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PATHWAYS OF SELECTION IN AVIAN REPRODUCTION: A FUNCTIONAL FRAMEWORK AND ITS APPLICATION IN THE POPULATION STUDY OF THE GREAT TIT (*PARUS MAJOR*)

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers referred to by their Roman numerals

I **Hõrak, P. 1994**: Effect of nestling history on adult size and reproduction in the Great Tit. — Ornis Fennica 71: 47–54.

II **Hõrak, P., Mänd, R., Ots, I. & Leivits, A. 1995**: Egg size variation in the Great Tit: individual, habitat and geographic differences. — Ornis Fennica 72: 97–114.

III **Hõrak, P. 1993**: Low fledging success of urban Great Tits. — Ornis Fennica 70: 168–172.

IV **Hõrak, P. & Lebreton, J.-D:** Survival of adult Great Tits in relation to sex and habitat: a comparison of urban and rural populations. (Submitted)

V **Hõrak, P. 1995**: Brood reduction facilitates female but not offspring survival in the Great Tit. — Oecologia 102: 515–519.

VI **Hõrak, P., Mänd, R. & Ots, I:** Identifying the targets of selection: a multivariate analysis of reproductive traits in the Great Tit. (Manuscript)

INTRODUCTION

Life-history theory views the reproductive traits as having been adjusted by evolution to optimize individual fitness. The cornerstone of the theory is the concept of trade-offs, representing the costs paid in the currency of fitness when a beneficial change in one trait is linked to detrimental change in another (Stearns 1989). Two basic trade-offs in life-history evolution are the trade-off between current and future reproduction (Williams 1966) and the trade-off between the number and quality of offspring (Lack 1947, Smith & Fretwell 1974).

Although the theory predicts negative correlations between life-history traits, attempts to demonstrate trade-offs often fail at the level of individuals within population because of inter-individual variation in acquisition and allocation of resources. Van Noordwijk and de Jong (1986) highlighted the role of individual phenotypic quality, demonstrating that the positive phenotypic correlations between life-history traits occur when some individuals spend much on several life-history traits while others spend little. Price *et al.* (1988) and Price and Liou (1989) applied the idea of the inequality of individuals with respect to their phenotypic quality in the models of selection on avian breeding traits, demonstrating that phenotypic plasticity of individuals may obscure the relationship between breeding traits and fitness: whenever a nonheritable trait, such as an individual condition, affects simultaneously both the expression of a character and fitness through separate pathways, a correlation between a heritable trait and fitness can persist at an evolutionary equilibrium (Fig. 1). The concept of selection on the environmental component of a trait therefore suggests that females laying early (and/or) large clutches may be the fittest because selection operates on their phenotypic quality (condition), not necessarily on clutch size or the laying date *per se*. Similar mechanisms have been proposed to explain the lack of response to selection on avian body size (van Noordwijk *et al.* 1988, Alatalo *et al.* 1990) and egg size (Bolton 1991).

The idea about different pathways of selection on reproductive traits is a general concept that has to be tested locally. However, the path scheme in Fig. 1 by itself is not a testable hypothesis since it contains a multitude of alternative scenarios of selection. To formulate explicitly testable hypotheses, the basic concept of different pathways of selection requires practical organizing, i.e. a framework theory to outline which scenarios of selection are relevant at the local level.

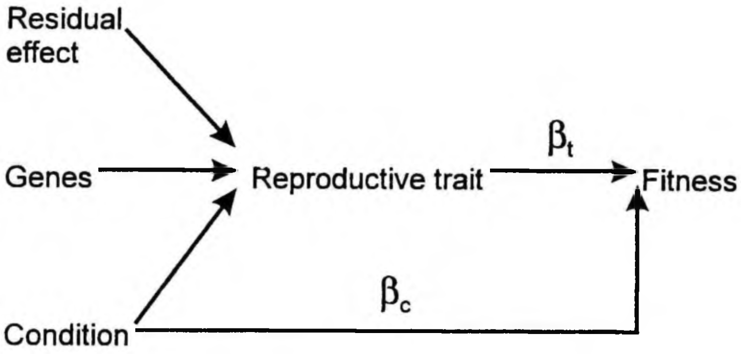

Fig. 1. Relationship between the breeding trait, individual phenotypic quality and fitness (after Price *et al.* 1988, modified). Arrows connect dependent variables (arrowheads) with independent variables. The breeding trait is determined by an additive genetic component, individual's condition (phenotypic quality), and a residual effect. β_t denotes direct selection on the trait, while β_c is a direct effect of the condition on fitness. Thus, fitness is affected by the direct effect of reproductive traits as indirectly influenced by genes and condition (β_t), but also by direct effects of the condition (β_c). Reproductive traits can therefore be potentially subjected to constant directional selection without any evolutionary response because selection acts on the environmentally determined condition of individuals rather than on reproductive traits. For related path models, see also Schluter and Gustafsson (1993), Møller (1994).

In this thesis I present a functional framework for applying the concept of different pathways of selection on avian reproductive traits. For that purpose, I decompose the model presented in Fig. 1 into different path schemes representing alternative scenarios of phenotypic selection. Doing so, I aim at making a clear distinction between different ways in which the phenotypic quality can affect the reproduction of individuals. In this aspect, my approach differs from that of traditional life-history studies which treat the individual's condition merely as a confounding nuisance parameter which has to be eliminated when examining the relationship between reproductive traits and fitness. This, however, does not mean that I will give an explanation of the origin and maintenance of phenotypic variation in the reproductive behaviour of individuals, which is alternative to that offered by concepts of trade-offs and optimization. Rather, my goal is to present a detailed description of optimization mechanisms.

In the first section of the thesis, I will show how the outcome of phenotypic selection depends on the relative importance of different causal links between breeding traits, individual condition (phenotypic quality), and reproductive success. I will describe different scenarios of selection on two avian reproductive traits — clutch size and the date of the initiation of breeding, as well as outline practical considerations for applying this concept to the examination of the phenotypic selection in natural populations. In the second section of the thesis, I will proceed from the framework presented in the first section in an attempt to identify primary targets of selection in the population study of Great Tit.

1. FUNCTIONAL FRAMEWORK

1.1. General concepts and assumptions

The functional framework for describing relationships between individual phenotypic quality, breeding traits and fitness is derived from the general model of Price *et al.* (1988) (Fig. 1) by decomposing it into eight submodels (Fig. 2). The decomposition of the initial model proceeds from the assumption that causal links between different components of the path diagram might be of different importance and, therefore, several alternative combinations of breeding trait, condition and fitness may be realized. Each of these combinations involves a specific predictions in respect of selection (and response to selection) on breeding traits and therefore, they are labelled as different scenarios of selection. For the sake of better understanding, these scenarios can be thought of as distinct, categorical models. In a natural situation, however, I would rather expect them to exist as a continuum resulting in a smooth shift from one scenario to another when some link between the components of the model becomes more (less) important as compared to the others. When defining the system, I proceed from the following concepts and assumptions.

Following Schluter and Gustafsson (1993), I define the individual phenotypic quality as a composite of nongenetic factors affecting the expression of reproductive traits including nutritional state, health, experience and amount of physiological wear-and-tear. Thus, the individual phenotypic quality (also labelled as condition or C) is a joint factor which summarizes all effects of nonrandom determinants of environmental variation in reproductive traits, such as foraging efficiency, parasite load, age, mate and territory quality etc.. Aspects of the condition affecting the reproduction of an individual involve a number of components, starting from short-term variation in nutritional state through to, for example, the lasting effects of growth period on an individual's reproduction.

The individual condition (in a broad sense) varies in parallel to the reproductive effort made. Hence, the relationship between the individual condition and reproductive traits is not necessarily unilateral, since reproductive decisions made in the early stages of the breeding cycle may have a feedback on the individual condition in later stages. These processes are beyond the scope of the present approach and, therefore, I will use the term phenotypic quality in this thesis in a narrower sense, to denote the component of the individual condition which is persistent throughout the breeding cycle (in the sense that its variation is parallel for all individuals). This means that individuals who are in a better condition than others in one stage of the breeding cycle are also in a relatively better condition in other stages. Since both breeding traits under investigation (clutch size and laying date) are female properties, the condition term refers, in fact, to the female phenotypic quality. According to the definition, C is nonheritable and its variation within a population is maintained regardless of phenotypic selection on it.

Reproductive success (labelled as W) is defined as a number of offspring that are produced by a female in a single breeding occasion and recruited into the breeding population. This is not a complete measure of individual fitness (although a rather good approximation in the case of a short-lived species). Therefore, extrapolations to Lifetime Reproductive Success (LRS) will be also made (Section 1.2).

Selection denotes phenotypic selection *sensu* Endler (1986). Populations are assumed not to be in the phase of an evolutionary change of the reproductive traits (T) under investigation.

In what follows, the relationships between the components of the path model in Fig. 2 will be explained on an example of clutch size:

The relationship between C and T in the model denotes the dependence of clutch size on the female condition. I assume here that this effect can only be direct and positive, i.e. all other things being equal, birds do not lay large clutches when their condition is poor or average. The stronger the dependence of T on C, the lower the heritability of clutch size.

The lack of relationship between C and T corresponds to a situation where the female condition does not influence the number of eggs laid. Such a situation arises when reaction norms in a (genetically heterogenous) population are so narrow that a bird in a good condition may lay a still smaller clutch than a bird in a poor condition because both are genetically predetermined to do so. Otherwise, the lack of relationship may arise from the low variation in T or from a situation where all females are in a similar condition before egg-laying. The latter case may occur, e.g. when females adjust rather the onset of laying than clutch size to their condition.

The relationship between T and W (β_t in Fig. 1) denotes a different reproductive success of different phenotypes, i.e. clutch size classes occurring in the form of positive directional, stabilizing, disruptive or oscillating selection.

The lack of the relationship between T and W indicates no selection on clutch size (a flat fitness profile; $\beta_t \approx 0$). This may be the result of the evolution of reproductive rates if other components of fitness (e.g. number of fledglings, condition, life span) contribute significantly more to its variation than the initial number of eggs laid. An effective brood reduction mechanism could lead to such a situation. In this case it is assumed that parents produce marginal offspring to cope with unpredictable variation in the food situation during the nestling period. If food proves short, the size of the brood will be reduced to the level that can be reared. The selection will operate on the adequate ***number of fledglings*** rather than on the ***number of eggs*** laid. If individuals are flexible enough for sufficient brood reduction, then initial clutch size is not necessarily related to final brood size.

The relationship between C and W denotes a dependence of female reproductive success on her condition (β_c in Fig. 1). I presume (as Price and Liou (1989)) that this can only be positive and directional, i.e. all other things being equal, females in a poor condition are not capable to rear more offspring than those in a good condition.

The lack of relationship between C and W means that all other things being equal, females in a different condition do equally well, i.e. there is no ***direct*** effect of the condition on fitness ($\beta_c \approx 0$). Note that this does not exclude the possibility that C could affect fitness through some breeding trait.

1.2. Scenarios of selection on clutch size (Fig. 2)

1. (CT, TW, CW). According to the first model (termed here as the model of Price and Liou), birds in a good condition lay more eggs than those in a poor condition and, at the same time, these birds recruit also more offspring. The independent effect of T on W in the model can be interpreted as follows:

1) Birds who lay large clutches are the fittest not only because they are in the best condition but also because a large clutch *per se* is advantageous (not only the quality but also the quantity of young is selected for). For instance, females lay as many eggs as their condition allows but laying even a larger clutch would be more beneficial since, e.g. feeding conditions allow to rear more young.

2) Though birds in the best condition lay large clutches, being also the fittest, a *large* clutch *per se* is not necessarily selected for (e.g. due to a trade-off between the quality and number of the young).

The model therefore predicts positive directional or stabilizing selection on T. In the first case the largest clutches are the most productive, and a positive directional selection on T may persist without inducing an evolutionary change of average T in a population. This is the situation modelled by Price and Liou (1989). In the second case, an intermediate most productive clutch size exists as a balance resulting from positive directional selection for good-conditioned phenotypes laying large clutches and negative directional selection against large clutches *per se*. The CW relationship in the model excludes the possibility of apparent negative directional, disruptive or fluctuating selection on T, since otherwise, birds in a poor condition (who cannot lay large clutches due to the CT relationship in the model) should be selected for.

2. (CT, CW). The second (apparent selection) model differs from the previous one by the lack of actual selection on clutch size. This is an extreme extrapolation of Price and Liou's model, which considers T simply as a covariate in basically important CW relationship. This means that the initial number of eggs (quantity) is less important than the fact that birds in a good C produce the young with better chances of survival (quality), while quantity and quality just correlate (CT relationship). If there exists adaptive brood reduction then the model predicts that birds who laid the largest clutches may fledge fewer (or equal number of) young when compared to smaller-clutched birds, but still recruit more offspring. Therefore, feeding conditions may fluctuate in different

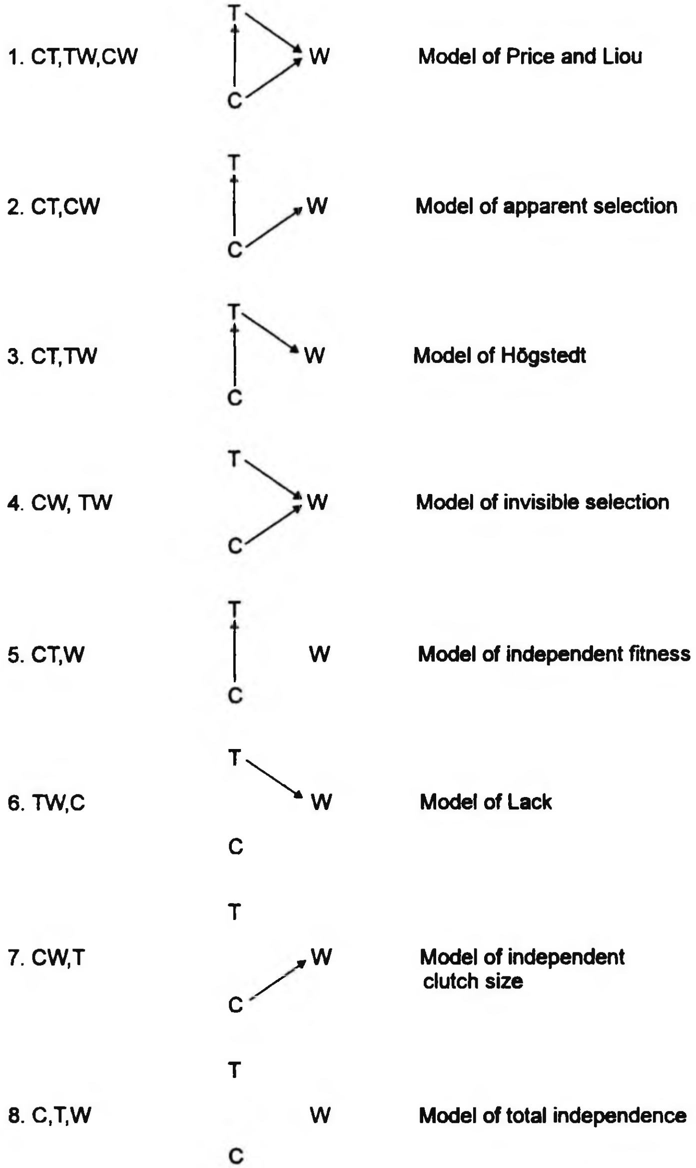

Fig. 2. Path models of relationships between the breeding trait (T), individual condition (C) and fitness (W) presented as eight different scenarios of selection. Pathways of the genetic component and residual effect are as in Fig. 1, they are similar in all cases and therefore not shown here. Arrows connect dependent variables (arrowheads) with independent variables. The lack of connection between variables denotes situations in which causal links between some components of the path scheme are of so small practical importance (as compared to more important, dominating pathways) that they can be regarded as lacking. See 1.1 for details.

years but the "apparent optimal clutch size" does not. The latter is the largest clutch size occurring in the population since CT and CW relationships lead to a positive correlation between T and W. However, selection on T is only apparent which means that the "clutch size term" becomes insignificant in the multiple analysis of selection if some other trait which is more strongly correlated to the individual condition is incorporated into the model.

3. (CT, TW). The third (termed as Högstedt's) model states that females in a good condition lay large clutches while selection on C is (entirely) mediated through selection on T. The latter does not need to be positive directional (since the CW relationship is lacking in the model, birds in the best C who lay the largest clutches need not be selected for as in previous models). Therefore all types of selection on T are possible. The model also allows that selection may indirectly act against females in a good condition.

4. (CW, TW). According to the fourth (invisible selection) model, birds in a good condition are the most successful but they do not necessarily lay the largest clutches. Because the clutch size of an individual is independent of its condition, there are both small-clutched and large-clutched individuals among birds in a good as well as in a poor condition. The model predicts that both clutch size and the individual's condition affect fitness but so that there is no persistent directional (neither disruptive or stabilizing) selection on clutch size. This is because, otherwise, also females in poor condition (who are represented among all clutch size classes) would be selected for. Such a situation is not allowed due to CW relationship in the model.

The model fits for a situation in which the direction of selection fluctuates temporally: in general, all birds in a good condition are successful; however, among them, individuals with large clutches do best in good years while individuals with small clutches do best in poor years. Birds in a poor C do always worse regardless of their clutch size. Note that although selection pressure fluctuates temporally (yearly), the selection differential does not necessarily differ from zero in individual years. This is because part of small-clutched birds do worse than larger-clutched birds even in poor years, while also part of birds with large clutches (the ones in a poor C) always do poorly. For visualizing selection on clutch size, one has to incorporate some measure of female phenotypic quality in the multiple analysis of selection. In this case, a significant "clutch size*condition" interaction term is expected in the statistical model, because the fitness value of clutch size depends on the condition of an individual.

5. (CT, W). The fifth (independent fitness) model states that the female condition affects clutch size but neither of them affects breeding success, since the model assumes no selection on T. The simplest interpretation of such a situation is the presence of an effective brood reduction mechanism. The difference from the apparent selection model is that birds in the best C (who lay the largest clutches) need not be the fittest ones, i.e. there is no "apparent optimal clutch size" and no "apparent selection" on clutch size.

6. (TW, C). The sixth (Lackian) model shows selection on clutch size but no CT relationship. The model differs from Högstedt's model by the lack of dependence of T on C and, therefore, a persistent positive selection differential on T cannot be maintained in populations at evolutionary equilibrium. Thus the model predicts that stabilizing selection should lead to a situation where the modal clutch size is the most productive — a Lackian prediction valid for cases where there exists no "average genotype" in a "better than average condition". In fact, Högstedt's (1980) contribution to Lack's hypothesis of clutch size optimization was to derive the third model from the present one.

The model also allows yearly fluctuating selection pressure which is likely to lead to the highest fitness for the long-term geometric mean clutch size (Gillespie 1977, Boyce & Perrins 1987). The difference from the outcome of the "invisible selection model" is that in the "Lackian model", a positive or negative directional selection on clutch size should be detectable in single years in univariate analysis, because relationship between clutch size and fitness is not confounded by the effects of the female condition.

7. (CW, T). The seventh (independent clutch size) model predicts no selection on T but birds in the best C do best. Since C does not influence T, good-conditioned birds are present in all clutch size categories. Brood reduction is again expected.

8. (C, T, W). The eighth (total independence) model shows the lack of relationships between clutch size, female condition and fitness.

Cost of reproduction

In the preceding approach the possibility of parental reproductive costs was not considered. Recruitment rate was used as a measure of reproductive success and, therefore, conclusions are restricted to the extent to which another main component of fitness, the reproductive life span, influences LRS. If parental cost of reproduction affects clutch size variation within a population, then the main prediction is that LRS of all clutch size categories is equal: by definition (e.g. Nur 1986, 1987), different clutch sizes are expected to reflect different reproductive tactics (small clutch — long life span, large clutch — short life span) but different tactics must have an equal outcome (fitness pay-off) for a population to be at an Evolutionary Stable State (ESS)[1]. Equality in pay-offs comes about through trade-offs between fecundity and survival; and because of the pay-offs to different tactics are the same, evolutionary stability is maintained. For these trade-offs to account for interpopulational variation in clutch size, differences among reproductive decisions of individuals must involve a genetic component (cf. Reznick 1985). This means that if the cost of reproduction is expected to account for intrapopulation clutch size differences, then trade-off between fecundity and survival of the parents is merely a necessary but not sufficient precondition. The presence of individuals possessing different tactics in the same population is also obligatory.

Using path schemes in Fig. 2 for the detection of the role of parental reproductive costs in clutch size variation within populations demands that both recruitment rate and female reproductive life span are used as criteria of fitness in the models. By definition, the necessary precondition is the lack of association between clutch size and LRS in stable populations. If this is met then parental cost will be manifested by the absence of a positive correlation between clutch size and female survival, and by the presence of positive correlations between clutch size and recruitment rate.

There are two models which allow above situation: model of Price and Liou and Högstedt's model.

For Högstedt's model the demonstration of reproductive costs is the easiest. The model allows a negative correlation between clutch size and female survival and a positive correlation between clutch size and recruitment rate. The possible trade-off is not obscured by the direct effect of the condition on fitness (lack of CW relationship in the model).

However, such situations are probably hardly realistic, since the phenotypic quality of individuals can affect either some or all life history traits simultaneously, so that the exhibition of reproductive costs is obscured. It means that the female condition affects both clutch size and female survival, and this is what is expected in the case of the Price and Liou's model.

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[1] Here ESS refers to an evolutionary stable state which consists of a stable mixture of genotypes

In this case the relationship curve between female survival and clutch size is concave as a result of trade-off between these traits on one side and a positive effect of C on both T and W on the another side. If the model fits the data then the role of reproductive trade-offs in intrapopulation clutch size variation can be manifested. Otherwise, the cost may be present but it does not necessarily have a causal relationship to clutch size differences within a population.

1.3. Implications

1.3.1. Individual optimization of clutch size

Distinction between different pathways of selection might be useful for clarifying some basic concepts in clutch size theory such as e.g. the individual optimization hypothesis which can be decomposed into four different scenarios of selection.

The individual optimization hypothesis was derived from the ideas of Lack (1954, 1966), chiefly by Perrins and Moss (1975), Högstedt (1980) and Nur (1986, 1987). It suggests that individual females lay that size of clutch from which they can maximize recruitment. By definition, the individual optimization hypothesis can be validated by testing whether individuals laying n eggs do best (better than if they had laid, say, n-1 or n+1 eggs instead). The value of n is not necessarily the same for all individuals.

The problem with the individual optimization hypothesis is that there are different causes why a female may lay the number of eggs which corresponds to her ability to rear the young. According to Liou *et al.* (1993) individual optimization of clutch size involves different causal mechanisms.

First, a decision to produce fewer eggs might be an adaptive response for individuals in a low condition, since individuals in a different condition have different costs of producing an equivalent number of young (adaptive explanation).

Second, the condition of an individuals may constrain both their ability to produce eggs and ability to rear offspring (nonadaptive explanation).

The output of both paths is identical in the sense that selection favours laying such a number of eggs that maximizes reproductive success (optimization of clutch size), while also individuals in the best condition are favoured. The critical point in making a distinction between the adaptive and nonadaptive explanation is whether the condition of the laying female sets constraints on her clutch size.

According to path schemes in Fig. 2, the nonadaptive explanation corresponds to the model of apparent selection, assuming selection on the female condition, dependence of clutch size on condition, and apparent but not actual selection on clutch size. Adaptive clutch size optimization in its purest form is in accordance with Lack's model in Fig. 2, while the model of Högstedt and that of Price and Liou allow both constraints and optimization to determine the clutch size of an individual. The difference between these is that in the model of Price and Liou, the female condition acts as a constraint limiting both the number of eggs laid and reproductive success, while in the Högstedt model, the independent effect of the individual's condition on fitness is lacking. These models can be interpreted as different outcomes of clutch size evolution and therefore worth distinction: if Price and Liou's model rather than Högstedt's model fits the data, then the contribution of both constraints and optimization is relatively equal. If Högstedt's model fits the data better, then optimization is prevailing.

