in fledgling size

Heritability estimates for tarsus length of about 60%, based on female — mid-offspring and mid-parent mid-offspring regressions, were generally comparable to those found in other studies of the Great Tit (Garnett 1981: $h^2 = 0.76$; van Noordwijk et al. 1988: $h^2 = 0.57$; Gebhardt-Henrich & van Noordwijk 1991: $h^2 = 0.39...1.05$). My estimates are also similar to those for several other passer-

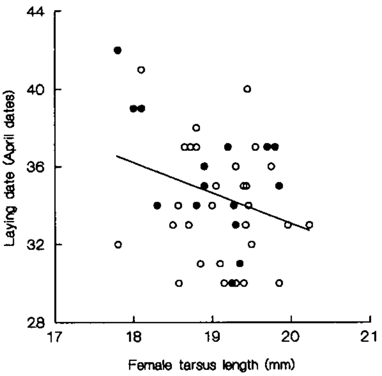

Fig. 4. Relationship between laying date and female tarsus length in the urban population in 1992. Filled symbols: yearlings, open symbols: older birds. Slope for the line: y=64.271–1.56(±0.74)x, P = 0.041, n = 47.

ine species, showing heritabilities of 60–70 % for morphological characters (review in Boag & van Noordwijk 1987). Heritabilities of this magnitude are commonly considered to imply a high potential for an evolutionary response to selection.

My data revealed also that despite the high heritability, the tarsus length of an individual is also sensitive to conditions experienced during growth. Similar results have been reached by several authors, e.g. Garnett (1981), van Noordwijk et al. (1988), Gebhardt-Henrich & van Noordwijk (1991) for Great Tit and Alatalo & Lundberg (1986), Boag (1987), Richner et al. (1989), Smith (1993) for other species. Lack of difference in heritability estimates for tarsus length for broods with and without nestling mortality (Fig. 1) implies the lack of genotype-environment interaction (Falconer 1989; see also Boag 1983).

Shorter tarsi of individuals, originating from broods where nestling mortality occurred indicated that despite of the high heritability the tarsus length of an individual is a good indicator of conditions experienced in ontogeny. This result is meaningful also in relation to the brood reduction hypothesis (Lack 1954, O'Connor 1978).

The brood reduction hypothesis has been applied also to the Great Tit (e.g. Slagsvold 1985, Slagsvold & Amundsen 1992) which is known to hatch asynchronously. In my study, survivors of brood reduction attained significantly shorter tarsi than nestlings in non-reduced broods. I.e., brood reduction did not improve the growth of the surviving nestlings. My data suggest therefore, that brood reduction did not fully compensate for poor feeding conditions. The similar results were found by Moreno et al. (1994) in the Chinstrap Penguin *Pygoscelis antarctica*.

Table 3. Test for population-specific relationship between clutch size and female tarsus length. $R^2 = 0.027$. Clutch sizes are standardized by expressing the individual values in relation to the yearly mean (for both populations separately).

Source of variation	df	Sum of squares	F value	P
Population	1	0.020	0.97	0.325
Female tarsus length	1	0.174	8.29	0.004
Population * Female tarsus length	1	0.020	0.97	0.324
Error	356	7.483		

4.2. Variation in adult size

Several authors have shown that selection during the period of major mortality acts mainly on the environmental component of the phenotypic variation in fledgling size (van Noordwijk et al. 1988, Lindén 1990 for Great Tits; Alatalo et al. 1990 for Collared Flycatcher). Excluding the work of Richner et al. (1989) on Carrion Crows, it has not been reported to my knowledge that the small size of not only fledglings but also of adult birds can be ascribed to the growth depression in the nest. In my study, birds born in poor years were on average smaller than those born in normal years (Fig. 2). This implies that there is a remarkable amount of environmental variation in body size which remains after elimination of the smallest and worst-conditioned individuals.

4.3. Female size and reproduction

4.3.1. Clutch size

Females with short tarsi laid slightly but significantly smaller clutches than larger birds. The similar result was shown by Alatalo & Lundberg (1986) in the Pied Flycatcher. In the Great Tit, van Noordwijk et al. (1988) found no correlations between female tarsus length and reproductive traits.

Was the relationship between clutch size and female tarsus length caused by the lasting effect of growth conditions? Although there is no reason to expect a priori the presence of a genetic correlation between clutch size and body size, this possibility can not be excluded theoretically. The effect of growth conditions, however provides a more simple explanation and is supported by the pattern in my data. The positive correlation between females' tarsus length and her clutch size was mostly due to very small females laying small clutches. This could be expected in the case of the adverse effect of poor growth conditions on clutch size. The latter has been demonstrated by Haywood & Perrins (1992) on captive Zebra Finches (*Taeniopygia guttata*) and on wild Great Tits. Effect of growth conditions on the clutch size was also shown experimentally by Schluter & Gustafsson (1993) in Collared Flycatcher. My results agree with those of aforementioned studies and suggest that the lasting effects of the individual's ontogeny upon its reproduction may well occur also in natural circumstances.

I could not reveal significant differences in the relationship between female size and clutch size between urban and rural population even though the difference in the average clutch size between the populations was as large as 2.3 eggs (Hõrak 1993; see also Fig. 3 in this paper). This indicates that the possible effect of adverse growth conditions did not reduce the clutch size to a definable amount but rather shifted it towards the lower limit of the reaction norm.

4.3.2. Laying date

Yearling Great Tits had a significant negative correlation between tarsus length and laying date in 1992. However, the sample size was small (15) and the pattern was evidently not typical since it was not revealed in other years nor in the pooled data.

Given that small birds laid small clutches and small clutches were laid late in the season (Hõrak in prep.), one would also expect small birds to lay late. The latter, however was generally not the case. The possible reason could be that small females reach the condition enabling to start laying more quickly because they need less food to pass the corresponding energetic threshold (Jones 1973, cited in Garnett 1976).

4.5. Implications

The main finding of the present study, i.e. that the small size of breeding individuals can be ascribed to growth depression during ontogeny, is meaningful in relation to the concept of selection against environmental variance of a trait (e.g. Price & Liou 1988, Alatalo et al. 1990). If the non-genetic variation in body size is common, and reproductive traits of individuals are size-dependent, then not only survival selection but also fecundity selection on body size can occur without producing genetic response.

Correlation between female size and clutch size, found in the present study, was in the direction expected by the hypothesis that poor nestling history can have a negative effect on reproduction of the breeding female. Although the effect was slight, this implies for a possibility that breeding performance of individuals affects not only the offspring number but also the next generation's reproductive success. The possibility of such an inter-generational effect deserves therefore more attention in the research on clutch size evolution (see also Andersson 1981, Smith 1988).

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