1.3.2. Brood reduction

Half of the path schemes presented above did not predict selection on clutch size. Thus, if the models of apparent selection, independent fitness, independent clutch size, or total independence fit the data, there is a reason to expect life-histories in which the initial number of eggs laid by the female is not of decisive importance with respect to her fitness perspectives. Such a situation can arise when individuals are capable of flexible brood reduction.

The main point of the brood reduction hypothesis (Lack 1947, 1954, 1968, O'Connor 1978) is that producing a marginal chick(s) is parental adaptation for contending with environmental unpredictability: a full brood can be reared when food is plentiful but when it is scarce, the number of offspring will be reduced to what can be reared. It has also been found that progeny choice, food caching, and insurance against the unexpected early failure of offspring are likewise possible and not mutually exclusive explanations for the evolution of clutches larger than the parents can normally rear (Forbes 1991 and references therein).

If individuals possess an ability for flexible brood reduction then there will exist no single optimal clutch size for a population or individual, but the target of selection is clutch size together with parental ability to adjust it downwards (i.e. to reduce the brood to an adequate size when necessary). Note that although the overproduction of eggs is expected, this innately does not lead to the selection for large clutches because large broods might be more difficult to reduce to an adequate size.

In numerous taxa (e.g. some eagles, cranes, boobies, pelicans and penguins) brood reduction is a widespread and obligate strategy (see e.g. Forbes 1991 for references). The problem becomes more interesting if one detects the best fit of the model which predicts no selection on clutch size in the species not belonging to obligate brood reductionists. A significant fit in the case of a model allowing no selection on clutch size in situations where brood reduction does not occur suggests that some component of individual fitness other than the number of fledglings raised, clutch size, or the female life span is of crucial importance. No doubt that this is most likely the female condition if apparent selection or independent clutch size models hold. Such a result for life history evolution would be in accordance with popular interpretation of Fisher's fundamental theorem which predicts minimal heritability in traits most closely related to fitness (see e.g. Falconer 1989).

The situation is more complicated if there is no efficient brood reduction but independent fitness or total independence models fit. This would suggest that some other (possibly random) fitness component is more important than brood size, clutch size, parental survival, or condition.

1.4. Selection on breeding dates

Previous sections described different pathways of selection on avian clutch size, individual phenotypic quality and their combinations. The concept of selection on parental phenotypic quality, however, has a broader meaning and it can be used for distinguishing between targets of selection also in the case of other reproductive traits which are both genetically and environmentally determined, such as e.g. the date of initiation of breeding.

In birds of the temperate zone, clutch size and other measures of reproductive success typically decline as the breeding season progresses (see Klomp 1970, Daan *et al.* 1989, Meijer *et al.* 1990, Briggs 1993, Crick *et al.* 1993 for reviews). This has lead several authors to suggest that natural selection generally favours earlier breeding dates, e.g. because food for nestlings decreases seasonally (Lack 1966, Perrins 1970), or because late-breeding parents have to avoid stress just prior to moult and/or migration (Hussell 1972). Since several studies have shown moderate to high heritabilities for the breeding date in natural populations (see e.g. van Noordwijk *et al.* 1981), there arises a question why selection has not induced the birds to evolve earlier breeding. A solution for this paradox was suggested by Price *et al.* (1988) who developed a quantitative-genetic model showing that directional selection for early breeding can persist at evolutionary equilibrium if a nonheritable trait, such as the individual condition (nutritional state) affects simultaneously both the date of initiation of breeding and fitness through separate pathways (Fig. 1 in Price *et al.* 1988 and in this thesis).

Analogously to the case of clutch size, one may assume that in different situations, some pathway of selection may be more important than others, and decomposing the initial model would enable to make a clearer distinction between the scenarios of selection on the breeding dates of birds. Substituting the term "clutch size" (T) in Fig. 2 with "breeding date" gives 8 different path schemes for the description of relationships between individual phenotypic quality, breeding time and fitness. The relationships between the components of path schemes can be interpreted analogously to these described in Section 1.1. (CT relationship means that individuals in a good condition lay earlier than others, and TW relationship denotes any kind of selection on breeding dates).

Using the path schemes of Fig. 2 for interpreting the scenarios of selection on breeding dates, however, requires a somewhat different approach than the one used in the case of clutch size. This is because the timing of breeding is not directly related to the initial number of offspring and, therefore, unlike in the case of clutch size, concepts of trade-offs between offspring number and quality, and between current and future reproduction cannot be applied for the interpretation of path schemes.

The similarity between the cases is that, analogously to the selection for individuals with large clutches, early breeders may be the fittest because of their superior phenotypic quality, or because the breeding time *per se* has a direct effect on reproductive success, or both.

Scenarios of selection

1. (CT, TW, CW). According to the first model in Fig. 2, individuals in a good condition breed early and have high breeding success both because of the direct effect of condition on their brood-rearing ability and the existence of some optimal breeding time within the season.

The model generally predicts positive directional selection for early breeding. CT and CW relationships exclude the possibility of negative directional, disruptive or fluctuating selection on the laying date because, otherwise, late-breeding individuals in a poor condition should be selected for. Thus the selection differential for early breeding persists without producing an evolutionary response as described by Price *et al.* (1988).

When optimal breeding time varies between years in an unpredictable manner, selection may sometimes act against the earliest breeders. The model predicts that in years favouring late breeding, females with an intermediate breeding date are the most fecund as a result of directional selection for good-conditioned females laying early and counteracting directional selection against early breeding *per se*.

2. (CT, CW). The second, apparent selection model, states that individuals of the best phenotypic quality are the earliest breeders and also the most fecund. Early breeding *per se*, however, is not the cause of their highest reproductive success. Such a situation occurs when the individual's condition is the most important determinant of its reproductive success and the effects of external factors are weak. Since the model does not assume a seasonal pattern in offspring survival perspectives, there arises a question why females with the best brood-rearing ability breed earlier than the others. One possible explanation is that early breeding may enhance parental fitness independently of that of offspring. For instance, an early onset of laying may enable multiple breeding attempts per season. This solution holds for single-brooded species as well, since in the case of nest failure, renesting is possible only within the range of the breeding season, and therefore, late breeders face greater risks of being deprived of time for repeat breeding. This would create selection pressure for breeding as early as the female condition allows in order to match the season, even when offspring fitness perspectives within the season are constant (lack of TW relationship).

Again, the model predicts positive directional selection for early laying but no evolutionary change in the population mean laying date. The true target of selection is individual phenotypic quality, not early laying *per se*, and therefore, there is no independent effect of the laying date on fitness.

3. (CT, TW). According to the third model, individuals in a good condition start laying early (CT relationship) but they are not necessarily the fittest because the CW relationship is lacking. Therefore the model allows any kind of selection on breeding dates. Analogously to the third model for clutch size, the model also allows indirect selection against individuals in a good condition (e.g. if unpredictable deterioration of weather conditions hits the earliest, but not late breeders).

4. (CW, TW). The fourth model assumes selection on the laying date and selection for individuals in a good quality but the independence of the onset of breeding on individual quality. The model predicts fluctuating selection pressure for breeding dates, on a similar ground as the fourth model for clutch size: in different years selection may favour either early or late breeding. The model excludes the possibility of directional, stabilizing, or disruptive selection since there are good-conditioned individuals among both early and late breeders. Because of CW relationship, these individuals are never selected against but do always well, regardless of whether they breed early or late.

5. (CT, W). The fifth model assumes that individuals in a good condition lay early but breeding success is independent of both, the laying date and the individual condition. Analogously to the second, apparent selection model, selection for matching the breeding season may be the cause of the CT relationship. Since CW relationship is lacking, some other breeding trait (e.g. clutch size) is expected to affect reproductive success independently of the individual condition and the breeding date.

6. (TW, C). The sixth model assumes that the laying date is independent of the individual's condition but is causally related to breeding success. Analogously to the Lackian model for clutch size, the stabilizing or fluctuating selection on breeding dates is expected. Since CT relationship is lacking, directional selection for the laying date cannot persist at equilibrium but should lead to an evolutionary change in the population mean laying date.

7. (CW, T). According to the seventh model, individual phenotypic quality determines breeding success independently of the laying date.

8. (C, T, W). The total independence model: analogously to the fifth, independent fitness model, selection on some trait other than the individual condition and laying date is expected to affect reproductive success.

1.5. Practical considerations

1.5.1. Measuring selection on individual phenotypic quality

In previous chapters of the thesis a functional framework was presented for describing eight different pathways of selection on two avian breeding traits. To apply this framework in the study of phenotypic selection in natural populations, one has to measure both selection on such a component of the female condition which is persistent during breeding and relationship between this component of condition and breeding traits.

Although obtaining direct measurements of female phenotypic quality is hardly a realistic task in field studies, some approximation to this dimension is possible since selection on the individual's condition can be detected in the multiple analysis (see e.g. Lande and Arnold 1983, Mitchell-Olds and Shaw 1987) of fitness effects of different reproductive traits.

Due to common covariance with condition, the contribution of different reproductive traits to fitness has an overlapping component. This component can be detected in multiple analysis: if the effects of different reproductive traits on fitness are mutually exclusive, then the true determinant of fitness is the third factor which correlates with both breeding traits and fitness. By definition, this trait is expected to be a condition (phenotypic quality) of a breeding individual, i.e. the sum of all nonrandom determinants of environmental variation in reproductive traits. This means, too, that the most condition-dependent trait included in multiple analysis should eliminate condition-dependent fitness effects of other traits. Alternatively, if traits affect fitness independently, then their effects in multiple analysis must remain significant. It is important to note that possibilities for the interpretation of multiple selection analysis are limited since it is difficult to distinguish whether a condition affects fitness proximately (*sensu* β_c), or through some unmeasured reproductive trait. This question is, however, of less practical importance as compared to the (answerable) question whether the effects of breeding traits of fitness are independent or not.

Including simultaneously many traits, for example, in multiple regression, reduces the statistical power of analysis. Therefore, increasing the probability of obtaining true targets of selection by the inclusion of more traits in the analysis must be based on the previous knowledge of the study system (see e.g. Larsson 1992), which would allow to incorporate only the most condition-dependent traits in analysis. Thus, before providing a multiple analysis of selection, a careful examination of all factors potentially affecting the phenotypic quality of individuals would be useful. Among these, traits correlating with components of condition which are persistent during the whole breeding cycle are of particular interest.

1.5.2. Taking account of gene flow

To understand variation in reproductive traits in an evolutionary context, the possibility that optimal reproductive decisions may be different in habitats of different quality should be taken into account. Gene flow between habitats of different quality may prevent local adaptations. This should be considered in case the functional framework is applied to the examination of phenotypic selection in natural populations.

First, the possibility that reproductive costs can affect clutch size variation within a population assumes an ESS in which a population consists of a continuum of individuals with different, genetically fixed tactics of resource allocation but with similar fitness pay-offs (1.2). The stability of such a system would be difficult to predict in the case of immigration of individuals with different resource allocation rules. Then the path schemes in Fig. 2 are hardly applicable in detecting the role of parental reproductive costs in clutch size variation within a population.

Second, predictions about the direction of and response to phenotypic selection on breeding traits depend on the occurrence of gene flow. This holds especially in the case of the sixth (Lackian) model and the fourth model (of invisible selection) which lack CT relationship suggesting high heritability of reproductive traits under investigation. Therefore, interpopulational variation in traits reflects genetic heterogeneity. If populations are subjected to perpetual gene influx from populations with different optimal clutch sizes or laying dates (possibly a common situation in sink-habitats *sensu* Pulliam 1988), then the predictions based on these models are different from those holding in the case of isolated populations (1.2 and 1.4):

1) The fourth model (of invisible selection) does not necessarily assume temporally fluctuating selection pressure. In the case of gene influx, individuals in a good condition (including the ones with genes for "wrong reproductive decisions") may be more successful than those in a poor condition (but with genes for "right reproductive decisions") because of CW relationship. However, due to TW relationship, individuals in a similar condition but with different "decision rules" possess different breeding success, depending on whether the "decision rule" fits current environment. Thus, there might be successful individuals among birds with large and small clutches (and likewise, among early and late breeders); some of them are successful because of their good condition (although they might possess a suboptimal "decision rule"), while others are successful because they have an inherent "optimal decision rule" for coping with current environment, although they might not be in the best possible trim.

2) The sixth (Lackian) model allows also directional selection, both negative and positive, to occur without inducing a change in the population mean in case individuals from populations with different optima permanently immigrate into the population. In the Lackian model, directional selection is likely to be more easily detected in univariate analysis than in the fourth model because selection

acts directly on breeding traits, and its outcome is not confounded by the effects of female phenotypic quality.

2. CASE STUDY OF THE GREAT TIT

In this section I apply a functional framework on the scenarios of selection in avian reproduction, presented in the first section of the thesis, for describing phenotypic selection in a population study of the Great Tit.

The Great Tit is a small (ca 19 g), mainly insectivorous passerine bird. Great Tits are monogamous and shortlived; only a small proportion of the fledged young reach breeding age, and more than half of those that breed do so only once. The Great Tit is common in the whole Eurasian continent and readily accepts nestboxes for breeding, which makes it a very convenient subject for ecological and behavioral research. Therefore the Great Tit has been used as a model species in many studies in different parts of Europe. The material used in this thesis is mainly collected during 1987–1994 in a long-term study of two Great Tit populations breeding in different (urban and rural) habitats in south-east Estonia. The study areas and method are described in the corresponding sections of original papers (I, II, IV, V, VI).

When examining the scenarios of phenotypic selection in the Great Tit, I will proceed from the practical considerations outlined in section 1.5.1, i.e. I start from the examination of factors potentially influencing the individual condition (I, II). Next, I will examine the possibility of the occurrence of gene flow and its possible causes (III, IV). Thereafter, I will test whether Great Tits are capable of flexible brood reduction (V) and, lastly, make an attempt to distinguish between the targets of selection in the multiple analysis of reproductive traits (VI).

2.1. Results and discussion

2.1.1. Female condition

The original paper I examines the effect of growth conditions on adult size and reproduction in the Great Tit. About 60% of variation in tarsus length (an index of body size) was heritable, but the tarsus length was also sensitive to growth conditions. Cohorts of adults born in poor breeding years had shorter tarsi than those born in normal years. Females with short tarsi laid smaller clutches than larger birds. The positive correlation between the female’s tarsus length and her clutch size was mostly due to very small females laying 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.

In the paper II, the question about the possible correlates of the female condition is addressed in the context of the egg size study. In two (urban and rural) Great Tit populations, clutch mean egg size correlated positively with female mass (independently of body size) in the second half of the nestling period (i.e. about one month after the onset of laying). Since females lose weight in the course of breeding, this result indicates that either females with large eggs were initially heavier, or/and they lost less weight during breeding. This, in turn, suggests that egg size reflects the component of the female condition which is persistent throughout the breeding period. The idea about close relationship between egg size and the female condition was further supported in the analysis of seasonal patterns in egg size. During the period of laying the first clutches, late-breeding females laid small eggs in the urban population. However, the significant relationship between egg size and laying date vanished when the effect of the female residual weight (in relation to body size) was taken into account in the partial correlation. The latter indicates that small eggs in late first clutches reflect the poor phenotypic quality of late-breeding females. It is probably symptomatic that seasonal decline in egg size was revealed only in the urban population breeding in more unfavourable conditions than their rural conspecifics. Under harsh conditions, individuals are likely to experience considerable energetic limitation in their activities, and therefore, differences in their physiological condition will affect reproduction most conspicuously.

In spite of the close relationship with the female condition, egg size was also highly heritable ($h^2=0.81\pm0.28$ SE). A possible explanation could be that nongenetic variation in egg size can nearly entirely be explained by the effects of the female condition and there is almost no random residual variance.

The paper also addresses the question of trade-offs between egg and clutch size, and concludes that these can be revealed as negative phenotypic correlations only under most favourable environmental conditions.

2.1.2. Gene flow

The original paper III attempts to explain the causes of low fledgling success in urban Great Tit populations. Great Tits in five urban study areas located in different parts of Europe fledged consistently fewer nestlings than their conspecifics from neighbouring rural areas, which suggests that average clutch sizes for urban populations are too large to match local breeding conditions. For example, in Tartu only 60% of eggs fledged, while in the neighbouring rural population fledging success was 75%. An analysis of literature data led to the conclusion that the most reliable explanation for the low fledging success of urban Great Tits is the immigration of individuals from richer habitats where the laying of large clutches is not selected against. Possibly, good wintering conditions resulting in enhanced survival attract birds to breed in towns. This idea was further tested in the paper IV, which examines differences in adult survival between urban and rural Great Tit populations in and near Tartu. Using the capture-recapture data of breeding adults and relying on modern methods of survival analysis, it was demonstrated that according to expectations, local adult survival was higher in the urban Great Tit population among both male and female birds.

2.1.3. Brood reduction

The paper V tests whether Great Tits are capable of flexible brood reduction. This problem is of central importance in making a distinction between different scenarios of selection: if the mechanism of brood reduction works efficiently then there will be no proximate selection on clutch size, since broods are always reduced to the adequate size, matching parental ability to provision nestlings (1.3.2). My results did not support the brood reduction hypothesis in its initial, Lackian sense, since partial brood loss was accompanied by a decrease in fledgling weight and recruitment rate. This suggests that in the case of the Great Tit populations studied, brood reduction could hardly be considered a mechanism of the efficient adjustment of brood size to match parental ability to rear viable offspring. Female survival was significantly higher in broods with high nestling mortality in the rural population, suggesting that female Great Tits may be able to reallocate resources for self-maintenance if food appears to be short for the successful raising of the brood.

2.1.4. Pathways of selection

The original paper VI aims at distinguishing between the targets of phenotypic selection in the multiple analysis of three reproductive traits: laying date, clutch size, and egg size. The recruitment analysis of the 5-year data-set for the urban Great Tit population revealed a persistent positive selection differential for egg

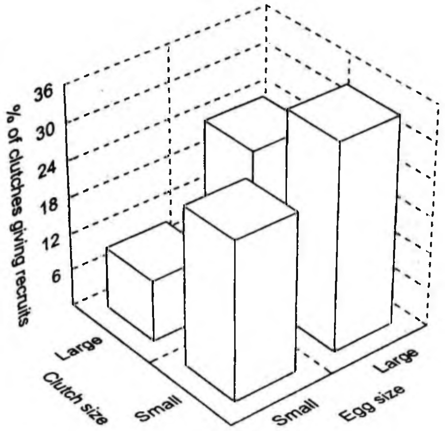

Fig. 3. Local recruitment rate in respect of clutch size and egg size. "Small" clutches and eggs are smaller than the yearly average while "large" ones are greater than the average. See the original paper VI for details.

size only. Great Tits laying large eggs recruited consistently more offspring to the breeding population, independent on their clutch size and laying date. Selection on clutch size fluctuated in direction over years and there appeared a general but weak tendency for early laying to be beneficial.

The mean egg size of a clutch was not related to the occurrence of embryonal or nestling mortality, which points to the possibility that relationship between egg size and recruitment rate was due to the effects of the female quality. This idea was further supported by the results of multiple analysis which revealed that the effect of laying date on recruitment rate disappeared when egg size was incorporated into the model. This indicates that the primary target of selection was not the laying date *per se* but some property of a female which had an effect on both the laying date and egg size. Fitting this result to the scenarios of selection described in the first part of the thesis (Fig. 2 and Section 1.4), suggests the best match of the second, apparent selection model (CT,CW).

Selection on clutch size fluctuated in sign during the five-year period, the net selection differential being close to zero (s=-0.04 SD). Unlike selection on the laying date, fluctuating selection on clutch size occurred independently of the factors affecting relationship between egg size and recruitment rate, since the "clutch size*year" interaction term remained significant after the egg size term had been incorporated into the model. If the clutch size was affected mostly by the phenotypic quality of laying female, I would have expected persistent selection for large clutches. Contrary to this expectation, the selection differential for clutch size sometimes even had a relatively large negative value (s=-0.45 SD in 1989), indicating that individuals with large clutches were not always the most efficient in brood rearing.

Selection against large clutches mainly hit the individuals with small eggs (Fig. 3). Since large eggs most likely reflect the good condition of a laying female (see above), my result possibly indicates that selection on clutch size was mediated through the effects of the female condition: a bird in a good condition can afford to lay a large clutch while a bird in a poor condition would be mistaken in doing so. This suggests the best fit of data with the fourth model (of invisible selection, CW,TW) under conditions of gene influx: assuming that large egg size reflects individual's good phenotypic quality while small clutch size indicates good adaptation to locally prevailing conditions, the result is consistent with the prediction (1.5.2) that some individuals do well because they are in a good condition (birds with large eggs, including those with large clutches in Fig. 3), while others do well because they are well adapted locally (birds with small clutches, including those in a poor condition (with small eggs) in Fig. 3). The idea that some individuals are likely to make wrong reproductive decisions (i.e. to lay too large clutches) is consistent with the expectation of gene influx into the urban Great Tit population (2.1.2). The hypothesis of nonadaptive clutch sizes is further supported by the finding that Great Tits are not capable of efficiently reducing their brood size to match parental ability to rear viable offspring (2.1.3).

My general conclusion is that the functional framework of different selection pathways, presented in the first section of the thesis, is suitable for describing the process of phenotypic selection in the wild.

REFERENCES

Alatalo, R. V., Gustafsson, L. & Lundberg, A. 1990. Phenotypic selection on heritable size traits: Environmental variance and genetic response. — Am. Nat. 135: 464–471.

Bolton, M. 1991. Determinants of chick survival in the Lesser Black-backed Gull: Relative contributions of egg size and parental quality. — J. Anim. Ecol. 60: 949–960.

Boyce, M. S. & Perrins, C. M. 1987. Optimizing Great Tit clutch size in a fluctuating environment. — Ecology 68: 142–153.

Briggs, S. V. 1993. A review of seasonal declines in clutch size of waterfowl (*Anatidae*) in the northern and southern hemispheres. — Ornis Fennica 70: 1–10.

Crick, H. Q. P., Gibbons, D. W. & Magrath, R. D. 1993. Seasonal changes in clutch size in British birds. — J. Anim. Ecol. 62: 263–273.

Daan, S., Dijkstra, C., Drent, R., H & Meijer, T. 1989. Food supply and the annual timing of avian reproduction. — In: Oullet, H. (ed.), Acta XIX Congr. Int. Ornithol. Univ. of Ottawa Press, Ottawa, pp. 392–407.

Endler, J. A. 1986. Natural selection in the wild. — Princeton University Press, Princeton, N. J.

Falconer, D. S. 1989. Introduction to quantitative genetics, 3rd ed. — Longman, New York.

Forbes, L. S. 1991. Insurance offspring and brood reduction in a variable environment — the costs and benefits of pessimism. — Oikos 62: 325–332.

Gillespie, J. H. 1977. Natural selection for variances in offspring numbers: a new evolutionary principle. — Am. Nat. 111: 1010–1014.

Högsted, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territory quality. — Science 210: 1148–1150.

Hussell, D. J. T. 1972. Factors affecting clutch size in arctic passerines. — Ecol. Monogr. 42: 317–364.

Klomp, H. 1970. The determination of clutch size in birds. A review. — Ardea 58: 1–124.

Lack, D. 1947. The significance of clutch size. — Ibis 89: 302–352.

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

Lack, D. 1968. Ecological adaptations for breeding in birds. — Methuen, London.

Larsson, K. 1992. Ecological and quantitative genetic processes in a population of the Barnacle Goose (*Branta leucopsis*). — Ph.D. Dissertation, Uppsala University.

Liou, L., Price, T., Boyce, M. S. & Perrins, C. M. 1993. Fluctuating environments and clutch size evolution in Great Tits. — Am. Nat. 141: 507–516.

Meijer, T., Daan, S. & Hall, M. 1990. Family planning in the kestrel (*Falco tinnunculus*): The proximate control of covariation of laying date and clutch size. — Behaviour 114: 117–136.

Mitchell-Olds, T. & Shaw, R. G. 1987. Regression analysis of natural selection: statistical inference and biological interpretation. — Evolution 41: 1149–1161.

van Noordwijk, A. J. & de Jong, G. 1986. Acquisition and allocation of rescources: their influence on variation in life history tactics. — Am. Nat. 128: 137–141.

van Noordwijk, A. J., van Balen, J. H. & Scharloo, W. 1981. Genetic variation in the timing of reproduction in the Great Tit. — Oecologia 49: 158–166.

van Noordwijk, A. J., van Balen, J. H. & Scharloo, W. 1988. Heritability of body size in a natural population of the Great Tit *Parus major* and its relation to age and environmental conditions during growth. — Genet. Res. 51: 149–162.

Nur, N. 1986. Is clutch size variation in the Blue Tit (*Parus caeruleus*) adaptive? An experimental study. — J. Anim. Ecol. 55: 983–999.

Nur, N. 1987. Alternative reproductive tactics in birds: individual variation in clutch size. — Perspect. Ethol. 7: 49–77.

O'Connor, R. 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide? - Animal Behaviour 26: 79–96.

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

Perrins, C., M. 1970. The timing of bird's breeding seasons. — Ibis 108: 132–135.

Price, T. & Liou, L. 1989. Selection on clutch size in birds. — Am. Nat. 134: 950–959.

Price, T., Kirkpatrick, M. & Arnold, J. 1988. Directional selection and evolution of breeding date in birds. — Science 240: 798–799.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. — Am. Nat. 132: 652–661.

Reznick, D. 1985. Cost of reproduction: an evaluation of the empirical evidence. — Oikos 44: 257–267.

Schluter, D. & Gustafsson, L. 1993. Maternal inheritance of condition and clutch size in the Collared Flycatcher. — Evolution 47: 658-667.

Stearns, S. 1989. Trade-offs in life-history evolution. — Funct. Ecol. 3: 259–268.

Williams, G. C. 1966. Natural selection, costs of reproduction and a refinement of Lack's principle. — Am. Nat. 100: 687–690.

ABSTRACT

Proceeding from the concept of different pathways of phenotypic selection on reproductive traits (selection directly on the traits and simultaneous selection on individual phenotypic quality), I present a functional framework describing eight different scenarios of selection in avian reproductive traits. The first section of the thesis describes how the outcome of phenotypic selection depends on the relative importance of different causal links between reproductive traits, individual condition (phenotypic quality), and reproductive success. Scenarios of selection are exemplified in the case of two avian breeding traits: clutch size and the date of initiation of breeding.

In the second section of the thesis, a functional framework is applied to the detection of primary targets of selection in the population study of the Great Tit. According to the practical considerations outlined in the first section, I examine the factors potentially affecting the condition of reproductive individuals (original papers I and II) as well as the possibility of the occurrence of gene flow and its possible causes (III, IV). I test whether Great Tits are capable of flexible brood reduction (V) and make an attempt to identify the true targets of selection in the multiple analysis of reproductive traits (VI). My results indicate that the functional framework of different selection pathways, presented in the first section of the thesis, can be successfully applied for describing the process of phenotypic selection in the wild. In the urban Great Tit population studied, selection on the breeding date is described by the model of "apparent selection" which predicts that the dependence of the laying date on the female condition and selection on the female condition result in a correlation between breeding time and fitness. However, the apparent effect of breeding time on fitness occurs only because the female condition affects both breeding time and breeding success. Selection on clutch size is described by the model of "invisible selection" according to which both the individual condition and clutch size affect breeding success, while the clutch size of an individual is not affected by its condition.

FENOTÜÜBILISE VALIKU STSENAARIUMID LINDUDE PESITSUSBIOLOOGIAS

Kokkuvõte

Fenotüübilise valiku (*sensu* Endler, 1986) märklauaks võivad olla nii pärilikud tunnused kui ka isendi mittepärilik fenotüübiline kvaliteet e. konditsioon. Viimane omakorda võib mõjutada isendi edukust (*fitness*) nii kaudselt (st. pärilike tunnuste kaudu, mille avaldumine sõltub konditsioonist), kui ka otseselt (joon. 1). Lähtudes eeldusest, et joonisel 1 toodud skeemi põhikomponente (tunnus, konditsioon, edukus) ühendavad lülid võivad olla erineva suhtelise tähtsusega, on eelnimetatud algskeemi põhjal konstrueeritud 8 fenotüübilise valiku stsenaariumi (joon. 2). Dissertatsiooni esimene osa kirjeldab erinevate valikustsenaariumide väljundit kahe sigimisparameetri — kurna suuruse ning pesitsusaja — näitel.

Dissertatsiooni teises osas on eeltoodud kontseptsiooni rakendatud fenotüübilise valiku märklaudade identifitseerimiseks rasvatihase populatsiooniuuringus. Lähtudes töö esimes osas osutatud praktilistest juhistest, uuriti isendi konditsiooni mõjutavaid faktoreid (publikatsioonid I ja II). Käsitleti geenisiiret erikvaliteediliste elupaikade vahel kui potensiaalset takistust lokaalsete adaptatsioonide tekkele, ning geenisiirde võimalikke põhjusi (III, IV). Samuti kontrolliti, kas rasvatihased on võimelised adaptiivseks pesakonna reduktsiooniks (V) ning rakendati mitmemõõtmelist analüüsi valiku tegelike märklaudade kindlakstegemiseks (VI). Leiti, et dissertatsiooni esimeses osas esitatud kaheksast valikustsenaariumist koosnev skeem on otstarbekas fenotüübilise valiku protsessi kirjeldamiseks looduses. Uuritud tihasepopulatsioonis oli valik pesitsusaja suhtes kirjeldatav "näilise valiku" mudeliga, mille kohaselt isendi konditsioon mõjutab nii uuritavat tunnust kui sigimisedukust nii, et tagajärjeks on tunnuse ja edukuse vaheline korrelatsioon. Viimane pole aga põhjuslik, sest tunnusel puudub iseseisev mõju edukusele. Kurna suuruse puhul sobis andmetega "nähtamatu valiku" mudel mille kohaselt nii uuritud tunnus kui ka isendi konditsioon mõjutavad edukust, kuid puudub seos tunnuse ja konditsiooni vahel.

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

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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-

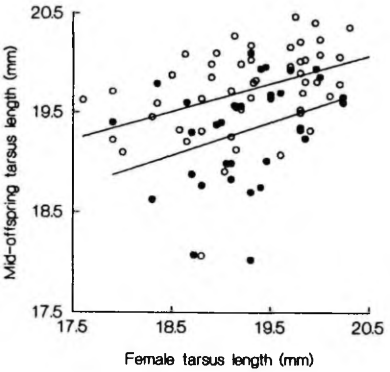

Fig. 1. Plot of mid-offspring tarsus length vs. female tarsus length. Filled symbols represent broods where at least one nestling died in the nest. Data are pooled over three years and two populations. Female tarsus is used instead of midparent tarsus because of larger sample size. Slopes for the lines: 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 ($r = -0.15$, $P = 0.422$, $n = 31$).

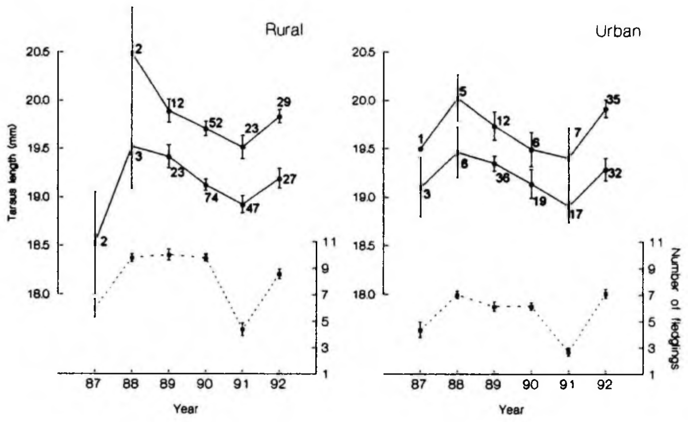

Fig. 2. Tarsus length (mean ± SE) of adult Great Tits plotted against the year of birth (lines, upper = males, lower = females). Data for individuals which were trapped at least three months after leaving the nest. Breeding conditions of a given year (dotted lines) are indicated by the average number 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.

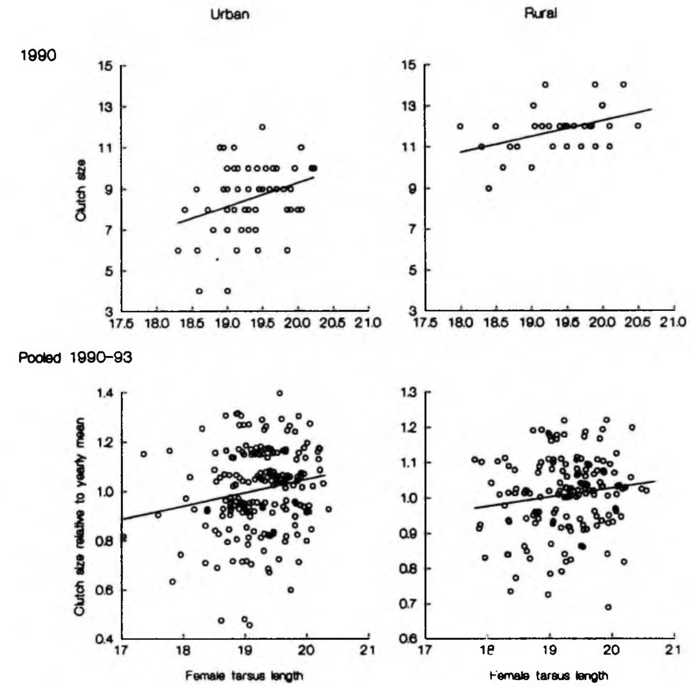

Fig. 3. Relationship between clutch size and female tarsus length in the urban (left) and rural (right) population. Upper: data for 1990; slopes for the lines: $y=-13.67+1.15(\pm0.45)x$, $P = 0.014$, $n = 59$, (urban) and $y=-3.01+0.76(\pm0.29)x$, $P = 0.012$, $n = 34$ (rural). Lower: Pooled data from 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: $y=0.01+0.05(\pm0.02)x$, $P = 0.016$, $n = 204$ (urban) and $y=0.52+0.03(\pm0.01)x$, $P = 0.076$, $n = 156$ (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-

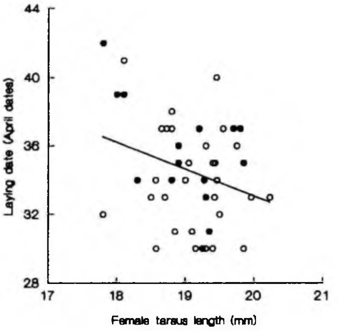

Fig. 4. Relationship between laying date and female tarsus length in the urban population in 1992. Filled symbols: yearlings, open symbols: older birds. Slope for the line: $y=64.271-1.56(\pm0.74)x$, $P = 0.041$, $n = 47$.

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).

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		

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*.

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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References

Alatalo, R. V. & Lundberg, A. 1986: Heritability and selection on tarsus length in the Pied Flycatcher (Ficedula hypoleuca). — Evolution 40:574–583.

Alatalo, R. V., Gustafsson, L. & Lundberg, A. 1990: Phenotypic selection on heritable size traits: Environmental variance and genetic response. — Am. Nat. 135:464–471.

Andersson, M. 1981: Natural selection of offspring numbers: some possible intergeneration effects. — Am. Nat. 112:762–766.

Boag, P. T. 1983: The heritability of external morphology in Darwin's Ground Finches (Geospiza) on Isla Daphne Major, Galapagos. — Evolution 37:877–894.

— 1987: Effects of nestling diet on growth and adult size of zebra finches (Poephila guttata). — Auk 104:155–166.

Boag, P. T & van Noordwijk, A. J. 1987: Quantitative genetics. — In: Cooke, F. & Buckley, P. A. (eds.), Avian genetics: a population and ecological approach: 45–78. Academic Press, London.

Garnett, M. C. 1976: Some aspects of the body size in the Great Tit. — D. Phil. Thesis, University of Oxford.

— 1981: Body size, its heritability and influence on juvenile survival among Great Tits, Parus major. — Ibis 123:31–41.

Gebhardt-Henrich, S. G. & van Noordwijk, A. J. 1991: Nestling growth in the Great Tit I. Heritability estimates under different environmental conditions. — J. Evol. Biol. 3:341–362.

Falconer, D. S. 1989: Introduction to quantitative genetics, 3rd ed. — Longman, New York.

Haywood, S. & Perrins, C. M. 1992: Is clutch size in birds affected by environmental conditions during growth? — Proc. R. Soc. Lond. B 249:195–197.

Hõrak, P. 1993: Low fledging success of urban Great Tits. — Ornis Fennica 70:168–171.

Jones, P. J. 1973: Some aspects of the feeding ecology of the Great Tit Parus major. — D. Phil. Thesis, University of Oxford.

Lack, D. 1954: The natural regulation of animal numbers. — Oxford University Press, Oxford.

Lessells, C. M. & Boag, P. T. 1986: Unrepeatable repeatabilities: a common mistake. — Auk 104:116–121.

Lindén, M. 1990: Reproductive investment and its fitness consequences in the Great Tit Parus major. — Ph. D. Thesis, Univ. Uppsala, Dept. of Zoology.

Moreno, J, Carrascal, L. M., Sanz, J. J., Amat, J. A. & Cuervo, J. J. 1994: Hatching asynchrony, sibling hierarchies and brood reduction in the Chinstrap penguin Pygoscelis antarctica. — Polar Biol. 14:21–30

van Noordwijk, A., J, van Balen, J., H & Scharloo, S. 1981: Genetic and environmental variation in the clutch size of the Great Tit (Parus major). — Neth. J. Zool. 31:342–372.

van Noordwijk, A. J., van Balen, J. H. & Scharloo, W. 1988: Heritability of body size in a natural population of the Great Tit Parus major and its relation to age and environmental conditions during growth. — Genet. Res. 51:149–162.

O'Connor, R. 1978: Brood reduction in birds: selection for fratricide, infanticide and suicide? — Anim. Behav. 26:79–96

Price, T. & Liou, L. 1989: Selection on clutch size in birds. — Am. Nat. 134:950–959.

Richner, H., Schneiter, P. & Stirnimann, H. 1989: Life-history consequences of growth rate depression: an experimental study on Carrion Crow (Corvus corone corone L.). — Funct. Ecol. 3:617–624.

Rising, J. D. & Somers, K. M. 1989: The measurement of overall body size in birds. — Auk 106:666–674.

Schluter, D. & Gustafsson, L. 1993: Maternal inheritance of condition and clutch size in the Collared Flycatcher. — Evolution 47:658–667.

Slagsvold, T. 1985: Asynchronous hatching in passerine birds: influence of hatching failure and brood reduction. — Ornis Scand. 16:81–87.

Slagsvold, T. & Amundsen, T. 1992: Do Great Tits adjust hatching spread, egg size and offspring sex ratio to changes in clutch size? — J. Anim. Ecol. 61:249–258.

Smith, H. G. 1988: Reproductive cost and offspring quality: the evolution of clutch size in Tits (Parus). — Ph. D. Dissertation, Lund University, Sweden.

Smith, H. 1993: Heritability of tarsus length in cross-fostered broods of the European Starling (Sturnus vulgaris). — Heredity 71:318–322.

Svensson, L. 1992: Identification guide to European passerines. — Naturhistoriska Riksmuseet, Stockholm 4th ed.

Wilkinson, L. 1987: SYSTAT: the system for statistics. — SYSTAT, Evanston, Illinois.

Hõrak, P., Mänd, R., Ots, I. & Leivits, A. 1995: Egg size variation in the Great Tit: individual, habitat and geographic differences. — Ornis Fennica 72: in press.

Ornis Fennica 72:97–114. 1995

Egg size in the Great Tit *Parus major*: individual, habitat and geographic differencess

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Factors affecting egg dimensions were investigated in two neighbouring Great Tit populations breeding in a poor urban and a rich rural habitat in southeast Estonia. About 80% of variation in egg size was heritable; however, the effects of female condition were also remarkable. In both populations, females laying large eggs were heavier during the second half of the nestling period, indicating that egg size reflects the component of female condition which is persistent throughout the breeding period. In the urban population, egg size decreased seasonally, most likely because of a poor phenotypic quality of late breeders. In the rural population, large clutches tended to contain small eggs, which points to a trade-off between the size and number of eggs. The analysis of literature data from 30 Great Tit populations revealed no evidence of a trade-off between egg size and clutch size at the inter-populational level, but rather a positive correlation between these traits among populations. Egg size increased with latitude.

1. Introduction

The size of eggs to lay is one of the first problems that an individual bird faces at the beginning of the reproductive cycle. Being hatched from a large egg could potentially be beneficial for a chick; from the viewpoint of the laying female, however, high investment into egg quality (size) might conflict with her own energetic demands and willingness to produce more offspring. Unveiling the causes and consequences of egg-size variation is necessary for understanding the relationship between the number and quality of offspring, a concept, central to the life-history theory.

There is little doubt that reproductive success is related to clutch size, and also some indication that egg size is closely linked to hatchling growth and survival (e.g., Ojanen 1983a, Martin 1987, Grant 1991, Magrath 1992, Potti & Merino 1994, Williams 1994). Considering that heritabilities for egg size, too, are generally higher than heritabilities for clutch size (Boag & van Noordwijk 1987), a trade-off between egg number and size in birds seems a plausible expectation. Most interestingly, however, the evidence for such a trade-off within a bird species has been claimed to be lacking (Williams 1994), and, in fact, often the positive phenotypic correlations between egg and clutch size have been found (see, e.g., Flint & Sedinger (1992) for references). Most likely, the reason for the latter is high inter-individual variation in the phenotypic quality of individuals which, according to van Noordwijk

& de Jong (1986), may lead to positive phenotypic correlations between life-history traits. Theoretically, trade-offs could be revealed by measuring genetic correlations; this, however, would require sample sizes which can seldom be obtained in field studies (see, e.g., Lessells et al. 1989).

To get an insight into the evolutionary causes and consequences of egg-size variation, alternative methods have thus to be used. One possible approach would be the study of relationships between egg and clutch size within habitats of different quality.

In this paper we examine inter-individual variation of egg size in two Great Tit populations breeding in contrasting environmental conditions in urban and rural habitats in southeast Estonia. Breeding conditions for our rural Great Tits are probably the most favourable, as indicated by large clutch sizes (one of the highest recorded for the species) and high fledging success (Hõrak 1993a). We predict that in such a situation, between-individual differences in the total amount of resources spent on reproduction are manifested to a lesser extent because individuals are less constrained by food availability in the habitat. Therefore, if there exists a trade-off between the number and size of eggs, we expect this to be revealed as a negative phenotypic correlation in our rural population. In the urban population, on the contrary, a positive correlation between egg and clutch size seems more probable, since urban Great Tits face far more difficult breeding conditions when compared to their rural conspecifics. In our study area, mean clutch size of urban Great Tits is about two eggs smaller than that of rural birds, while the nestling mortality is high (Hõrak 1993a). It is therefore tempting to suggest that between-individual differences in the phenotypic quality, leading to positive correlations between life-history traits, will be manifested in such a situation.

Another possibility for examination of the trade-off between egg and clutch size would be to study their covariation among populations breeding in different environmental conditions. The average amount of resources available for reproduction is likely to vary with respect to local breeding conditions. Hence, the optimal patterns of resource allocation between the number and quality of offspring may also depend on the locality. In this case, a trade-off at the inter-populational level could be revealed as a negative correlation between mean egg and clutch size among different geographical populations. To test this possibility, we will investigate covariation between egg and clutch size among 30 Great Tit populations breeding over a wide range of conditions in different parts of Europe. To reveal adaptive variation in egg size at the population level, we will also check for the presence of the latitudinal trend in egg size.

The second objective of our study is to extract information about the relationship between egg size and female condition. The simultaneous effect of female condition (nutritional state, phenotypic quality) on both clutch size (or laying date) and brood-rearing ability is a central element in the recent developments of the clutch-size theory (Price & Liou 1989), and in explanations for the evolution of breeding dates in birds (Price et al. 1988). Testing both of these requires the measuring of female condition at different stages of the breeding cycle, which means an examination of correlates of condition. Some authors (e.g., Ojanen et al. 1979, Murphy 1986, Järvinen & Pryl 1989) have shown that egg size might be one such correlate. In this study we test this possibility, again checking whether the relationships are similar in populations breeding in habitats of different quality.

Understanding the selective importance of variation in traits requires knowledge about the genetic basis of variation. Therefore, we will estimate repeatabilities and heritabilities of egg and clutch size in both populations. In line with other studies on egg morphology, we also examine variation in egg shape and linear measurements.

2. Material and methods

2.1. Study area and data sets

Data were collected in two main study areas: in the town of Tartu (human population about 120 000) and in the rural area of Tõrvandi, 5 km from Tartu (58°22'N 26°43'E). Egg measurements were recorded during 1987–1991. When calculating heritabilities for clutch size, we also used an enlarged data set covering eight years from 1987 to 1994. Measurements of adult morphology were started in 1990, so we had a two-year data set for examination of relationships between egg size and female morphology.

The urban study area in Tartu consisted of two large and two small parks (about 22 ha) and avenues with a total length of 9 km. The distance between the nestboxes was 30–40 m. The main tree species were *Tilia cordata, Acer platanoides, Betula pendula, Quercus robur*, and *Populus suaveolens*. All streets in the urban study area bordered on gardens where winter feeding of birds was common.

The rural study area was located at a distance of 5 km from the southern boundary of Tartu and comprised two woods (Tõrvandi and Ropka, 2.5 km apart) surrounded by cultivated land. About two-thirds of the 72 ha area of Tõrvandi wood is covered with a moist birch forest, while the remaining third accounts for a poor mixed spruce forest; the tree species include *Picea abies, Pinus sylvestris, Betula pendula* and *Populus tremula*. The 550 ha Ropka wood is mostly covered with a rich mixed spruce forest with a deciduous understory. In the understory and on roadsides *Corylus avellana* was the most common woody plant. In the rural study area the nestboxes were placed at every 40–50 meters in lines (total length 11 km) running along forest edges and roadsides.

When examining relationships between egg and clutch size we used, in addition, data on three Great Tit populations in southwest Estonia (58°09'N 24°56'E) collected in 1983. The first study site was located in the small town of Kilingi-Nõmme (human population about 2500) with a high density of breeding Great Tits. The second study site at Vanajärve was located about 20 km from Kilingi-Nõmme and consisted mainly of deciduous wood patches and strips among cultivated land. So the first two habitats were roughly analogous to our main urban and rural study areas. The third study site at the Nigula forest was in a large natural mixed forest area with a very sparse Great Tit population (Vilbaste & Leivits 1990).

2.2. Methods

The number of Great Tit pairs breeding in our study area in different years varied from 36 to 61 and from 43 to 93 in rural and urban populations, respectively (the first clutches only). The birds bred in nestboxes mounted at a height of about 2.5 m. The dimensions of the box cavity were approximately 11 × 11 × 30 cm, the diameter of the entrance hole being 3.5 cm. Old nest materials were removed every year.

Nestboxes were checked regularly to determine clutch size and laying date, assuming that one egg is laid every day. Adults were captured during the second half of the nestling period and, since 1988, were aged using plumage characteristics (see Svensson 1992).

Tarsus length was used as a measure of the overall body size of individuals. Although caution is needed for interpreting the single variables as representative to structural size in birds (e.g., Freeman & Jackson 1990), tarsus length is probably the best indicator of size among single external measures (e.g., Rising & Somers 1989, Freeman & Jackson 1990). Tarsi were measured (see fig. 18b in Svensson 1992) with a sliding caliper to the nearest 0.1 mm by the same person (PH). In an attempt to separate mass from structural size, 'condition indices' (residual weights) were computed, as the residuals from linear regressions of weight on cubed tarsus length. Diurnal weight changes were eliminated by the inclusion of weighing time into partial correlations between female weight or condition and egg size. Females were weighed with a Pesola spring balance with a precision of 0.1 g.

When collecting oomorphological data, whole clutches were photographed after the sixth day of incubation using a stand described in Mänd et al. (1986). A graphics digitizer was used for the input of egg contours from photographs, and a special program OMELETTE (Mänd et al. 1986) for smoothing data and for estimating egg dimensions and volume. The volume of an egg was calculated from the contour using trapezoidal integration instead of deriving it from linear measurements. Thus, individual differences in egg shape did not influence the accuracy of volume estimation.

For describing the size and shape of eggs we used four parameters: L = egg length (mm), B = egg breadth (mm), V = egg volume (cm^3), and SPH = sphericity or the egg shape index (B/L). We preferred this ratio to the elongation index (L/B) because, in our opinion, SPH is more a figurative estimate of egg shape as it expresses egg breadth in percentages of egg length. Thus, the larger the SPH, the rounder the eggs. Measurement errors of egg dimensions (coefficient of variation of 10 measurements of the same egg) were negligible as compared to total and interclutch variation (Fig 1). Vari-

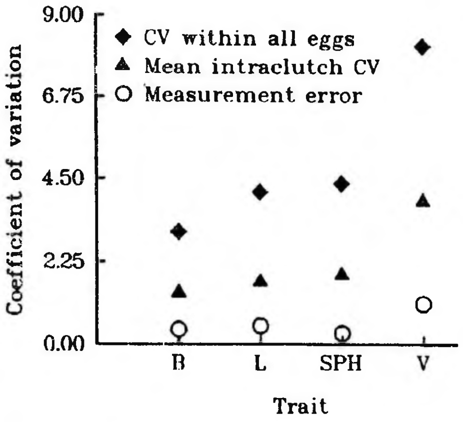

Fig. 1. Variation among egg dimensions.

ation was highest for egg volume, evidently because it is a three-dimensional trait.

To avoid pseudoreplications, the clutch means of egg parameters were used in all statistical analyses, except in Table 1. To minimize the influence of a few aberrant eggs on clutch means, one egg per clutch, the most contrasting to the others by its size, shape or appearance, was excluded before the clutch mean was calculated. The rejection was based on the preliminary visual observation of the researcher, not on the basis of calculated egg measurements.

When comparing data on egg size in literature, we recalculated egg volumes according to the formula $V = \pi/6 \times L \times B^2$, or adjusted it accordingly in case the authors had not presented original data on egg length and breadth. We consider this especially important because several authors have used different coefficients, which leads to considerable differences in estimates for egg volume.

Table 1. Pearson correlation coefficients between egg traits. All are significantly different from zero ($p < 0.0001$) except the correlation between SPH and egg volume. N = 3060 individual eggs.

Trait	r	
	B	V
L	0.27	0.64
B		0.87
SPH		–0.02

Statistical analyses were performed using the SAS statistical package (SAS Institute 1985). All significance levels are for two-tailed tests. When pooled data were used for calculations, clutch size, laying date and egg size were yearly normalized by expressing trait values relative to the annual means of the population. Repeatabilities were calculated according to Lessells and Boag (1987). Heritabilities were estimated from mother-daughter regressions according to Falconer (1989).

3. Results

3.1. Variation and relationships between egg traits

In the analysis of individual eggs, all traits except shape and size were significantly correlated with each other (Table 1), although the correlation between egg length and breadth was rather low. Variation in egg breadth was slightly lower than variation in egg length (Fig. 1; see also SD's in Table 4).

3.2. Repeatability

Repeatability expresses the proportion of the variation between measurements that is due to consistent differences between the objects measured. In quantitative genetics, repeatability provides an upper limit for the degree of genetic determination of a trait (Falconer 1989). It is calculated as the intraclass correlation coefficient, $s^2_A/(s^2 + s^2_A)$, where s^2_A is the among-groups variance component and s^2 is the within-group variance component derived from one-way ANOVA (Lessells & Boag 1987).

Egg dimensions revealed moderate to high repeatabilities in both populations when the first clutches of the same female were compared in different years (Table 2). Repeatabilities were remarkably lower when egg dimensions of individual females were compared within a year. This was evidently because egg volume and linear dimensions tended to increase from the first clutches to the repeat or second clutches. However, the difference was significant at a 5% level only in the case of egg length ($t_{19} = 2.116$, $p = 0.048$), which increased on the average by 0.26 mm (1.5%).

Repeatabilities for linear measurements were generally higher than repeatabilities for egg size.

Egg length had, on the average, about 20% higher repeatability than egg breadth.

Repeatabilities for clutch size in the data set, which was included in calculations with egg dimensions, were significantly different from zero only for the urban population ($r = 0.64, p < 0.0001$). The difference between the populations, however, was probably due to the smaller sample size of the rural population because in the enlarged data set (including data from three additional years) the repeatabilities of clutch size were of a similar magnitude in both populations ($r = 0.59$, $p < 0.0001$, $N = 185$ for the urban population; $r = 0.57$, $p < 0.0001$, $N = 115$ for the rural population).

To estimate the role of breeding territory quality upon the repeatabilities of breeding traits, we calculated repeatabilities for the same nestboxes inhabited by different females in different years. In none of the data sets did the repeatabilities differ significantly from zero. The result is convincing given that our sample sizes in the 8-year data set were rather large (N = 173...285 clutches).

3.3. Heritability

Since between-population differences in egg parameters were in most cases only marginally significant (see below), we found it justified, in order to increase the sample size, to rely on the data pooled over two populations. Heritability estimates for egg traits, as calculated from the pooled data, were high and significantly different from zero, although standard errors were relatively large (Table 3). Heritability estimates were generally close to repeatability estimates. Again, estimates were highly different for egg length and breadth.

In the five-year sample used for calculations with egg traits, the heritability of clutch size was not significantly different from zero in any of the

Table 2. Repeatability of egg size and shape among females. Data from 1987 to 1991. Traits are presented in descending order of repeatability value (average for four measurements). N = number of clutches, n_a = average number of observations per individual. P levels (from ANOVA) if not shown are smaller than 0.001 (in most cases smaller than 0.0001).

Trait	First clutches in different years			First vs. repeat and second clutches in the same year	
	Urban $N = 112, n_a = 2.11$	Rural $N = 43, n_a = 2.15$	Urban+Rural $N = 157, n_a = 2.12$	Urban+rural $N = 40$,	$n_a = 2$
SPH	0.87	0.66	0.84	0.63	
L	0.83	0.74	0.81	0.61	
V	0.64	0.69	0.64	0.34	$p = 0.064$
B	0.62	0.60	0.61	0.35	$p = 0.054$

Table 3. Heritability estimates for egg size and shape based on mother-daughter regressions. Regression coefficients and their standard errors (SE) are doubled. For individuals trapped more than once, trait values are averaged over all their breeding events. Traits are presented in descending order of their heritabilities (pooled data). Data from 1987 to 1991, first clutches only. N = number of clutches.

Trait	Urban, N = 19		Rural, N = 24		Urban + Rural, N = 43	
	h^2 (SE)	p	h^2 (SE)	p	h^2 (SE)	p
L	1.15 (0.45)	0.020	0.95 (0.44)	0.042	1.00 (0.29)	0.001
V	0.84 (0.41)	0.055	0.86 (0.44)	0.067	0.81 (0.28)	0.006
SPH	1.18 (0.50)	0.030	0.29 (0.46)	0.540	0.81 (0.32)	0.016
B	0.89 (0.47)	0.075	0.30 (0.37)	0.429	0.59 (0.29)	0.051

populations. In the enlarged data set covering eight years from 1987 to 1994 the heritability estimate for clutch size was significant for the rural population ($h^2 = 0.66 \pm 0.28$ (SE), $p = 0.021$, $N = 35$), but not for the urban birds ($h^2 = 0.48 \pm 0.38$ (SE), $p = 0.217$, $N = 39$).

3.4. Effects of year, habitat and age

Egg volume, breadth and shape (but not length) revealed slight but significant inter-annual variation (Table 4). Egg volume, length and breadth tended to be slightly larger in the rural population. The differences were, however, only marginally significant except for egg breadth. The average egg shape index (SPH) was similar for both populations. The proportion of variance in egg traits, explained by the year and habitat term together was generally low ($R^2 = 0.02...0.07$). Rural Great Tits laid, on the average, 2.3 more eggs per clutch than their urban conspecifics.

To estimate the effect of female age upon egg parameters, we compared changes in egg traits between the first and second years of breeding for the same females. By the second year of breeding, egg volume had increased on the average by 0.03 cm^3 (1.6%; $t_{35} = 2.099$, $p = 0.043$) and length on the average by 0.12 mm (0.7%; $t_{35} = 2.028$, $p = 0.050$), changes in other parameters being not significantly different from zero.

Table 4. Effect of year and habitat (urban vs. rural) on egg dimensions and clutch size of the Great Tit, estimated from ANOVA. Data from first clutches during 1987–91. In none of the models did 'year*habitat' interaction term differ significantly from zero. Sums of squares (SS) are type III of SAS allowing for an unbalanced design.

Trait	Effect	DF	SS	F	P	R^2	Mean ± SD (Range)	
							Urban, N = 317	Rural, N=218
	Year	4	0.350	6.04	< 0.0001		1.69 ± 0.12	1.71 ± 0.12
V	Habitat	1	0.049	3.35	0.067		(1.3–2.02)	(1.26–2.06)
	Model	5	0.403	5.56	< 0.0001	0.04		
Residual variance		529	7.677					
Total variance		534	8.081					
	Year	4	4.126	2.13	0.076		17.92 ± 0.66	18.03 ± 0.72
L	Habitat	1	1.748	3.61	0.058		(16.05–19.91)	(15.62–20.01)
	Model	5	5.706	2.36	0.039	0.02		
Residual variance		529	255.894					
Total variance		534	261.600					
	Year	4	3.683	7.80	< 0.0001		13.60 ± 0.35	13.68 ± 0.35
B	Habitat	1	0.755	6.40	0.012		(12.46–14.50)	(12.63–14.62)
	Model	5	4.590	7.77	< 0.0001	0.07		
Residual variance		529	62.466					
Total variance		534	67.056					
	Year	4	0.010	2.88	0.022		0.76 ± 0.03	0.76 ± 0.03
SPH	Habitat	1	< 0.001	0.11	0.740		(0.68–0.86)	(0.68–0.84)
	Model	5	0.010	2.31	0.043	0.02		
Residual variance		529	0.453					
Total variance		534	0.463					
Clutch	Year	4	54.704	6.13	< 0.0001		8.80 ± 1.66	11.10 ± 1.30
size	Habitat	1	634.094	284.26	< 0.0001		(3–12)	(7–14)
	Model	5	695.768	62.38	<0.0001	0.39	N = 297	N = 206
Residual variance		497	1108.63					
Total variance		502	1804.40					

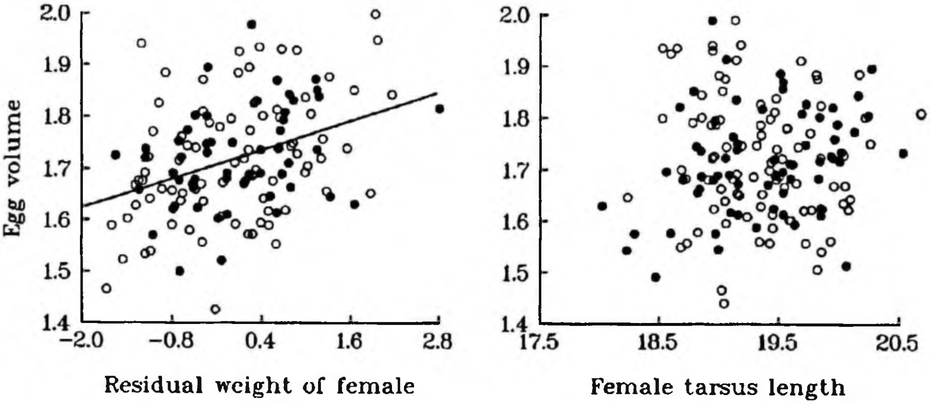

Fig. 2. Relationship between egg size and female condition (left), and between egg size and female size (right). Pooled data for 1990–91. ○ – urban population, ● – rural population. Slope for the line, calculated on data pooled over urban and rural population: $y = 1.718(\pm 0.009) + 0.046(\pm 0.010)x$; $p < 0.0001$, $N = 142$, $R^2 = 0.14$.

3.5. Effects of female condition and size

In both populations females laying large eggs were in a better condition (i.e., relatively heavier) in the nestling stage (Fig. 2). The partial correlation coefficient (adjusted to weighing time) between egg volume and the residual weight of a female was 0.35 ($p = 0.010$, $N = 56$) for the rural population and 0.43 ($p < 0.0001$, $N = 86$) for the urban population. Also, female weight revealed a similar relationship with egg size ($r_{partial} = 0.41$ for both populations).

We found no significant relationship between egg volume and tarsus length in either of the populations when the data were pooled for 1990 and 1991 (Fig 2). Examining the years and populations separately, however, revealed that small females laid larger eggs in the urban population in 1990 ($r = -0.29$, $p = 0.049$, $N = 46$).

3.6. Seasonal variation in egg size

Egg volume declined seasonally in the urban population when data were pooled over five years (Fig. 3; $r = -0.16$, $p = 0.006$, $N = 295$, both variables yearly normalized). For individual years, the pattern was significant only in 1991 ($r = -0.31$, $p = 0.012$, $N = 64$). Since we had female weight data for 1991, it was possible to test whether the seasonal decline in egg size could be ascribed to the poorer condition of late-breeding females. When the residual weight of the female was kept constant in the partial correlation, the relationship between egg size and laying date became insignificant: $r_{partial} = -0.15$, $p = 0.350$, $N = 40$ vs. $r = -0.36$, $p = 0.018$, $N = 40$ for ordinary Pearson correlation (sample sizes are smaller than in the previous analysis because morphometric data for all females were not known). For the rural population we found no seasonal changes in egg size.

3.7. Egg size and clutch size

Egg size decreased with increasing clutch size in the rural population of Tõrvandi (Fig. 4). The correlation between them was, however, only marginally significant in the pooled data ($r = -0.12$, $p = 0.080$, $N = 206$, both variables yearly normalized). For the individual years, the correlation between egg size and clutch size was significant in 1988 and nearly so in 1991. The latter relationship became clearer when female weight was kept constant in the partial correlation ($r_{partial} = -0.41$, $p = 0.024$, $N = 23$).

In the urban population of Tartu we found no consistent relationship between clutch and egg size, either for individual years or for pooled

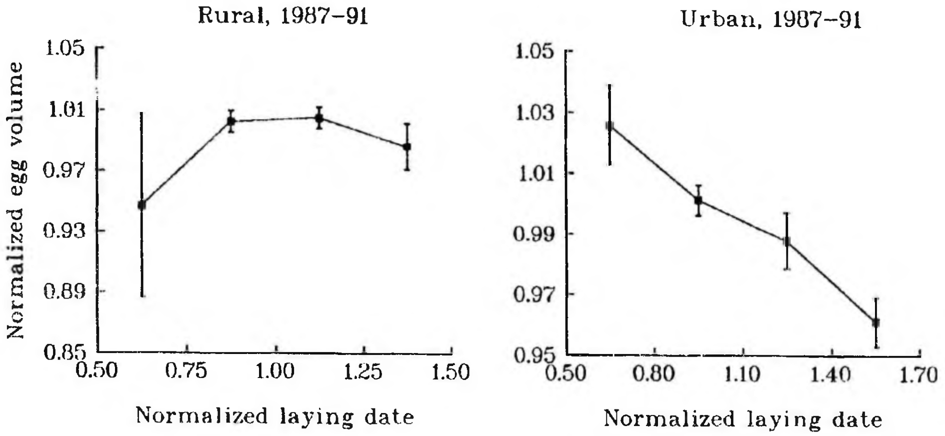

Fig. 3. Seasonal variation in egg size. Laying date and egg size are normalized by dividing the individual values to yearly averages for first clutches (i.e., expressing them in percents of yearly mean). Vertical bars denote standard errors. Grouping of data on X-axis bases on the division of total range of observations into four equal parts. Only data from first clutches are used.

data, despite the larger sample size (297 observations).

In the case of Great Tit populations from southwest Estonia, we found a negative correlation between egg and clutch size in the rural population at Vanajärve (Fig. 3). Great Tits breeding in a large forest at Nigula and in the urban population of Kilingi-Nõmme revealed no consistent relationship between egg and clutch size (r = –0.093, p = 0.733, N = 16 and r = 0.07, p = 0.500, N = 93, respectively).

3.8. Inter-populational trends

Eggs tended to be larger in populations with high average clutch sizes (Fig. 5). The relationship between egg and clutch size was distorted by three observations (1, 29 and 30) which had a profound effect on the regression (absolute values of Studentized residuals > 2). When these aberrant data points were excluded from the analysis, a positive correlation between egg and clutch size at the inter-populational level was significant (r = 0.42, p = 0.028, N = 27).

Egg size increased towards the north (Fig. 6). A single observation (# 30) had a large Studentized residual (–2.9); however, the relationship was still significant when this point was omitted from the analysis (r = 0.49, p = 0.009, N = 29).

Further analysis revealed that the positive correlation between egg and clutch size might have been caused by the latitude effect. The partial correlation coefficient (adjusted for latitude) between egg and clutch size was not significant at the 5% level ($r_{partial}$ = 0.34, p = 0.092, N = 27), while partial correlation between egg size and latitude (adjusted for clutch size) still was significant ($r_{partial}$ = 0.48, p = 0.020, N = 29).

4. Discussion

4.1. Egg size

4.1.1. Genetic variation

Our estimates for the repeatability of egg size in the first clutches were relatively high (0.64...0.69), and similar to those recorded in other Great Tit studies (Jones 1973 cited in van Noordwijk 1987): r = 0.72; Ojanen et al. 1979: r = 0.49...0.62; van Noordwijk et al. 1981: r = 0.59...0.80. However, the repeatability of egg size (and linear measurements) was remarkably lower when the repeat and second clutches were compared to the first clutches of the

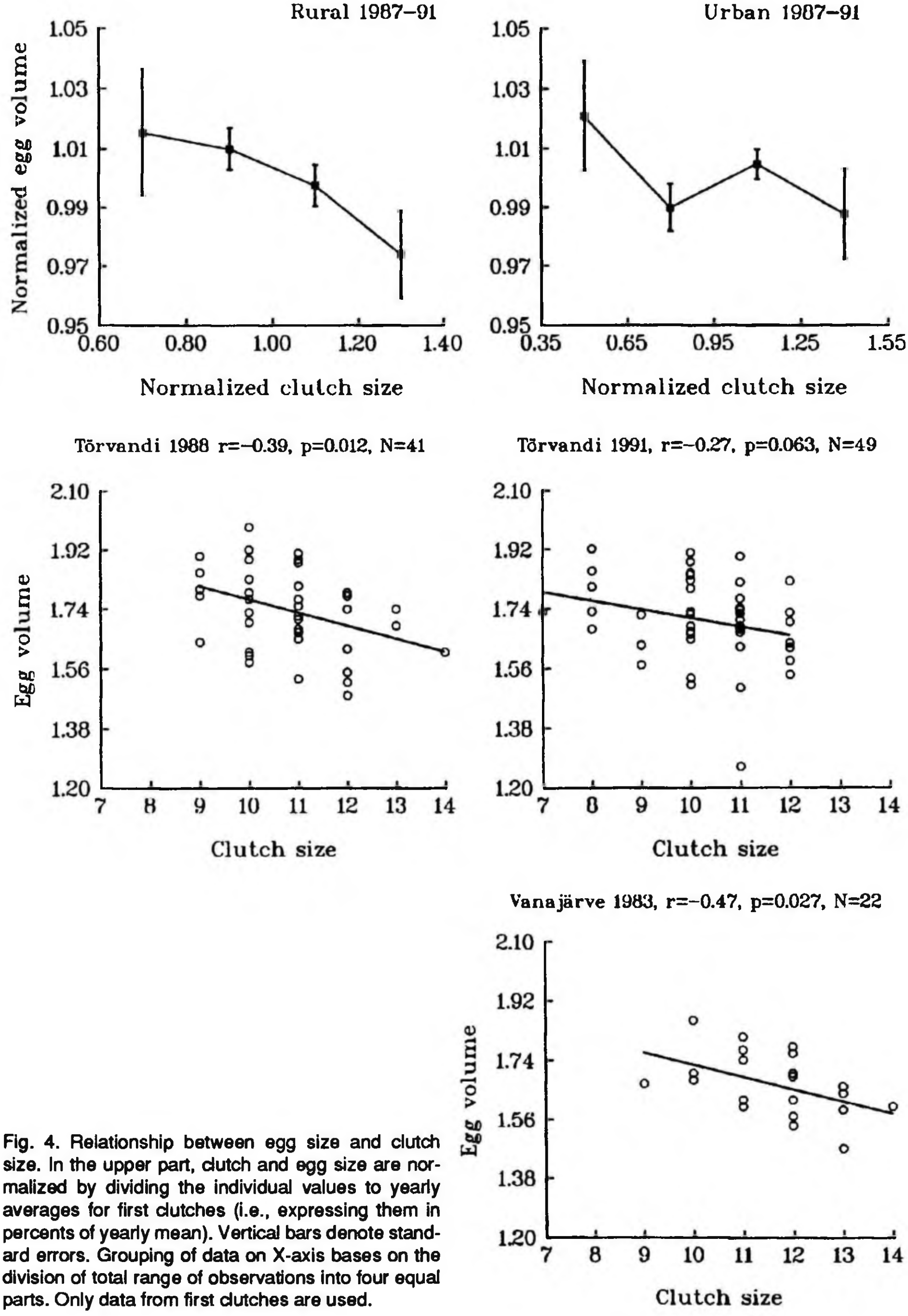

Fig. 4. Relationship between egg size and clutch size. In the upper part, clutch and egg size are normalized by dividing the individual values to yearly averages for first clutches (i.e., expressing them in percents of yearly mean). Vertical bars denote standard errors. Grouping of data on X-axis bases on the division of total range of observations into four equal parts. Only data from first clutches are used.

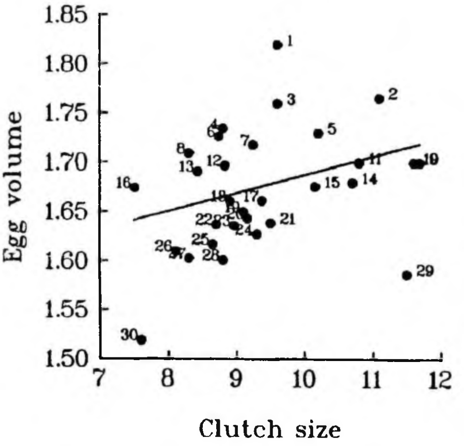

Fig. 5. Relationship between clutch size and egg size at the population level. Numbers denote ID numbers in Appendix. All egg volumes are calculated from the formula $V = \pi/6 \times L \times B^2$, or adjusted correspondingly. Slope for the line: $y = 1.503(\pm 0.075) + 0.019(\pm 0.008)\,x$. Line is fitted excluding three aberrant observations (1, 29 and 30).

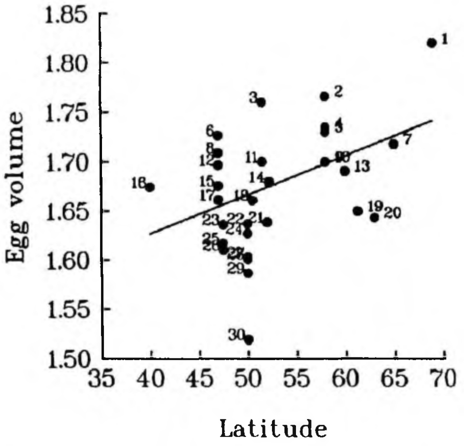

Fig. 6. Latitudinal trend in egg size. Legend as in Fig. 5. Slope for the line: $y = 1.468(\pm 0.076) + 0.004(\pm 0.001)\,x$. Line is fitted excluding the observation # 30.

same year (Table 2). A decrease of the female component in the repeat or second clutches can also be seen from the works of Ojanen et al. (1979) and van Noordwijk et al. (1981) in the Great Tit. Similarly, with other Great Tit studies (Haftorn 1985, Ojanen et al. 1979, Van Noordwijk et al. 1981, Yaremchenko 1989, Verhulst & Tinbergen 1991, Nager & Zandt 1994), we found that eggs tended to increase in the repeat/second clutches, which suggests that physiological and/or environmental processes affecting egg size and shape during the laying of the first and repeat/second clutches are different.

Heritability for egg volume was high (0.81 ± 0.28). This estimate, too, fell within the range found in other studies on the Great Tit (Jones 1973 cited in van Noordwijk 1987): $h^2 = 0.72 \pm 0.22$; Ojanen et al. 1979: $h^2 = 0.86 \pm 0.29$; van Noordwijk et al. 1981: $h^2 = 0.66 \pm 0.24...0.72 \pm 0.30$; and four other species ($h^2 = 0.55...0.99$, van Noordwijk & Boag 1987, Lessells et al. 1989). We found no effect of territory quality on egg size when repeatability of the same nestboxes with different females was calculated. This suggests that high heritability of egg size in our study was not caused by relatives sharing a similar environment. However, we concede that there might have been some hidden effect of habitat since 'nestbox quality' alone might not be a precise indicator of the quality of the breeding territory.

4.1.2. Yearly and age-related differences

In spite of highly significant inter-annual variation, the year and habitat term together explained only 4% of total variation in egg size (Table 4). Yearly differences in egg volume could have been caused by differences in air temperature (and correspondingly the development of food items) during the laying period (e.g. Ojanen et al. 1981, Järvinen 1994), while breeding density could be important, too (Perrins & McCleery 1994). However, considering high heritability of egg size, the possibility of differential elimination of genotypes as a potential source of yearly variation in egg size cannot be excluded either.

The result that egg size increased by the second year of life is in agreement with that of a Great Tit study in southwest Estonia (Mänd 1988, Mänd et al. 1990). Also, in a number of other species young females are known to lay smaller eggs than older ones (Ojanen 1983a).

4.1.3. Relationship with female condition and size

Our result that heavier and better-conditioned birds lay larger eggs, while egg volume generally does not depend on the size of the female, is in agreement with four other Great Tit studies (Ojanen et al. 1979, Mänd 1988, Järvinen & Pryl 1989, Nager & Zandt 1994). A similar tendency was found in a northern Pied Flycatcher population (Järvinen & Väisänen 1983) and in Eastern Kingbirds (Murphy 1986), Canada Goose (Leblanc 1989), Blue Tit (Nilsson & Svensson 1993), and Starling (Smith et al. 1993).

The positive correlation between egg size and female condition/weight is particularly interesting, because in our study (as well as in several others) females were weighed during the second half of the nestling period. It means that about one month after the first egg was laid, the females laying large eggs were heavier than those laying small eggs. Since females lose weight during breeding, our result indicates that either 1) females with large eggs were initially heavier, or/and 2) they lost less weight during the breeding. We therefore suggest that egg size reflects the component of female condition which is persistent throughout the breeding period.

The evidence that egg size variation within a population is related to the structural size of females is more rare. A few exceptions are the works of Larsson and Forslund (1992) in the Barnacle Goose, and Potti (1993) in the Pied Flycatcher, which found a positive correlation between egg size and female tarsus length. Several authors (e.g., Otto 1979, Järvinen & Väisänen 1984, Järvinen 1991, Potti 1993) have found positive correlations between egg size and female wing length. These studies might indicate the dependence of egg size on the structural size of the female; however, there have been claims that wing length is not a representative measure of body size (Rising & Somers 1989). It is also possible that wing length rather reflects the individual's condition during moult (see, e.g., Rätti et al. 1993).

The lack of positive correlations between female tarsus length and egg size is noteworthy in the context of another study (Hõrak 1994), which revealed positive correlations between clutch size and female tarsus length in the same populations in 1990. Since tarsus length depends on growth conditions during the nestling period, these correlations were interpreted as a possible lasting effect of the individual's ontogeny upon its reproduction. The present study suggests that growth conditions of the female do not necessarily affect her egg size.

4.1.4. Seasonal pattern

During the period of laying the first clutches, late-breeding females laid small eggs in the urban, but not in the rural population. A similar tendency has been recorded for Great Tits in southwest Estonia (Mänd 1988, Mänd et al. 1990), as well as for several other bird species (see, e.g., Ojanen 1983a, Flint & Sedinger 1992 for references).

What might cause seasonal patterns in egg size? Birkhead and Nettleship (1982) and Ojanen (1983a) have suggested that small egg size might be adaptive, allowing birds to lay early. However, Great Tits in our study clearly did not lay small eggs in early clutches. The seasonal decline of egg size in the urban population could hardly be caused by the proximate effect of food, since food availability generally increases during the laying of the first clutches. An alternative explanation would be that the quality of food decreases seasonally (e.g., vegetation growth and drying of soil could possibly make it more difficult for birds to find gastropods and other calcium-rich food items). This explanation, however, contradicts the finding that egg size increases again during the laying of repeat and second clutches. In addition, our personal observations confirm that snails are abundant during the whole Great Tit breeding period in our urban study area. Therefore, we suggest that small eggs in late first clutches just reflect the poor phenotypic quality of late-breeding females. This explanation is convincingly supported by the fact that the significant relationship between egg size and laying date vanished when the residual weight of the female was included in the analysis.

It is probably symptomatic that seasonal decline in egg size was revealed only in the urban population breeding under more unfavourable conditions than their rural conspecifics. Under harsh conditions individuals are likely to experience considerable energetic limitation in their activities, and, therefore, differences in their physiological condition will affect reproduction most prominently. In line with this explanation, the seasonal decline in clutch size, too, was steeper in our urban population than in the rural population (Hõrak 1993b).

4.1.5. Relationship with clutch size within populations

When data were pooled over five years, rural Great Tits at Tõrvandi tended to lay small eggs in large clutches. A similar pattern was present also during two individual years and in the rural population of Vanajärve in 1983. A negative correlation between clutch and egg size has been also reported in three other Great Tit studies (Jones 1973, cited in Ojanen et al. 1978; Haftorn 1985; Järvinen & Pryl 1989, but see Busse 1967 and Ojanen et al. 1978 for the opposite), and some other passerines (Ojanen et al. 1978, Greig-Smith et al. 1986, Hillström 1992) and non-passerines (Koskimies 1957, Myrberget 1977, Manning 1978).

Positive correlations between egg and clutch size have been recorded in the Starling (Ojanen et al. 1978, Smith et al. 1993) and several non-passerine species (Coulson 1963, Batt & Prince 1979, Rohwer & Eisenhauer 1989, Lessells et al. 1989, Flint & Sedinger 1992). Still, most egg size studies have revealed no clear trend in the relationship between egg size and number.

Two points can be made on the basis of these data: 1) Although it has been claimed that the evidence for a trade-off between egg size and clutch size within a bird species is lacking (Williams 1994), some populations do reveal negative correlations between clutch size and egg size. 2) Although the trade-off between clutch size and egg size is most likely to be expected in 'capital breeders' (*sensu* Drent & Daan 1980) who lay their eggs on the basis of a fixed amount of resource, the evidence of such a trade-off has been found also in small passerines laying eggs on the basis of daily energetic income.

We suggest that this is so because small passerines, in spite of being 'income breeders', also deplete their body reserves to a remarkable extent during laying (e.g., Jones & Ward 1976, Pinowska 1979, Ojanen 1983b). Since the laying of large eggs is energetically more demanding, the laying of smaller eggs in large clutches can be adaptive for 'income breeders', if it enables a female to start incubation with a lesser extent of depletion of body reserves during egg-laying. Thus, there is reason to expect a conflict between the number and size of eggs. We propose that the mechanism for a trade-off between egg size and clutch size works as follows: selection has fixed alleles for the strategy, which allows the clutch size to increase by laying small eggs. Clutch size, however, approaches its genetically determined maximum (upper limit of reaction norm) only under the most favourable environmental conditions. If a female is not in the best possible trim during the laying period, laying will cease before the maximum possible clutch size is attained, and the bird ends up with a small or average clutch containing small eggs. This explanation agrees with the fact that heritabilities for egg size are always higher than for clutch size (Boag & van Noordwijk 1987, Lessells et al. 1989, this study). In this context, it is noteworthy that in our study, the heritability estimate for clutch size was significantly different from zero in the rural, but not in the urban, population with small clutches. Negative correlations between egg and clutch size occurred only in the rural habitats of Tõrvandi and Vanajärve where breeding conditions are probably among the best recorded for the Great Tit (compare clutch sizes in Appendix).

4.1.6. Inter-populational trends

The study of 30 Great Tit populations revealed no evidence of a trade-off between egg size and clutch size at the inter-populational level (Fig. 5). This suggests that in the Great Tit, adaptations to locally prevailing breeding conditions do not involve different resource allocation patterns between the number and size of eggs at the population level.

Great Tits tended to lay larger eggs in populations with large average clutch sizes. To some extent, the phenomenon might be explained by proximate food limitations on both clutch and egg size at the population level. Proximate food limitations is a plausible explanation for the coexistence of very small eggs and clutches in Frankfurt on Main where breeding conditions for Great Tits seem to be poorest among the populations studied. On the other hand, the partial correlation analysis revealed that the simultaneous increase of egg and clutch size might have been largely due to latitude effect. In this case, the phenomenon can have a different reason: if individuals in northern populations of Great Tit have larger body size (Bergmann's rule) and also the clutch size increases towards the north, then the positive correlation between egg and clutch size would result as a byproduct of geographic trends in body size and clutch size. Whether the latitudinal trend in body size occurs in the Great Tit would require a further research; for the clutch size trend the evidence is contradicting (see Orell & Ojanen 1983 and references therein).

4.2. Egg shape

Like other researchers (Preston 1969, Ojanen et al. 1978, van Noordwijk et al. 1981, Järvinen & Väisänen 1983, and references in these) we found that egg length was more variable than breadth. Theoretically, the higher repeatability of egg length in comparison with that of egg breadth could, to some extent, be caused by its higher variation, because repeatabilities generally tend to be higher with greater differences between individuals in a sample (e.g., Harper 1994). Nevertheless, we believe that this was not the case, since the repeatability of egg volume, which showed the highest variation among egg traits, was much lower than that of egg length. Our data suggest, therefore, that among egg dimensions egg length possesses the highest level of genetic determination. This conclusion is convincingly supported by the comparison of heritability estimates from mother-daughter regressions (Table 3.).

Our finding about the high repeatability/heritability of egg length compares favourably with the results of Ojanen et al. (1979) and Mänd (1988) on the Great Tit. A similar tendency has been found also in some other species (Ojanen et al. 1979, Potti 1993 — Pied Flycatcher; Hendricks 1991 — American Pipit). Another Great Tit study (van Noordwijk et al. 1981), however, revealed the highest repeatability/heritability for the egg shape index, while heritabilities for egg length (but not breadth) were not significantly different from zero in one of the two study areas.

Grant (1982; see also Järvinen & Väisänen 1983, Hendricks 1991) suggested that egg shape is a function of egg size and female body size, mediated by the maximum extensibility of the oviduct. According to Grant's hypothesis, the maximum width of the oviduct sets an upper limit to egg breadth among eggs of various sizes, egg length being not so constrained.

The results of this study agree with those of many others which have shown that egg length is more variable than breadth. However, in our study egg length had also the highest heritability. This finding seems to be at odds with Grant's hypothesis, which suggests that egg length is most sensitive to non-genetic variation. Contrary to this expectation, we found that the most plastic egg trait was breadth (Tables 2 and 3), suggesting that the oviduct diameter is highly dependent on the physiological condition of the female, while factors determining egg length are most constant within individuals. Grant's hypothesis also suggests that small eggs must be more spherical in shape than large ones. Several authors (e.g., Myrberget 1977, van Noordwijk et al. 1981, Järvinen & Pryl 1989, Potti 1993) have presented similar evidence. Nevertheless, we failed to find any consistent relationship between egg size and shape in a sample of 3060 eggs (Table 1). Our result is similar to that of Mänd (1988) and Mänd et al. (1990).

Another explanation for differences in the female component among egg dimensions is the notion of van Noordwijk et al. (1981), who suggested on the basis of high repeatabilities of egg shape that it is not the diameter but the expansibility of the oviduct that is under genetic control. This can explain why we, too, found the highest repeatabilities for egg shape. The heritability estimate for the egg shape index, however, had only a penultimate rank among other egg dimensions in our study (Table 3).

An ultimate explanation for the higher heritability of egg length as compared to that of breadth agrees with the popular interpretation of Fischer's Fundamental Theorem: egg breadth is more directly related to egg volume than egg length, and since egg volume most likely has a fitness value, one can expect that directional selection has weeded out more genetic variation in egg breadth than in egg length (see also Hendricks 1991).

4.3. Conclusions

Egg size in the Great Tit is highly heritable but also sensitive to the female condition. The component of the female condition affecting egg size is persistent also about one month later, during the second half of the nestling period. The relationship between egg size and female condition was similar for populations breeding in rich and poor habitats, which suggests that egg size may be potentially useful for the examination of differences in the phenotypic quality of individuals. Nevertheless, egg size reflects the female condition probably best in the poor habitat, as indicated by the seasonal decline in egg size in our urban but not in the rural population.

Within populations, a trade-off between egg size and clutch size in small passerines is possible, as far as negative correlations have been observed between these traits. However, the trade-off can become apparent only when the female condition during egg laying is sufficient to approach the upper limit of the reaction norm for clutch size.

A trade-off between egg size and clutch size is not likely to occur at the inter-populational level in the Great Tit. On the contrary, egg and clutch size tend to correlate positively among populations. This might indicate that both egg size and clutch size are proximately food-limited in some populations. Alternatively, a simultaneous increase of egg and clutch size might be a by-product of latitudinal trends in body size and clutch size.

The genetic component is much higher for egg length than for egg breadth, possibly because egg length is more neutral in respect to fitness than breadth which is more strongly related to egg volume.

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Selostus: **Talitiaisen munan koko: yksilöiden, elinympäristöjen ja eurooppalaisten populaatioiden erot**

Minkä kokoinen muna naaraan tulisi munia? Poikaselle on edullista, jos se on kuoriutunut suuresta (laadukkaasta) munasta, koska se saattaa lisätä myöhempää hengissä selviytymisen mahdollisuutta, mutta naaraalle suuren munan tuottaminen voi olla energeettisesti rankkaa ja pienentää munalukua. Munakoon vaihtelun syiden ja seurausten tutkiminen on tärkeää, jotta ymmärrettäisiin jälkeläisten lukumäärän ja laadun välistä yhteyttä.

Pesimistulos liittyy ilman muuta jälkeläismäärään, mutta myös munakokoon, jos se vaikuttaa poikasen kasvuun ja selviytymiseen. Ottaen huomioon, että munan koon periytyvyys on yleensä suurempaa kuin pesyekoon, on oletettavissa, että nämä rajoittavat toisiaan (eli niiden välillä tulisi olla negatiivinen korrelaatio), mistä ei kuitenkaan ilmeisesti ole todellista tietoa. Päin vastoin: muna- ja pesyekoko ovat useissa tutkimuksissa korreloineet keskenään positiivisesti. Tämä johtunee yksilöiden välisistä fenotyyppisistä eroista, jotka voivat korreloida geneettisten elinkierto-ominaisuuksien kanssa.

Tietoa muna- ja pesyekoon keskinäisestä rajoittavuudesta on saatavissa tutkimalla niiden suhdetta yhtenäisten elinympäristötyyppien sisällä ja välillä. Me tutkimme kaupunkilaistuneiden ja maaseutuympäristössä pesivien talitiaisnaaraiden munakoon vaihtelua Kaakkois-Virossa. Tutkimme myös munakoon ja naaraan kunnon välistä suhdetta, jolla teoriassa on keskeinen merkitys sekä pesyekoon että jälkeläisten kasvatuskyvyn ja lisäksi pesintäajankohdan evoluution kannalta. Näiden testaaminen edellyttää naaraiden kunnon mittaamista pesintäkierron eri vaiheissa. Me tutkimme mahdollisuutta, että munan koko kuvastaisi naaraan kuntoa erilaisten ympäristöjen populaatioissa.

Aineisto kerättiin pääosin Tarton puistoissa ja puistokatujen varsilla sekä lehti- ja sekametsissä Tõrvandissa Tarton läheisyydessä vuosina 1987–91, pesyekoon perityvyyden arviointia varten vuoteen 1994 asti.

Maaseututalitiaistemme pesimisympäristöt ovat luultavasti mitä suotuisimmat, koska niiden pesyekoko on suuri (yksi suurimmista on talitiaisella on havaittu) ja pesintätulos erinomainen. Näissä oloissa ennustimme, että yksilöiden väliset erot lisääntymiseen käytettyjen resurssien määrässä ovat vähäisiä, koska ravintoa on tarjolla riittämiin. Siksi odotimme, että munien koon ja lukumäärän välillä on negatiivinen fenotyyppinen korrelaatio, jos niiden välillä ylipäätään on toisiaan rajoittava suhde.

Kaupunkipopulaatiossa munakoon ja pesyekoon välille on odotettavissa positiivinen korrelaatio, koska kaupunkilaistalitaiset elävät paljon vaikeammissa oloissa kuin lajitoverit maalla. Tutkimusalueellamme kaupunkilaistalitiaisten pesyekoko on suunnilleen kahta munaa pienempi kuin maalla ja poikaskuolleisuus on suurta. Siksi on odotettavissa, että yksilöiden väliset fenotyyppiset laatuerot, jotka voisivat johtaa elinkierto-ominaisuuksien positiiviseen korrelaatioon, korostuvat.

Suunnilleen 80% munan koon vaihtelusta oli periytyvää, mutta myös naaraan kunnon vaikutus oli huomattava. Molemmissa populaatioissa suuria munia munineet naaraat olivat painavia myös poikaskauden jälkipuoliskolla. Tämä osoittaa, että munan koko heijastaa naaraan kuntoa, joka pysyy samanlaisena läpi pesimäkauden. Kaupunkipopulaatiossa keskimääräinen munakoko pieneni munintakauden edistyessä luultavimmin siksi, että myöhäiset munijat olivat varhaisia huonokuntoisempia. Maaseutupopulaatiossa suurten pesyeiden munat olivat pieniä, mikä viittaa (ennustettuun) munaluvun ja -koon keskiseen rajoittavuuteen.

Toinen mahdollisuus tutkia muna- ja pesyekoon keskinäistä rajoittavuutta on selvittää, miten ne vaihtelevat toisiinsa nähden erilaisissa pesintäoloissa. Keskimääräinen pesintään käytettävien resurssien määrä luultavasti vaihtelee kunkin paikan olojen mukaan. Siten resurssien optimaalisen jakamisen jälkeläisten laadun ja lukumäärän kesken tulisi riippua paikasta. Tällöin muna- ja pesyekoon keskinäisen rajoittavuuden voi olettaa ilmenevän negatiivisena korrelaationa eri maantieteellisten populaatioiden välillä. Kirjallisuudesta eri puolilta Eurooppaa 30 populaatiosta kerättyjen tietojen pohjalta ei löytynyt todisteita siitä, että munakoon ja -luvun välillä olisi populaatiotasolla rajoittavuutta, ennemminkin näiden välillä oli positiivinen korrelaatio. Tutkimme myös munan koon etelä-pohjoissuuntaista vaihtelua, selvittääksemme, onko siinä havaittavissa sopeutuneisuutta populaatiotasolla. Munakoko kasvoi leveyspiirien suuntaisesti etelästä pohjoiseen.

Tutkimuksemme perusteella munakoko ja -luku rajoittavat toisiaan, mutta vain niin hyvissä olosuhteissa, että ravinnon saanti ei ole esteenä naaraan hyvälle kunnolle.

References

Batt, B. D. I. & Prince, H. H. 1979: Laying dates, clutch size and egg weight of captive Mallards. — Condor 81:35–41.

Báldi, A. & Csörgö, T. 1993: Effect of habitat on the clutch size and egg dimensions of the Great Tit (Parus major). — Aquila 100:201–209.

Birkhead, T. R. & Nettleship, D. N. 1982: The adaptive significance of egg size and laying date in Thick-billed Murres (Uria lomvia L.). — Ecology 63:300–306.

Boag, P. T. & van Noordwijk, A. J. 1987: Quantitative Genetics. — In: Cooke, F. & Buckley, P. A. (eds.), Avian Genetics:45–78. Academic Press, London.

Busse, P. 1967: Zmiennosc wielkosci, ksztaltu i ubarwienia jaj podvarszawskich populacji sikor: Parus major L. i Parus caeruleus L. — Notatki Orn. 8:33–50.

Coulson, J. C. 1963: Egg size and shape in the Kittiwake (Rissa tridactyla) and their use in estimating age composition of populations. — Proc. Zool. Soc. Lond. 140:211–227.

Drent, R. H. & Daan, S. 1980: The prudent parent: energetic adjustments in avian breeding. — Ardea 68:225–252.

Eeva, T. & Lehikoinen, E. 1995: Egg shell quality, clutch size and hatching success of the Great Tit (Parus major) and the Pied Flycatcher (Ficedula hypoleuca) in air pollution gradient. — Oecologia 102:312–323.

Freeman, S. & Jackson, W. M. 1990: Univariate metrics are not adequate to measure avian body size. — Auk 107:69–74.

Falconer, D. S. 1989: Introduction to quantitative genetics., 3rd ed. — Longman. New York.

Flint, P. L. & Sedinger, J. S. 1992: Reproductive implications of egg-size variation in the Black Brant. — Auk 109:896–903.

Grant, M. C. 1991: Relationships between egg size, chick size at hatching, and chick survival in the Whimbrel Numenius phaeopus. — Ibis 133:127–133.

Grant, P. R. 1982: Variation in the size and shape of Darwin's Finch eggs. — Auk 99:15–23.

Greig-Smith, P. W., Feare, C. J., Freeman, E. M. & Spencer, P. L. 1986: Causes and consequences of egg size variation in the European Starling Sturnus vulgaris. — Ibis 130:1–10

Haftorn, S. 1985: Variations in clutch size and egg dimensions of the Great Tit Parus major. — Fauna Norv. Ser. C. 8:106–115.

Hamann, H.-J., Schmidt, K.-H. & Simonis, S. 1989: Der Einfluss der Höhenlage auf Ei- und Gelegegrösse bei Kohlmeisen (Parus major). — J. Ornithol. 130:69–74.

Harper, D. C. G. 1994: Some comments on the repeatability of measurements. — Ringing & Migration 15:84–90.

Hendricks, P. 1991: Repeatability of size and shape of American Pipit eggs. — Can. J. Zool. 69:2624–2628.

Hillström, L. 1992: Patterns of hatching and adult body mass change in the Pied Flycatcher Ficedula hypoleuca: adaptations and constraints. — Ph. D.-thesis, University of Uppsala.

Hõrak, P. 1993a: Low fledging success of urban Great Tits. — Ornis Fennica 70:168–172.

— 1993b: Age-related differences in seasonal pattern of clutch size in the Great Tits (Parus major): proximate vs. ultimate explanation. — In: Proceedings of the

Fourth Congress of the European Society for Evolutionary Biology:179. Montpellier.

— 1994: Effect of nestling history on adult size and reproduction in the Great Tit. — Ornis Fennica 71:47–54.

Järvinen, A. 1991: Proximate factors affecting egg volume in subarctic hole-nesting passerines. — Ornis Fennica 68:99–104.

— 1994: Global warming and egg size of birds. — Ecography 17:108–110.

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

Järvinen, A. & Väisänen, R. A. 1983: Egg size and related reproductive traits in a southern passerine Ficedula hypoleuca breeding in an extreme northern environment. — Ornis Scand. 14:253–262.

— 1984: Reproduction of Pied Flycatchers (Ficedula hypoleuca) in good and bad breeding seasons in a northern marginal area. — Auk 101:439–450.

Jones, P. J. 1973: Some aspects of the feeding ecology of the Great Tit Parus major. — Ph. D.-thesis, University of Oxford.

Jones, P. J. & Ward, P. 1976: The level of reserve protein as the proximate factor controlling the timing of breeding and clutch-size in the Red-billed Quelea Quelea quelea. — Ibis 118:547–574.

Kıziroğlu, I. 1982: Brutbiologische Untercuchungen an vier Meisenarten (Parus) in der Umgebung von Ankara. — J. Ornithol. 123:409–423.

Koskimies, J. 1957: Variation in size and shape of eggs of the Velvet Scoter, Melanitta fusca (L.). — Arch. Soc. Vanamo 12:58–69.

Larsson, K. & Forslund, P. 1992: Genetic and social inheritance of body and egg size in the Barnacle Goose (Branta leucopsis). — Evolution 46:235–244.

Leblanc, Y. 1989: Variation in size of eggs of captive and wild Canada Geese. — Ornis Scand. 20:93–98.

Lessells, C. M. & Boag, P. T. 1987: Unrepeatable repeatabilities: a common mistake. — Auk 104:116–121.

Lessells, C. M., Cooke, F. & Rockwell, R. F. 1989: Is there a trade-off between egg weight and clutch size in wild Lesser Snow Geese (Anser c. caerulescens)? — J. Evol. Biol. 2:457–472.

Magrath, R. D. 1992: The effects of egg mass on the growth and survival of Blackbirds: a field experiment. — J. Zool., Lond. 227:639–653.

Manning, T. H. 1978: Measurements and weights of eggs of the Canada Goose Branta canadensis, analyzed and compared with those of other species. — Can. J. Zool. 56:676–687.

Martin, T. E. 1987: Food as a limit on breeding birds: a life-history perspective. — Ann. Rev. Ecol. Syst. 18:453–487.

Murphy, M. T. 1986: Body size and condition, timing of breeding, and aspects of egg production in Eastern Kingbirds. — Auk 103:465–476.

Mänd, R. 1988: Intrapopulational variation of avian eggs (In Russian with English summary). — Valgus. Tallinn.

Mänd, R., Nigul, A., & Sein, E. 1986: Oomorphology: A new method. — Auk 103:613–617.

Mänd, R., Vilbaste, H. & Leivits, A. 1990: The effect of ecological factors on the variability of eggs of the Great Tit. — In: Viksne, J. & Vilks, I. (eds.), Proceedings of the Fifth Conference on the Study and Conservation of Migratory Birds of the Baltic Basin:266–269., Vol. I. Zinatne Publishers, Riga.

Myrberget, S. 1977: Size and shape of eggs of Willow Grouse Lagopus lagopus. — Ornis Scand. 8:39–46.

Nager, R. G. & Zandt, H. S. 1994: Variation in egg size in Great Tits. — Ardea 82:315–328.

Nilsson, J.-Å: & Svensson, E. 1993: Causes and consequences of egg mass variation between and within Blue Tit clutches. — J. Zool., Lond. 230:469–481.

van Noordwijk, A. J., Keizer, L. C. P., van Balen, J. H. & Scharloo, W. 1981: Genetic variation in egg dimensions in natural populations of the Great Tit. — Genetica 55:221–232.

van Noordwijk, A. J. 1987: Quantitative ecological genetics of Great Tits. — In: Cooke, F. & Buckley, P. A. (eds.), Avian Genetics: A Population And Ecological Approach:363–380. Academic Press, London.

van Noordwijk, A. J. & de Jong, G. 1986: Acquisition and allocation of resources: their influence on variation in life history tactics. — Am. Nat. 128:137–141.

Ojanen, M. 1983a: Significance of variation in egg traits in birds, with special reference to passerines. — Ph. D.-thesis, Dept. of Anatomy and Dept. of Zoology, University of Oulu.

— 1983b: Egg development and the related nutrient reserve depletion in the Pied Flycatcher, Ficedula hypoleuca. — Ann. Zool. Fennici 20:293–300.

Ojanen, M., Orell, M. & Väisänen, R. A. 1978: Egg and clutch sizes of four passerine species in northern Finland. — Ornis Fennica 55:60–68.

— 1979: Role of heredity in egg size variation in the Great Tit Parus major and the Pied Flycatcher Ficedula Hypoleuca. — Ornis Scand. 10:22–28.

— 1981: Egg size variation within passerine clutches: effects of ambient temperature and laying sequence. — Ornis Fennica 58:93–108.

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

Otto, C. 1979: Environmental factors affecting egg weight within and between colonies of Fieldfare Turdus pilaris. — Ornis Scand. 10:111–116.

Perrins, C. M. & McCleery, R. H. 1994: Competition and egg-weight in the Great Tit Parus major. — Ibis 136:454–456.

Pinowska, B. 1979: The effect of energy and building resources of females on the production of House Sparrow (Passer domesticus (L.)) populations. — Ekol. Polska 27:363–393.

Potti, J. 1993: Environmental, ontogenetic, and genetic variation in egg size of Pied Flycatchers. — Can. J. Zool. 71:1534–1542.

Potti, J. & Merino, S. 1994: Heritability estimates and maternal effects on tarsus length in Pied Flycatchers, Ficedula hypoleuca. — Oecologia 100:331–338.

Preston, F. W. 1969: Shapes of birds' eggs: extant North American families. — Auk 86:419–428.

Price, T. & Liou, L. 1989: Selection on clutch size in birds. — Am. Nat. 134:950–959.

Price, T., Kirkpatrick, M. & Arnold, J. 1988: Directional selection and evolution of breeding date in birds. — Science 240:798–799.

Rising, J. D. & Somers, K. M. 1989: The measurement of overall body size in birds. — Auk 106:666–674.

Rätti, O., Dufva, R. & Alatalo, R. V. 1993: Blood parasites and male fitness in the Pied Flycatcher. — Oecologia 96:410–414.

Rohwer, F. C. & Eisenhauer, D. I. 1989: Eggs mass and clutch size relationships in geese, eiders, and swans. — Ornis Scand. 20:43–48.

SAS Institute 1985: SAS User's Guide, Version 6 Edition. — SAS Institute Inc., Cary, NC.

Smith, H. G., Ottosson, U. & Ohlsson, T. 1993: Interclutch variation in egg mass among Starlings Sturnus vulgaris reflects female condition. — Ornis Scand. 24:311–316.

Svensson, L. 1992: Identification guide to European passerines. 4th edn. L. Svensson. Stockholm.

Török, J. & Csörgö, T. 1988: Breeding ecology of hole-nesting passerines in different habitats in the Pilis mountains. — Aquila 95:67–76.

Verhulst, S. & Tinbergen, J. M. 1991: Experimental evidence for a causal relationship between timing and success of reproduction in the Great Tit Parus major major. — J. Anim. Ecol. 60:269–282.

Vilbaste, H. & Leivits, A. 1990: Programmes for long-term observations of dynamics of bird populations in the Nigula Nature Reserve (In Russian with English summary). — In: Renno, O. (ed.), Communications of the Baltic Commission for the Study of Bird Migration, Vol. 22:64–83.

Williams, T. D. 1994: Intraspecific variation in egg size and egg composition in birds: Effects on offspring fitness. — Biol. Rev. Cambridge Phil. Soc. 69:35–59.

Winkel, W. 1970: Experimentelle Untersuchungen zur Brutbiologie von Kohl- und Blaumeise (Parus major und P. caeruleus). — J. Ornithol. 111:154–174.

Yaremchenko, O. A. 1989: Reproduction of the Great Tit in artificial nests (In Russian). — In: Shurakov, A. I. (ed.), Gnezdovaja zhizn ptits:133–142. Pedagogical Institute of Perm, Perm.

Appendix

Data used in Figures 5 and 6. Egg sizes are presented in descending order. All egg volumes are calculated from the formula $V = \pi/6 \times L \times B^2$ or adjusted correspondingly. N is the number of clutches if not otherwise indicated.

L	B	V Mean ± SD (N)	Clutch size Mean ± SD (N)	N. Latitude	ID	Source
		1.82 ± 0.09 (20)	9.6 (20)	69°03'	1	Järvinen 1991
18.03	13.68	1.77 ± 0.12 (218)	11.10 ± 1.30 (206)	58°22'	2	This study, Tõrvandi
		1.76 ± 0.90 (13)	9.6 ± 1.1 (13)	51°	3	Verhulst & Tinbergen 1991
17.92	13.60	1.74 ± 0.12 (317)	8.80 ± 1.66 (297)	58°22'	4	This study, Tartu
17.90	13.60	1.73 ± 013 (93)	10.21 ± 1.27 (93)	58°09'	5	This study, Kilingi-Nõmme
18.02	13.53	1.73 ± 0.11 (51)	8.74 ± 1.42 (61)	47°15'	6	Báldi & Csörgő 1993
17.93	13.53	1.72 ± 0.12 (5007)*	9.24 (55)	65°00'	7	Ojanen et al. 1978
		1.71 ± 0.29 (414)*	8.30 ± 1.31 (54)	47°	8	Hamann et al. 1989
17.80	13.50	1.70 ± 0.11 (16)	11.69 ± 1.78 (16)	58°09'	9	This study, Nigula
17.60	13.60	1.70 ± 0.10 (22)	11.60 ± 1.67 (22)	58°09'	10	This study, Vanajärve
		1.68 ± 0.10 (10)	10.8 ± 1.1 (10)	51°	11	Verhulst & Tinbergen 1991
18.03	13.41	1.70 (168)*	8.83	57°	12	Török & Csörgő 1988
17.86	13.45	1.69 ± 0.10 (99)	8.43** (89)	60°15'	13	Järvinen & Pryl 1989
17.61	13.49	1.68 (1289)*	10.7 (122)	52°	14	Busse 1967
17.86	13.39	1.68 (147)*	10.15	57°	15	Török & Csörgő 1988
17.95	13.35	1.52 (45)*	7.51 (193)	40°	16	Kiziroglu 1982
17.76	13.37	1.66 (120)*	9.37	47°	17	Török & Csörgő 1988
		1.66 ± 0.15 (479)*	8.9 ± 1.53 (73)	50°30'	18	Hamann et al. 1989

contd.

contd.

		1.65 ± 0.02 (78)*,†	9.10 ± 0.11 (213)	61°20'	19	Eeva & Lehikoinen 1995
17.54	13.38	1.64 ± 0.11 (11)	9.16 ± 1.04 (31)	61°25'	20	Haftorn 1985
17.70	13.30	1.64 (42)	9.5	58°18'	21	Winkel 1970
		1.64 ± 0.15 (716)*	8.7 ± 1.57 (69)	50°	22	Hamann et al. 1989
		1.64 ± 0.10 (93)	8.97 ± 1.33 (93)	47°33'	23	Nager & Zandt 1994 + unp.
		1.63 ± 0.15 (2380)*	9.3 ± 1.48 (182)	50°	24	Hamann et al. 1989
		1.62 ± 0.11 (187)	8.65 ± 1.31 (187)	47°33'	25	Nager & Zandt 1994 + unp.
		1.61 ± 0.12 (137)	8.11 ± 1.45 (137)	47°33'	26	Nager & Zandt 1994 + unp.
		1.60 ± 0.14 (1993)*	8.3 ± 1.54 (227)	50°	27	Hamann et al. 1989
		1.60 ± 0.14 (1816)*	8.8 ± 1.46 (183)	50°	28	Hamann et al. 1989
17.40	13.2	1.59 (569)*	11.5	50°	29	Yaremchenko 1989
		1.52 ± 0.15 (497)*	7.6	50°	30	Hamann et al. 1989

* – number of eggs, not clutches; ** – value calculated by us, possibly not exact; † – only unhatched eggs measured

III

Hõrak, P. 1993: Low fledging success of urban Great Tits. — Ornis Fennica 70: 168–172.

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, inspite 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 – Hõrak 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) (1967–91)	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, Lehikoinen 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 kehno 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 syotyään 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 houkuttelevat jatkuvasti uusia lintuja ympäröivältä maaseudulta. Maaseudun talitiaiset ovat sopeutuneet munimaan suuria pesyeitä, koska kuoriutuville poikasille riittää runsaasti ravintoa. Geenivirta maaseudulta kaupunkeihin estää kaupunkipopulaatioiden paikallisen sopeutumisen huonoon poikasaikaiseen ravintotilanteeseen.

References

Balen, J. H. van 1980: Population fluctuations of the Great Tit and feeding conditions in winter. — Ardea 68:143–164.

Bejer, B. & Rudemo, M. 1985: Fluctuations of tits (Paridae) in Denmark and their relations to winter food and climate. — Ornis Scand. 16:29–37.

Berressem, K. G., Berressem, H. & Schmidt, K.-H. 1983: Vergleich der Brutbiologie von Höhlenbrütern in innnerstädtischen und stadtfernen Biotopen. — J. Ornithol. 124:431–445.

Berndt, R. & Frantzen, M. 1964: Von Einfluss des strengen Winters 1962/63 auf den Brutbestand der Höhlenbrüter bei Braunschweig. — Orn. Mitt. 16:126–130.

Cowie, R. J. & Hinsley, S. A. 1987: Breeding success of Blue Tits and Great Tits in suburban gardens. — Ardea 75:81–90.

Dhondt, A. A. 1971: The regulation of numbers in Belgian populations of Great Tits. — Proc. Adv. Study Inst. Dynamics Numbers Popul. (Oosterbeek 1970):532–547.

Dhondt, A. A., Adriaensen, F., Matthysen, E. & Kempenaers, B. 1990: Nonadaptive clutch sizes in tits. — Nature 348:723–725.

Drent, P. J. 1979: Territory occupancy in the autumn, seed food supply in the winter and local survival during the annual cycle. — Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., 2c Reeks 73:310–314.

Eeva, T., Lehikoinen, E. & Veistola, S. 1989: Habitat preference and breeding performance in four hole-nesting passerines at the northern limit of their range. — Ornis Fennica 66:142–150.

von Haartman, L. 1973: Talgmespopulationen på Lemsjöholm. — Lintumies 8:7–9.

Haggard, W. H. 1990: Urban weather. — Intern. J. Environmental Studies 36:73–82.

Hamann, H.- J., Schmidt, K.- H. & Simonis, S. 1989: Der Einfluss der Höhenlage auf Ei- und Gelegegrösse bei Kohlmeisen (Parus major). — J. Orn. 130:69–74.

Hansson, L. 1986: Breeding bird communities in relation to distance from winter food supply. — Ornis Fennica 63:47–49.

Hildén, O. & Koskimies, J. 1969: Effects of the severe winter of 1965/66 upon winter bird fauna in Finland. — Ornis Fennica 46:22–31.

Hildén, O. & Solonen, T. 1990: Helsingin puistojen pönttölintututkimus 1987–89. — Tringa 17:66–70.

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

Krebs, J. R. 1971: Territory and the breeding density in the Great Tit, Parus major L. — Ecology 52: 1–22.

Källander, H. 1981: The effects of provision of food in winter on a population of the Great Tit Parus major and the Blue Tit Parus caeruleus. — Ornis Scand. 12:244–248.

Lehikoinen, E. 1986: Dependence of winter survival on size in the Great Tit Parus major. — Ornis Fennica 63:10–16.

Lindén, M. 1990: Reproductive investment and its fitness consequences in the Great Tit Parus major. — Acta Univ.Upsaliensis, Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science 260, Uppsala.

van Noordwijk, A. J., van Balen, J. H. & Scharloo, S. 1981: Genetic and environmental variation in the clutch size of the Great Tit (Parus major).— Neth. J. Zool. 31:342–372.

Orell, M. 1989: Population fluctuations and survival of Great Tits Parus major dependent on food supplied by man in winter. — Ibis 131:112–127.

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

— 1990: Concluding remarks: dispersal and gene flow. — In: Blondel, J., Gosler, A., Lebreton, J.-D. & McCleery, R. (eds.), Population biology of passerine birds: an integrated approach: 475–480. Springer Verlag, Berlin.

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.

Schmidt, K.-H. & Einloft-Achenbach, H. 1984: Können isolierte Meizenpopulationen in Städten ihren Bestand erhalten? — Vogelwelt 105:97–104.

Schmidt, K.-H. & Wolff, S. 1985: Hat die Winterfütterung einen Einfluss auf Gewicht und Überlebensrate von Kohlmeisen (Parus major)? — J. Ornithol. 126:175–180.

Smith, H. G., Källander, H. & Nilsson, J.-A. 1989: The trade-offbetween offspring number and quality in the Great Tit Parus major. — J. Anim. Ecol. 58:383–401.

Tomiałojć, L. 1985: Urbanization as a test of adaptive potentials in birds. — In: Ilyichev, V. D. & Gavrilov, V. M. (eds.), Proc. XVIII Int. Congr. Ornithol. Vol. 2:608–614, Nauka, Moscow.

Vilbaste, H. 1976: Operatsioon "Parus-75". — In: Loodusvaatlusi 1975, Vol. 1:64–84, Valgus, Tallinn.

New journal in parasitology

A new journal in parasitology, **Bulletin of the Scandinavian Society for Parasitology**, has been established. Besides presenting society information it will publish articles on all aspects of parasitology, with priority given to contributors from the Nordic countries and other members of the Society. It will include review articles and short articles/communications. Comments on any topic within the field of parasitology may be sent as letters to the editor. The bulletin is also open for short presentations of new projects. All contributions should be written in English. Correspondence should be addressed to:

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IV

Hõrak, P. & Lebreton, J.-D. Survival of adult Great Tits in relation to sex and habitat: a comparison of urban and rural populations. (Submitted)

Survival of adult Great Tits in relation to sex and habitat: a comparison of urban and rural populations

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ABSTRACT

We examined capture-recapture data on adult survival in Great Tits in two (urban and rural) populations in south-eastern Estonia. Urban birds survived better than rural ones and females better than males. Proportion of yearling breeders was higher among females than among males, contrary to what could have been expected on the basis of survival estimates.

INTRODUCTION

Fecundity and survival are the basic components of fitness. Reliable methods for studying survival rates, accounting for the incompleteness of recapture rates became available with the recent development of specialized software (see reviews by Lebreton *et al.* 1992 and 1993). Recent applications have already revealed some interesting patterns, questioning such ecological dogmas as the high survival of tropical or insular birds (Karr *et al.* 1990, Blondel *et al.* 1992). Applying new methods for checking old paradigms can thus be useful.

Such a paradigm is sex specificity in survival, among birds. There is extensive evidence that adult sex ratios are male-biased in many bird species, a reason to believe in differential survival among sexes (reviews by Breitwisch 1989, Payevsky 1993). However, the presence of sex differences in survival and its possible causes require careful examination in case studies with proper methodology.

Another properly untested assumption is the higher survival rate of urban birds. Urban mesoclimate is warmer than in rural surroundings (Haggard 1990) and supplementary food resources due to winter feeding for birds are available. This probably enhances the suitability of urban areas for winter survival compared to rural woodlands (e.g. Hõrak 1993). However the survival differences between urban and rural populations have not been demonstrated yet.

In the present study we analyze capture-recapture data to estimate the local survival rates of Great Tits (*Parus major*) from two populations, breeding in urban and rural habitat in south-eastern Estonia. We examine the age structure of breeders, check for the presence of sex-related differences in survival and test for the prediction about higher survival rates of urban Great Tits.

METHODS

Study area

Data were collected in two main study areas: in the town of Tartu (human population about 120,000) and in the rural area of Tõrvandi, 5 km from Tartu (58°22'N 26°43'E) in 1987-93. The urban study area in Tartu consisted of two large and two small parks (about 22 ha) and avenues with a total length of 9 km. The distance between nestboxes was 30-40 m. The 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. The dominant tree species were *Picea abies, Pinus sylvestris, Betula pendula, Corylus avellana* and *Populus tremula*. Nestboxes were placed at every 40-50 m in lines (total length 11 km) running along forest edges and roadsides.

Total number of nestboxes varied from 327 to 497 over the years. On the average, 24 % of nestboxes were occupied by Great Tits in the rural and 38 % in the urban population in the period of first clutch laying. The proportion of occupied nestboxes did not vary significantly between years (χ^2_6=10.88, n.s.; LOGIT analysis). Altogether, 182 individual breeding females were captured in the rural population and 257 in the urban population; corresponding figures for males are 102 and 186. The average trapping efficiency (number of caught/number of breeding in the nestboxes) was 0.72 for rural females, 0.79 for urban females, 0.38 for rural males and 0.53 for urban males. Birds were aged and sexed according to Svensson (1984).

Survival analysis

For analyzing the capture-recapture data, we followed the approach in Lebreton *et al.* (1992), i.e. start from a global model of which the fit can be checked by contingency table tests; then proceed to more parsimonious models by dropping main effects or interaction terms of factors suspectable to influence survival and capture probabilities. Three factors considered were time (t), sex (s) and habitat (h). As a consequence the global model from which we started was model Φ_{t*s*h}, p_{t*s*h}, i.e. the Cormak-Jolly-Seber model (Φ_t, p_t) fitted separately to each of four data subsets: urban males, urban females, rural males, rural females. The notation, derived from generalized linear models, is that of Lebreton *et al.* (1992).

The fit of this initial model was checked using program RELEASE (Burnham *et al.* 1987). The sparseness of data lead to use the Fischer exact tests for testing independence in the 2*2 contingency tables provided by RELEASE. The levels p_i of the test were combined as $-2\ \Sigma \text{ Log } p_i$, which follows under the null hypothesis a distribution χ^2 (2n), where n is the number of terms in the sum (e.g. Hedges & Olkin 1985 p. 37).

Parsimonious models were fitted using SURGE (Pradel 1989), version 4.0. Because there were 361 possible models, we proceeded by looking for a parsimonious model alternatively for survival and capture probabilities. The list of the 40 models tested is given in the appendix. Model selection among the series of models tested was based on the Akaike's Information Criterion (AIC), to maximize external validity (Lebreton *et al.* 1992, Anderson *et al.* 1994). Likelihood ratio tests were used to test for the significance of biologically relevant effects from the linear model. All AIC calculations and tests were done conditional on parameters on a boundary (e.g. capture probability equal to 1).

RESULTS

Survival analysis

The fit of the global model (Φ_{t*s*h}, p_{t*s*h}) was good: none of the tests provided by RELEASE was significant. The overall Goodness of fit statistics indicated indeed too good a fit (males $\chi^2_{50}=19.163$, $P=1.000$; females $\chi^2_{38}=11.165$, $P=1.000$). Because of the sparseness of data, a number of P-levels of the Fisher exact tests were equal to 1, i.e. to Log $p_i=0$. The distribution of $-2\ \Sigma$ Log p_i tended then to be shifted to low values, its χ^2 distribution being valid only for continuous distributions of p_i. The global model had 40 identifiable parameters, with AIC=1305.776.

Among 38 models fitted with SURGE (Appendix), the one with the lowest AIC was model Φ_{t+s+h}, $p_{t*s+t*h}$ (AIC=1289.647) for 22 identifiable parameters. All other models had an AIC at least bigger by one. The final model (Φ_{t+s+h}, $p_{t*s+t*h}$) did not differ significantly from the global model Φ_{t*s*h}, p_{t*s*h} ($\chi^2_{18}=19.871$, $P=0.340$), indicating that the reduction achieved in the number of parameters was quite acceptable.

The complexity of the recapture structure resulted largely from the difficulty to spread evenly the effort over sites and habitats, hence the term t*h. Females are more prone to capture in tits (e.g. Clobert *et al.* 1988, Blondel *et al.* 1992): this was reflected by the sex effect. The presence of an interaction between sex and time was more surprising, since it indicated a change in the difference of capturability over the years. The resulting capture probabilities are shown in Fig. 1.

The time effect on survival probabilities, t, was on the verge of significance ($\chi^2_5=9.927$, $P=0.0773$). The sex effect was significant ($\chi^2_1=6.857$, $P=0.0088$). Survival in the urban population was significantly better than in the rural one (one-tailed test; standardized gaussian deviate, $Z=1.837$, $P=0.0331$). The resulting survival probabilities are shown in Fig. 2. Absence of interaction terms makes all survival curves parallel over time. Moreover, the shifts due to sex and habitat are additive. The logit link used here approximates closely the log-log link (Aitkin & Stasinopoulos 1989) used in proportional hazard models. As a consequence, the hazard rates, i.e. instantaneous mortality rates can be considered as proportional in the absence of interaction terms. This means that, in the final model, there were independent multiplicative effects of respectively habitat and sex on the instantaneous mortality rate.

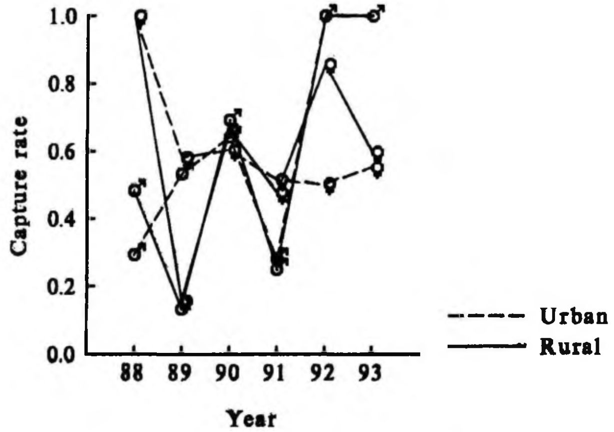

Fig. 1. Capture rates of Great Tits on the basis of model Φ_{t+s+h}, $p_{t*s+s*h}$. Six year averages are 0.59 for rural males and 0.63 for the rest of bird categories.

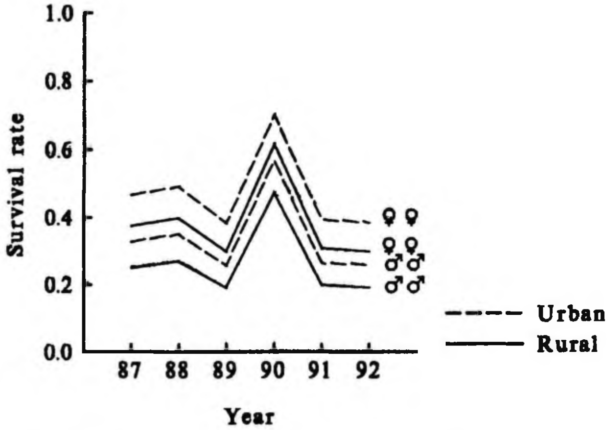

Fig. 2. Survival rates of Great Tits on the basis of model Φ_{t+s+h}, $p_{t*s+s*h}$. Six year averages are 0.47 for urban females, 0.38 for rural females, 0.26 for rural males and 0.34 for urban males.

Table 1. Proportion of yearlings among breeders (data pooled over six years).

Population	Sex	Number aged	Number and percentage of yearlings
Urban	Females	363	175 (48%)
	Males	234	60 (26%)
	Pooled	497	235 (44%)
Rural	Females	236	135 (57%)
	Males	114	44 (39%)
	Pooled	350	179 (51%)
Pooled	Females	599	310 (52%)
	Males	348	104 (30%)

Table 2. The most parsimonious model explaining the differences in proportion of yearlings between sexes, populations and years in LOGIT analysis of multiway contingency tables (SAS CATMOD procedure). Significant sex*year interaction indicates that in different years the magnitude of difference in proportion of yearlings between females and males varied. Probability for likelihood ratio, larger than 0.05 shows that model fits the data reasonably well.

Effect	d.f.	χ^2	P
Sex	1	38.67	<0.0001
Population	1	12.18	0.0005
Year	5	15.74	0.0076
Sex*Year	5	18.99	0.0019
Likelihood ratio	11	15.23	0.1722

Age of breeders

The proportion of yearling breeders was generally higher among females and in the rural population (Table 1). LOGIT analysis (SAS Institute 1985) indicated that these differences were statistically significant (Table 2).

DISCUSSION

The estimated local survival rates for adult Great Tits (0.26...0.47) were generally lower than in other studies, ranging from 0.43 to 0.56 (see review by Orell & Ojanen 1979). We found clear differences in survival rates between sexes and populations. The prediction about higher survival of urban Great Tits was verified. Due to relatively mild temperatures and winter feeding, urban areas are probably more suitable for wintering than rural woodlands.

Higher survival of males than females has been reported in most of earlier studies of Great Tits (Orell & Ojanen 1979), as well as many other bird species (reviews by Breitwisch 1989, Payevsky 1993). In our study, adult female Great Tits survived better than males, which seems to be inconsistent with the general pattern of sex differences in survival. However, our results are not so striking when compared to those of studies which used capture-recapture data. Clobert et. al (1988) found no consistent differences between survival of adult male and female Great Tits in Wytham, Oxford. Dhondt *et al.* (1990) found no sex differences in survival in the Blue Tit population in Belgium. Females survived slightly better on the Corsica while males survived better on the mainland among Mediterranean Blue Tits (Blondel *et al.* 1992).

Our most contradictory result is that, in spite of higher female survival, yearling females outnumbered yearling males among breeders. In the stable population, one would expect the members of the sex with higher survival to outnumber those of the opposite sex. Accordingly, not all members of prevalent sex could breed because of deficiency of partners. Therefore one could have expected a higher proportion of yearlings among males than among females because more females than males are expected to skip breeding at their first year when there are no sufficient mates to pair with. This was not so. Theoretically, the phenomenon can have the following explanations:

1) Although there are more females than males in the population, females are not the "limiting resource" for breeding. More males than females skip breeding in their first year because some other factor than the availability

of mates is limiting. Since males compete for territories, the availability of suitable nesting sites could potentially be such a factor. However, this explanation does not seem very realistic because nestboxes were distributed sparsely and more than half of them remained unoccupied by Great Tits.

2) Our estimates of survival are confounded with different 'nestbox fidelity' of males and females. In this scenario, males would survive no worse than females, but a higher proportion of males would disperse between breeding occasions and breed outside nestboxes without ever coming back. This permanent emigration inflates artificially their mortality rates, estimated from capture-recapture data.

The proportion of individuals not breeding in the nestboxes is high when the capture rate is low compared to the trapping efficiency (Nur & Clobert 1989, Blondel *et al.* 1992). In our study, the trapping efficiencies of females were higher than those of males, but the capture rates did not differ systematically between sexes. Therefore our data suggest that the proportion of birds alive but breeding outside nestboxes is higher for females than for males. This could potentially inflate the male survival estimates but not the female ones. Consequently, a difference in site fidelity does not seem to be responsible for the higher female survival estimates.

3) All observed differences are genuine and are compensated by a difference in juvenile survival or/and recruitment rates. I.e., the proportion of yearlings will be lower among male breeders if males reveal higher juvenile mortality than females, or alternatively, if yearling males are less likely to breed in nestboxes than yearling females. This might be more plausible in particular because nestboxes may induce unusual patterns of recruitment because of their attractiveness.

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REFERENCES

Anderson, D. R., Burnham, K. P. & White, G. C. 1994. AIC model selection in overdispersed capture-recapture data. Ecology 75: 1780-1793.

Aitkin, M. & Stasinopoulos, M. 1989. Likelihood analysis of a binomial sample size problem. *In* Gleser, L. J., Perlman, M. D., Press, S. J. & Sampson, A. R. (eds) Contributions to probability and statistics: essays in honor of Ingram Olkin: 399-411. New York: Springer Verlag.

Blondel, J., Pradel, R. & Lebreton, J.-D. 1992. Low fecundity insular blue tits do not survive better as adults than high fecundity mainland ones. J. Anim. Ecol. 61: 205-213.

Breitwisch, R. 1989. Mortality patterns, sex ratios, and parental investment in monogamous birds. *In* Current Ornithology, Vol. 6: 1-50. New York: Plenum Press.

Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C. & Pollock, K. H. 1987. Design and analysis of methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5.

Clobert, J., McCleery, R. H., Perrins, C. M. & Gosler, A. G. 1988. Survival rate in the Great Tit *Parus major* in relation to sex, age, and immigration Status. J. Anim. Ecol. 57: 287-306.

Dhondt, A. A., Matthysen, E., Adriaensen, F. & Lambrechts, M. M. 1990. Population dynamics and regulation of a high density Blue Tit population. *In* Blondel, J., Gosler, A., Lebreton, J.-D. & McCleery, R. (eds), Population Biology of Passerine Birds: 39-53. Berlin: Springer Verlag.

Haggard, W. H. 1990. Urban Weather. Intern. J. Environmental Studies 36: 73-82.

Hedges, L.V. & Olkin, I. 1985. Statistical methods for meta-analysis. Boston: Academic Press.

Hõrak, P. 1993. Low fledging success of urban Great Tits. Ornis Fennica 70: 168-172.

Karr, J. R., Nichols, J. D., Klimkiewicz, K. & Brawn, J. D. 1990. Survival rates of tropical and temperate forest birds: Will the dogma survive? Am. Nat. 136: 277-291.

Lebreton, J.-D., Burnham, K. P., Clobert, J. & Anderson, D. R. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecol. Monogr. 62: 67-118.

Lebreton, J.-D., Pradel, R. & Clobert, J. 1993. The statistical analysis of survival in animal populations. Trend. Ecol. Evolut. 8: 91-95.

Nur, N. & Clobert, J. 1989. Measuring Darwinian fitness in birds: a field guide. *In* Proc. Int. Orn. Comgr. XVI: 2121-2130.

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

Payevsky, V. A. 1993. The sex structure of bird populations and its variations (in Russian with English summary). Zoologitcheski Zhurnal 72: 85-97.

Pradel, R. 1990. User's manual for program SURGE Version 4.0. Montpellier: CEPE/CNRS.

SAS Institute 1985. SAS User's Guide, Version 6 Edition. Cary, NC: SAS Institute Inc.

Svensson, L. 1984. Identification guide to European passerines. Stockholm: Naturhistoriska Riksmuseet.

Appendix. Capture-recapture models for Great Tit data

In a first step, among the four preferable models from 19 under p_{t*s*h}, the model Φ_{t+s+h} is kept for the sake of simplicity.

Survival Φ	Capture p	n	AIC=dev+2n
t*s*h	t*s*h	40	1305.776
t*s+t*h+s*h	t*s*h	35	1297.681
t*s+s*h	**t*s*h**	**31**	**1292.035**
t*h+s*h	t*s*h	33	1298.774
t*s+t*h	t*s*h	34	1295.732
t+s*h	t*s*h	30	1295.335
t*s+h	**t*s*h**	**31**	**1292.118**
t*h+s	t*s*h	32	1297.231
t*s	t*s*h	31	1294.289
s*h	t*s*h	26	1297.631
t*h	t*s*h	32	1300.762
t+s+h	**t*s*h**	**29**	**1293.671**
t+s	**t*s*h**	**28**	**1292.574**
t+h	t*s*h	29	1297.870
s+h	t*s*h	25	1296.085
t	t*s*h	28	1296.272
s	t*s*h	24	1295.568
h	t*s*h	25	1300.513
	t*s*h	24	1299.455

In a second step, under Φ_{t+s+h}, the recapture structure can be simplified to $p_{t*s+s*h}$, among six further models.

Survival Φ	Capture p	n	AIC=dev+2n
t+s+h	t*s+t*h+s*h	23	1291.581
t+s+h	t*s+s*h	20	1300.419
t+s+h	t*h+s*h	20	1299.796
t+s+h	**t*s+t*h**	**22**	**1289.647**
t+s+h	t+s*h	16	1302.283
t+s+h	s+t*h	19	1297.977

Finally, the survival structure can not be simplified further (13 further models).

Survival Φ	Capture p	n	AIC=dev+2n
t*s+h	t*s+t*h	26	1290.025
t*h+s	t*s+t*h	26	1294.366
t*s	t*s+t*h	26	1293.875
s*h	t*s+t*h	19	1293.518
t*h	t*s+t*h	26	1301.503
t+s+h	**t*s+t*h**	**22**	**1289.647**
t+s	t*s+t*h	21	1290.922
t+h	t*s+t*h	21	1294.504
s+h	t*s+t*h	18	1291.574
t	t*s+t*h	22	1298.601
s	t*s+t*h	17	1294.252
h	t*s+t*h	18	1298.425
	t*s+t*h	18	1301.261

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ORIGINAL PAPER

Peeter Hõrak

Brood reduction facilitates female but not offspring survival in the great tit

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Abstract The long-term fitness consequences of brood reduction were examined in two (urban and rural) great tit populations in south-eastern Estonia during 1987–1994. The brood reduction hypothesis in its initial, Lackian sense was not supported since partial brood loss was accompanied by a decrease in fledgling weight and recruitment rate. Female survival was significantly improved in broods with high nestling mortality in the rural population. My results suggest that female great tits might be able to reallocate resources for self-maintenance if food appears to be short for the successful raising of the brood. However, parents are not capable of efficiently reallocating resources between nestlings.

Key words Brood reduction · Fledgling recruitment · Reproductive cost · *Parus major*

Introduction

The optimal clutch size for altricial birds is expected to correspond to the maximum number of nestlings that parents can adequately feed (Lack 1954) without depleting their own resources required for future reproduction (Williams 1966). If food availability for nestlings varies unpredictably, the laying female encounters difficulties in predicting the optimal clutch size at the time of egg-laying. One possible solution for parents in such a situation could be to create more offspring initially than can be normally reared and to reduce the brood size later if food proves to be short for raising the whole brood (Lack 1954; O'Connor 1978). The mechanism for the latter can be provided by asynchronous hatching, which is a result of parents starting incubation before the completion of a clutch. Under conditions of low food supply, asynchronous hatching creates size hierarchies among siblings, facilitating flexible brood reduction through the starvation of the youngest nestling(s) without adversely affecting older nestlings (Lack 1947, 1954, 1968).

Although Lack's brood reduction hypothesis has attracted considerable attention since its conception, its life-history consequences have remained virtually unexplored until very recently (Mock and Forbes 1994), since the majority of field studies have been confined to the investigation of relationships between hatching asynchrony, nestling size hierarchies and nestling mortality (see Amundsen and Stokland 1988; Magrath 1990; Amundsen and Slagsvold 1991a,b; Mock and Forbes 1994). Compared to the short-term effects of brood reduction, disproportionately little is known about its long-term fitness consequences for the nestlings which survive it. To my knowledge, the only study which has found a (positive) effect of brood reduction on postfledging survival of nestlings was that of Husby (1986) on the black-billed magpie. Therefore, more long-term studies are needed for a proper evaluation of the hypothesis (Amundsen and Slagsvold 1991a).

As critical is the need for empirical data about the consequences of brood reduction for parental survival. If parents save resources by early elimination of some nestlings, those resources can be invested not only in the remaining nestlings but also in the survival and reproduction of the parents themselves (e.g. Mock and Ploger 1987). Accordingly, the lack of brood reduction in a poor food situation could result in a survival penalty for parents. A rigorous test for these possibilities is also lacking since parental survival has not been assessed directly in studies of brood reduction (Mock and Forbes 1994).

In this paper I examine the consequences of brood reduction on both adult and fledgling survival (recruitment rate) in a long-term study of the great tit (*Parus major*) in south-eastern Estonia. The great tit is the species most often used by avian ecologists for testing the predictions of life-history theory. Therefore knowledge about its family-planning abilities is essential. Great tits start incubation during the egg-laying period and the young hatch more or less asynchronously, usually within a peri-

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od of 3 days (e.g. Haftorn 1985a). Average fledging success in the great tit may be lower than 50%, especially in poor habitats (see e.g. Hõrak 1993). Hatching asynchrony and its short-term consequences in the great tit have been interpreted and examined in the light of the brood reduction hypothesis (e.g. Haftorn 1985b; Slagsvold 1985; Slagsvold and Amundsen 1992). Nevertheless knowledge on the adaptive significance of brood reduction for great tits (as for the majority of facultative brood reductionists) is lacking. Here I attempt to answer this question by examining the effect of naturally occurring brood reduction on both fledgling and parental survival. If brood reduction is adaptive in its initial, Lackian sense (i.e. it facilitates the survival of remaining offspring), I would expect the brood reduction rate to correlate positively with or to be independent of fledgling weight and offspring recruitment rate. If brood reduction is adaptive in the sense that it facilitates parental survival, I would expect the brood reduction rate to correlate positively with the probability of adult survival to the next breeding season. To cover a wider range of environmental conditions, I will examine the outcome of brood reduction in two great tit populations, breeding in different types of (urban and rural) habitat.

Materials and methods

The study was conducted during 1987–1994 in two neighbouring (urban and rural) great tit populations, breeding in nestboxes in and near Tartu (58°22′N, 26°43′E; human population about 120 000), in south-eastern Estonia. A description of the study area is given in Hõrak (1994).

The number of nestboxes at the beginning of breeding seasons varied from 192 to 257 and from 135 to 240 in rural and urban areas, respectively. Nestboxes were fastened at a height of about 2.5 m. The dimension of the box cavity was approximately 11x11x30 cm, and the diameter of the entrance hole was 3.5 cm. Old nest materials were removed every year.

Nestboxes were checked regularly during the breeding season to determine breeding parameters (laying and hatching date, clutch size, number of dead and fledged young). Rate of brood reduction (number of died nestlings) was determined by searching for dead nestlings and unhatched eggs in nest material. Therefore clutches with no brood reduction were probably overrepresented in the sample since in many cases it could not be detected whether the number of fledglings was smaller than the clutch size due to nestling mortality or due to the presence of unhatched (but destroyed) eggs. I therefore used approximate brood reduction rate [= clutch size –(number of fledglings + number of unhatched eggs, if found)] in some analyses in order to enlarge the sample size and the power of the tests. This data set probably also included some broods with no nestling mortality, classified as brood reductionists, but this bias was less likely for clutches with high rates of nestling mortality (there is only a minor chance that addled eggs will not be found if the difference between clutch size and number of fledglings is larger than, for example, three units and no nestling mortality occurs).

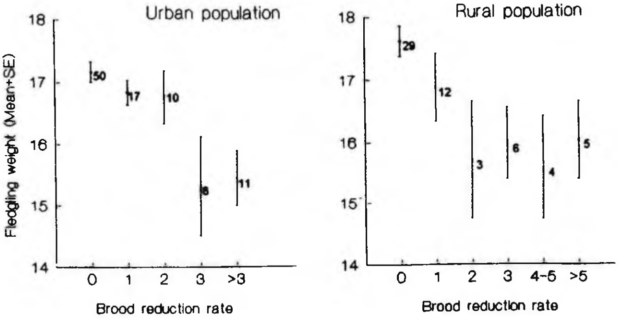
Young were ringed in the second half of the nestling period. Since 1990, nestlings were weighed with a precision of 0.1 g with Pesola spring balances when the average brood age was greater than 14 days (by that age the weight of nestlings corresponds to fledgling weight which is a good predictor of postfledging survival: see e.g. Tinbergen and Boerlijst 1990 and references therein). Parental survival and local recruitment rate of nestlings were determined by identifying the breeding adults captured on the nests during the second half of the nestling period.

The relationship between adult survival and brood reduction rate was analyzed by logistic regression using SAS CATMOD procedure (SAS Institute 1985). The same procedure was used in calculations concerning recruitment rate, which was transformed into a binary variable (clutches which recruited more than one offspring were weighted by the number of recruits). In the notation, π stands for the probability of a brood yielding a recruit, or for the probability of a female or male parent being alive (recaptured) in one of the following breeding seasons. (For regression with binary data, see also e.g. Turner et al. 1992.) If not otherwise stated, the models fitted the data reasonably well, i.e. probability for log-likelihood ratio was greater than 0.05. Significance levels were calculated for two-tailed tests except for the analysis of adult survival data where the presence of a positive relationship was tested for.

Results

Brood reduction was accompanied by a decline in prefledging nestling weight in both populations, average nestling weight being highest for broods with no nestling mortality (Fig. 1). An analogous decrease in the recruitment rate occurred with increasing brood reduction (Fig. 2), although this trend was significant at a 5% level only in the urban population. Low recruitment rate in broods with a high level of brood reduction was not caused by smaller absolute numbers of fledged young, since the proportion of recruited fledglings also decreased with increasing nestling mortality (Fig. 3).

Fig. 1 Relationship between brood mean pre-fledging weight and brood reduction rate. *Numbers* indicate sample sizes in all figures. Pooled data from 1990–1994. Totally failed broods are excluded. Trend is significant for both urban ($r = 0.46$, $P < 0.0001$, $N = 96$) and rural ($r = 0.45$, $P = 0.0004$, $N = 59$) populations



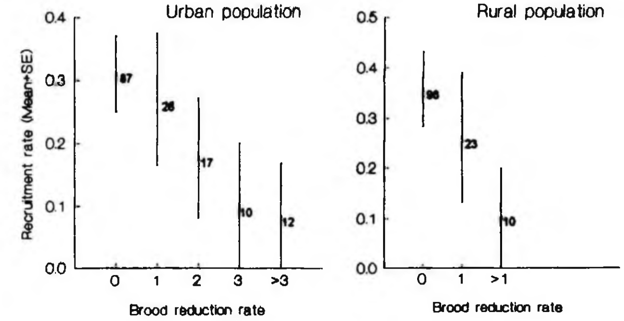


Fig. 2 Relationship between local recruitment rate and brood reduction rate. Totally failed broods are excluded. Pooled data from 1987–1994. Trend is significant for urban population: $\pi = 1/\{1+\exp[0.83+0.37(\pm0.18)$ brood reduction rate$]\}$, $P = 0.038$, $N = 152$ broods, but not for rural population: $\pi = 1/\{1+\exp[0.73+0.51(\pm0.32)$ brood reduction rate$]\}$, $P = 0.108$, $N = 131$ broods

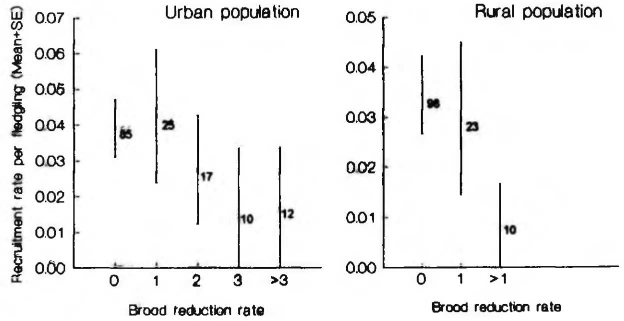


Fig. 3 Relationship between proportion of recruited fledglings and brood reduction rate. Pooled data from 1987–1994. Totally failed broods are excluded

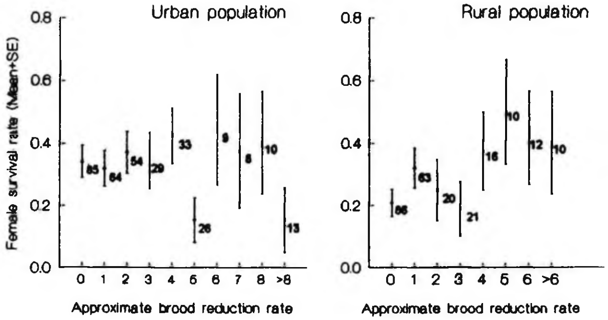


Fig. 4 Relationship between female survival rate and approximate (see methods) brood reduction rate. Pooled data from 1987–1994. Trend is significant for rural population: $\pi = 1/\{1+\exp[1.21-0.13(\pm0.06)$ brood reduction rate$]\}$, one-tailed $P = 0.014$, $N = 228$, but not for urban population: $\pi = 1/\{1+\exp[0.61 -0.03(\pm0.05)$ brood reduction rate$]\}$, one-tailed $P = 0.238$, $N = 331$

The probability of female survival increased with brood reduction rate in the rural population: $\pi = 1/\{1+\exp[1.34 -0.24(\pm0.15)$ brood reduction rate$]\}$, one-tailed $P = 0.050$, $N = 116$. The pattern was even more clear in the enlarged data set with approximate brood reduction rate as a predictor variable (Fig. 4). In the urban population the probability of female survival did not reveal a consistent relationship with brood reduction rate (Fig. 4). I tested whether this was caused by yearly differences in female survival by adding the year and year x "approximate brood reduction rate" terms as explanatory variables to the model. The explanatory power of those models was weak because they fitted the data poorly (P for log-likelihood ratio = 0.039 and 0.013 respectively). Probability of male survival was not related to brood reduction in any of the data sets.

Discussion

Lack's original brood reduction hypothesis was developed from the inductive evidence that siblings differ in size and vigor in many altricial bird species which hatch their eggs asynchronously, and that parents sometimes have difficulties in successfully rearing the whole brood. This innately suggests that brood reduction (and everything facilitating it) should be selected for, if the early mortality of some nestlings will avoid wasting parental resources on runts with poor survival perspectives.

The vast majority of studies on brood reduction (see e.g. Magrath 1990; Amundsen and Slagsvold 1991a,b) have examined the effects of hatching asynchrony on nestling growth and mortality patterns. These studies have yielded considerable controversy in their results and several alternative explanations for hatching asynchrony (see e.g. Magrath 1990; Nilsson 1993) but only a minor insight into the long-term fitness consequences of brood reduction. In this study, I was able to test for the adaptive significance of brood reduction, relying on the local recruitment rate as the most rigorous criterion of offspring fitness.

Data from the urban great tit population showed clearly that brood reduction did not facilitate postfledging survival of the remaining nestlings. The decline of recruitment rate with increasing nestling mortality was not significant at the 5% level in the rural population, but it showed the opposite tendency to that, predicted by the hypothesis. The prefledging weight of nestlings (which is commonly considered to be a good predictor of breeding success) also revealed a remarkable decrease with brood reduction rate in both populations. A decline in the proportion of fledglings recruited with increasing brood reduction rate indicates that the overall decline in recruitment rate was not caused by a decrease in fledgling numbers, but rather by the lower survival/establishment prospects of surviving young from broods with high nestling mortality.

In principle, one might argue that the efficiency of brood reduction can not be judged on the basis of the low quality of nestlings from broods with high nestling mortality since, in this case, brood reduction rate may exceed the range of hatching asynchrony (mostly only one or two last-hatched nestlings are much smaller than the others). However a decrease in both fledgling weight and recruitment rate was noticeable even in broods with only the slightest nestling mortality, indicating that even the death of a few "reserve offspring" did not help siblings reach a condition comparable to that of fledglings from broods with no nestling mortality. This suggests that for the great tit populations studied, brood reduction could hardly be considered to be a mechanism for efficiently coping with poor breeding conditions. Therefore the brood reduction hypothesis, in its initial Lackian sense, was not supported by my data. Instead, my results tend to agree with the view of Clark and Wilson (1981) classifying the great tit as a species with a pattern of lingering starvation. The lingering starvation results in the death of younger offspring taking so long that it should not be considered as an adaptation.

The second question investigated was whether brood reduction facilitates parental survival. The concept of reproductive cost suggests that one function of brood reduction might be the improvement of parental chances for future reproduction. Theoretically, the possibility for parental survival gain may be a key factor in the cost/benefit ratio of brood reduction strategy, as modelled by Mock and Forbes (1994). Yet future parental success has not been measured directly in studies assessing the adaptive significance of brood reduction. The closest indirect approximations in this dimension have involved measuring parental effort during the period of offspring provisioning. The notion that the absence of brood reduction may lead to parental costs was supported in two studies on cattle egrets (Fujioka 1985; Mock and Ploger 1987) in which parents increased food delivery rates in experimentally synchronized broods. Slagsvold and Lifjeld (1989) also found that female (but not male) pied flycatchers with asynchronous broods were heavier by the end of the nestling period than females with more synchronized broods, perhaps because of reduced work levels.

My study provides the first direct evidence for a positive relationship between parental survival and brood reduction rate. The result is notable, although a significant association was only found for females in the rural population. Lack of correlation for males is perhaps not surprising, given that in small passerines generally females tend to be subject to greater reproductive stress than males (see e.g. Amundsen and Slagsvold 1991a). More puzzling is the lack of survival gain from brood reduction among females in the urban great tit population. One possible explanation for the latter could be that smaller clutches and broods in the urban population (Hõrak 1993) resulted in a smaller adult survival penalty for adopting a brood survival strategy compared to the rural population with larger brood sizes. It is also possible that survival penalty for not being a brood reductionist was smaller in town because adult survival was generally higher for the studied urban population (P. Hõrak and J.D. Lebreton, unpublished work).

What was the reason for the positive relationship between nestling mortality and female survival in the rural population? For short-lived parents, the "suicidal" reproductive investment in the current brood might result in a similar risk of reproductive failure as decreased investment into the current brood for the sake of expected future reproduction. One theoretical possibility is, therefore, that different (genetically determined) reproductive strategies, yielding similar average fitness pay-offs (brood survival and brood reduction strategy), coexist in the same population. In this case, fluctuating selection pressure may assist in the preservation of genes for both strategies, i.e. brood reduction being selected for in poor food situations and brood survival in plentiful conditions.

An alternative (and probably simpler) explanation would be that all females have been selected to recognize (and respond to) the situation in which the amount of investment needed for successfully rearing the brood (even at the cost of their own impaired future reproduction) is so high that reallocation of resources to self-maintenance would be a better option anyway. In both cases, brood reduction should be considered as a by-product of adaptive reproductive decisions rather than a causal agent for improving reproductive success.

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References

Amundsen T, Slagsvold T (1991a) Asynchronous hatching in the pied flycatcher: an experiment. Ecology 72:797–804

Amundsen T, Slagsvold T (1991b) Hatching asynchrony: facilitating adaptive or maladaptive brood reduction? In: Acta XX Congressus Internationalis Ornithologici, Christchurch, New Zealand, 1990. New Zealand Ornithological Congress Trust Board, Wellington, pp 1707–1719

Amundsen T, Stokland JN (1988) Adaptive significance of asynchronous hatching in the shag: a test of the brood reduction hypothesis. J Anim Ecol 57:329–344

Clark AB, Wilson DS (1981) Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. Q Rev Biol 52:253–273

Fujioka M (1985) Food delivery and sibling competition in experimentally even-aged broods of the cattle egret. Behav Ecol Sociobiol 17:67–74

Haftorn S (1985a) Recent research on titmice in Norway. In: Ilychev VD, Gavrilov VM (eds) Acta XVIII Congressus Internationalis Ornithologici, Moscow, 1982. Nauka, Moscow, pp 137–155

Haftorn S (1985b) Variations in clutch size and egg dimensions of the great tit *Parus major*. Fauna Norv Ser C 8:106–115

Hõrak P (1993) Low fledging success of urban great tits. Ornis Fenn 70:168–172

Hõrak P (1994) Effect of nestling history on adult size and reproduction in the great tit. Ornis Fenn 71:47–54

Husby M (1986) On the adaptive value of brood reduction in birds: experiments with the magpie *Pica pica*. J Anim Ecol 55:75–83

Lack D (1947) The significance of clutch size. Ibis 89:302–352

Lack D (1954) The natural regulation of animal numbers. Oxford University Press, Oxford

Lack D (1968) Ecological adaptations for breeding in birds. Methuen, London

Magrath RD (1990) Hatching asynchrony in altricial birds. Biol Rev 65:587–622

Mock DW, Forbes LS (1994) Life-history consequences of avian brood reduction. Auk 111:115–123

Mock DW, Ploger BJ (1987) Parental manipulation of optimal hatch asynchrony in cattle egrets: an experimental study. Anim Behav 35:150–160

Nilsson J-Å (1993) Energetic constraints on hatching asynchrony. Am Nat 141:158–166

O'Connor R (1978) Brood reduction in birds: selection for fratricide, infanticide and suicide? Anim Beh 26:79–96

SAS Institute (1985) SAS user's guide, version 6 edn. SAS Institute, Cary

Slagsvold T (1985) Asynchronous hatching in passerine birds: influence of hatching failure and brood reduction. Ornis Scand 16:81–87

Slagsvold T, Amundsen T (1992) Do great tits adjust hatching spread, egg size and offspring sex ratio to changes in clutch size? J Anim Ecol 61:249–258

Slagsvold T, Lifjeld JT (1989) Hatching asynchrony in birds: the hypothesis of sexual conflict over parental investment. Am Nat 134:239–253

Tinbergen JM, Boerlijst MC (1990) Nestling weight and survival in individual great tits *Parus major*. J Anim Ecol 59:1113–1128

Turner DL, Ralphs MH, Evans JO (1992) Logistic analysis for monitoring and assessing herbicide efficiency. Weed Technol 6:424–430

Williams GC (1966) Natural selection, costs of reproduction and a refinement of Lack's principle. Am Nat 100:687–690

VI

Hõrak, P., Mänd, R. & Ots, I. Identifying the targets of selection: a multivariate analysis of reproductive traits in the Great Tit. (Manuscript)

Identifying the targets of selection: a multivariate analysis of reproductive traits in the great tit

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Abstract

In order to distinguish between the targets of phenotypic selection, we carried out a multivariate analysis on three reproductive traits in an urban population of great tits breeding in Tartu, south-east Estonia, during 1987-1994. Individuals laying large eggs recruited consistently more offspring for the breeding population, independent on the clutch size and laying date. However, the mean egg size of a clutch was not related to the occurrence of embryonal or nestling mortality, which points to the possibility that relationship between egg size and recruitment rate was due to the effects of female quality. Early breeders recruited more offspring into the breeding population, but the effect of laying date disappeared when egg size was incorporated into the model. The latter indicates that the primary target of selection was not the laying date *per se* but some property of a female which had an effect on both laying date and egg size. Selection on clutch size fluctuated in direction between years. Selection against large clutches mostly operated on individuals with small eggs, suggesting that the fitness consequences of similar reproductive decisions are different for individuals of different quality.

Introduction

Reproductive performance of individuals and its fitness consequences are affected by a combination of genetic and environmental factors. Among environmental factors, the condition of the reproductive individual is of central importance, since it can simultaneously affect both reproductive traits and fitness.

An individual's condition (or phenotypic quality) is a composite of nongenetic factors affecting the expression of reproductive traits including nutritional state, health, experience and amount of physiological wear-and-tear (cf. Schluter and Gustafsson 1993). It can be thought of as a joint factor which summarizes all nonrandom determinants of environmental variation in reproductive traits, such as foraging efficiency, parasite load, age, mate and territory quality etc.. Aspects of condition which affect the reproduction of an individual consist of a number of components, starting from short-term variation in nutritional state through to, for example, the lasting effects of growth period on an individual's reproduction.

In respect to the study of the evolution of reproductive traits, the components of individual condition which are persistent during the breeding period are of particular interest. Price et al. (1988) postulated that a correlation between heritable trait and fitness can persist at an evolutionary equilibrium whenever a nonheritable trait, such as nutritional state (or condition in broader meaning), simultaneously affects both the expression of a character and fitness through separate pathways (Fig. 1). Such models of phenotypic selection on avian breeding dates (Price et al. 1988) and clutch size (Price and Liou 1989) show that females laying early (and/or) large clutches may be fittest because selection operates on a correlated, environmentally determined trait (individuals' condition, phenotypic quality, health, nutritional state). Analogously, the concept of selection on the environmental component of traits has been applied for explaining the phenotypic selection on avian body size (van Noordwijk et al. 1988, Alatalo et al. 1990) and egg size (Bolton 1991).

The concept of phenotypic selection on individuals' condition (phenotypic quality) raises a question about the primary determinants of fitness. Selection may favour some trait value for a population or individual because it is an optimal solution *per se*; however selection may also act on the phenotypic quality of individuals, both directly and through correlated traits. To answer this question, in an ideal case, one has to substitute the path symbols in Fig. 1 with partial regression coefficients and estimate the relative importance of different causal links. In practice this task would be hardly realistic since it would require the exact measuring of that component of individuals' condition which is persistent during the whole breeding cycle. Nevertheless, some approximation to this dimension is possible. A feasible tool for this would be a multiple analysis of the fitness effects of different reproductive traits (e.g. Lande and Arnold 1983, Mitchell-Olds and Shaw 1987).

Due to common covariance with condition, the contribution of different reproductive traits to fitness has an overlapping component. This component can

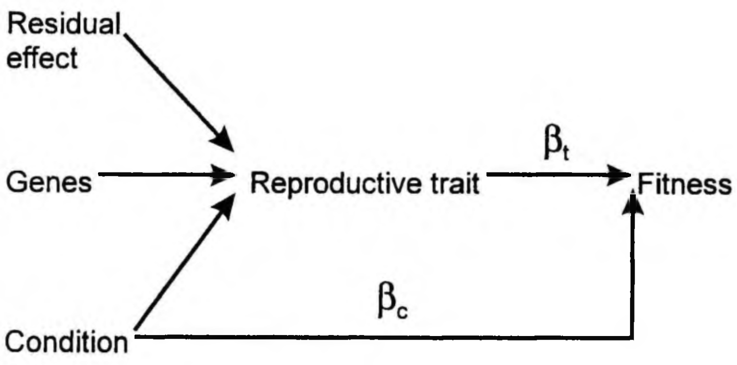

Fig. 1. Relationship between reproductive trait, individual's condition (phenotypic quality) and fitness (after Price et al. 1988, Møller 1994). Arrows connect dependent variables (arrowheads) with independent variables. Reproductive trait is determined by an additive genetic component, condition of the reproductive individual, and a residual effect. β_b denotes direct selection on trait, while β_c is a direct effect of condition on fitness.

be detected in a multiple analysis: if the effects of different reproductive traits on fitness are mutually exclusive, then the true determinant of fitness is the third factor, correlated with both breeding traits and fitness. By definition, we expect this trait to be a condition (phenotypic quality) of the breeding individual (= sum of all nonrandom determinants of environmental variation in reproductive traits). This also means that the most condition-dependent trait which is included in the multiple analysis should eliminate the condition-dependent fitness effects of other traits. Alternatively, if the traits affect fitness independently, then their effects in the multiple analysis should remain significant.

In this paper we present a multiple analysis of fecundity selection in the great tit (*Parus major* L.). Our aim is to distinguish between the targets of selection by examining the relationship between the local recruitment rate and three reproductive traits - breeding date, clutch size and egg size. We address the question of whether the effects of these traits on the reproductive success of individuals are independent of each other (and hence, independent of the condition of breeding individuals), or mutually exclusive, which would suggest the primary role of individuals' condition (phenotypic quality) in determination of the reproductive success.

To our knowledge the present study is first one to use as rigorous a measure as recruitment rate for examining the selection on egg size in a passerine bird species. Our previous work in the same great tit population (Hõrak et al. 1995), as well as the results of several other authors (see e.g. Ojanen et al. 1979, Murphy 1986, Järvinen and Pryl 1989, Williams 1994 and references in these) have revealed a close connection between the mean egg size of a female and components of her condition. Therefore we have reason to expect that inclusion of the egg size term into the analyses of selection on laying date and clutch size will help to clarify the role of individual phenotypic quality in selection on these traits.

Methods

The study was conducted during the period 1987-1994 in an urban great tit population breeding in Tartu, south-east Estonia (58°22'N 26°43'E). The study area consisted of two large and two small parks (about 22 ha) and of avenues with a total length of 9 km. The main tree species were *Tilia cordata, Acer platanoides, Betula pendula, Quercus robur,* and *Populus suaveolens.* The number of great tit pairs breeding in study area varied from 43 to 93 (first clutches only) in different years. The birds bred in nestboxes, mounted at a height of about 2.5 m. The dimensions of the box cavity were approximately 11*11*30 cm, the diameter of the entrance hole being 3.5 cm. Old nest materials were removed every year.

Nestboxes were checked regularly to determine clutch size and laying date (= date of laying the first egg), assuming that one egg is laid every day. Unhatched eggs were classified as infertile if no embryo development had occurred. Adults were captured and nestlings ringed in the second half of the nestling period. For measuring egg size, whole clutches were photographed after the sixth day of incubation using a stand described in Mänd et al. (1986). A graphics digitizer was used for the input of egg contours from photographs and a special program OMELETTE (Mänd et al. 1986) for smoothing data and for estimating egg dimensions and volume. The volume of an egg was calculated from the contour using trapezoidal integration instead of deriving it from linear measurements. Thus, individual differences in egg shape did not influence the accuracy of volume estimation. The clutch means of egg volume were used in all analyses. To minimize the influence of a few aberrant eggs on clutch means, one egg per clutch, the one most dissimilar to the others in size, shape or appearance, was excluded before the clutch mean was calculated. The rejection was based on the preliminary visual observation of the researcher, not on the basis of calculated egg measurements. Only data on first clutches are used. Depredated nests are excluded from the analysis.

Local recruitment rate was used as a measure of offspring fitness. Egg measurements were recorded during 1987-91 but recruitment was recorded up to 1994. Hence the length of the study period did not affect the chances of recapturing nestlings ringed in different years. In analyses of selection, clutch size, laying date and clutch mean egg size were standardized within years (mean=0, standard deviation=1). Average trait values for broods recruiting young for the breeding population (weighted by the number of recruits per brood) was thus equal to selection differential (s) in standard deviation units (Falconer 1989). The significance of selection differentials was tested by t-tests, comparing the means of individuals with and without recruitment (see e.g. Lindén et al. 1992). When analyzing net selection over five years, we used logistic regression (PROC CATMODE, SAS Institute 1985). Recruitment rate was transformed into a binary variable (clutches which recruited more than one offspring were weighted by the number of recruits). Year term was included as a factor in all analyses to eliminate the effect of yearly differences in recruitment rate. (For regression with binary data, see also e.g. Turner et al. 1992). Occurrence of stabilizing and disruptive selection was tested by comparing variances in trait values between the individuals with and without recruitment, as well as in logistic regression including squared trait values. All significance levels are for two-tailed tests.

Results

Selection on laying date

Compared to late breeders, early breeding females recruited significantly more offspring into the breeding population in 1988 (standardized selection differential, s=-0.77, $t_{17,51}$=2.89, p=0.005). Net selection differential (s on the data pooled over five years) was not significant (s=-0.26, $t_{52,173}$=-1.50, p=0.134). However, the date effect was marginally significant in the LOGIT analysis including the year term (Table 1).

We found no clear evidence for the fluctuating selection pressure on laying date since the 'year*laying date' interaction term was not significant at a 5% level (χ^2_4=7.53, p=0.110). However, at this p-level we can not entirely exclude the possibility that there was some inconsistency between years in respect to the direction of selection on laying date.

Table 1. Effect of laying date on local recruitment rate in LOGIT analysis. Significant year term indicates that average recruitment rate differs between years. Coefficient (Coef.) for the laying date (0.30±0.16) means that slope for the line describing relationship between standardized Laying date (D) and probability of a brood yielding a recruit equals to 1/{1+exp [0.30(±0.16)D]}. Intercept and year coefficients are not shown. Probability for likelihood ratio, greater than 0.05 indicates that model fits the data reasonably well.

Effect	DF	χ^2	Coef.±SE	p
Laying date	1	3.36	0.30±0.16	0.067
Year	4	21.11		<0.001
Likelihood ratio	209	214.33		0.386

The direction of selection on laying date was independent of the values of clutch size and egg size since inclusion of the corresponding interaction terms did not improve the fit of the model significantly (χ^2_1=0.23, p=0.632 for 'laying date*clutch size' and χ^2_1=1.09. p=0.297 for 'laying date*egg size' interactions respectively). Adding the main effect of clutch size did not improve the model significantly (χ^2_1=2.38, p=0.123), while adding the egg size term did so (χ^2_1=5.53, p=0.019). At the same time, the independent effect of laying date on recruitment rate disappears (Table 2), indicating that the effect of laying date on recruitment rate was due to the same factors which affected the relationship between egg size and recruitment rate.

Table 2. Joint effect of laying date and egg size on local recruitment rate. Interpretation as in Table 1.

Effect	DF	χ^2	Coef.±SE	p
Laying date	1	2.20	0.25±0.17	0.138
Egg size	1	5.33	-0.41±0.18	0.021
Year	4	21.34		<0.001
Likelihood ratio	208	208.80		0.471

We found no evidence for stabilizing or disruptive selection on laying date, when variances in laying dates of females with and without recruitment were compared (both in individual years and pooled data). Neither did adding the date squared term improve the fit of the LOGIT model (in Table 1) significantly (χ^2_1=1.19, p=0.275).

Selection on clutch size

Selection favoured large clutches in 1987 (s=0.69, $t_{9,13}$=3.54, p=0.002) while small clutches did best in 1989 (s=-0.45, $t_{16,23}$=-2.43, p=0.020). Net selection differential did not differ significantly from zero (s=-0.04, $t_{52,178}$=-0.81, p=0.420), and the clutch size did not affect the recruitment rate significantly in the LOGIT analysis with main effects of clutch size and year (χ^2_1=0.67, p=0.413). Adding the 'clutch size*year' term improved the fit of the model significantly (χ^2_4=15.23, p=0.004), further demonstrating that selection on clutch size fluctuated in direction between years.

Adding the egg size term to the model increased its fit significantly (χ^2_1=5.62, p=0.018). At the same time, the 'clutch size *year' interaction still remains significant (Table 3), indicating that fluctuating selection pressure on clutch size was independent of the factors affecting the relationship between egg size and recruitment rate. The fit of the previous model improved further when the 'clutch size*egg size' interaction term was added (χ^2_1=4.63, p=0.031). Fig. 2 reveals that interaction between clutch size and egg size was caused by the disproportionately low reproductive success of individuals with large clutches and small eggs.

Table 3. Joint effect of egg size and clutch size on local recruitment rate. Interpretation as in Table 1.

Effect	DF	χ^2	Coef.±SE	p
Egg size	1	5.50	-0.43±0.18	0.010
Year	4	16.39		0.003
Clutch size*Year	4	10.24		0.037
Likelihood ratio	205	197.07		0.548

As in the case of laying date, we found no evidence for stabilizing nor disruptive selection on clutch size neither by comparing the variances, nor in the LOGIT analysis with year, clutch size, and the clutch size squared term (χ^2_1=0.63, p=0.427, for adding the clutch size squared).

Table 4. Effect of egg size on recruitment rate. Interpretation as in Table 1.

Effect	DF	χ^2	Coef.±SE	p
Egg size	1	6.45	-0.45±0.18	0.011
Year	4	20.37		<0.001
Likelihood ratio	209	211.03		0.448

Selection on egg size

Unlike the cases of laying date and clutch size, the net selection differential for egg size was positive and significantly different from zero (s=0.38, $t_{53,179}=-2.35$, p=0.020). Out of five individual years, we found a statistically significant positive selection differential for egg size in 1989 (s=0.62, $t_{16,23}=2.94$, p=0.006). The positive effect of egg size on recruitment rate was also detected in the LOGIT analysis adjusting for year effects (Table 4). The effect of egg size was consistent in direction during all the years since the 'egg size*year' interaction term did not improve the fit of the model significantly ($\chi^2_4=4.51$, p=0.341). The final model, including the effects of all factors and those interaction terms which were previously found to be significant (Table 5), shows that the effect of egg size on breeding success was still present when the effect of other factors on recruitment rate was accounted for.

To distinguish between the components of breeding success related to egg size variation, we examined the relationships between egg size, hatching success and prefledging nestling mortality. We found no effects of egg size on either of these traits (Table 6). Test power however, was low; so we can not entirely exclude the possibility that differences might have been insignificant due to small sample sizes.

Analogously to clutch size and laying date, we found no sign of stabilizing nor disruptive selection on egg size (no difference in variances and insignificant effect of adding egg size squared to the model in Table 4: $\chi^2_1=1.15$, p=0.284).

Discussion

Of the three breeding traits investigated, we found a clear and persistent positive selection differential for egg size only. Great tits laying large eggs recruited

Table 5. Factors affecting local recruitment rate in the model summarizing main effects of all breeding traits and these interaction terms which were found significant in previous analyses. Interpretation as in Table 1.

Effect	DF	χ^2	Coef.±SE	p
Egg size	1	4.73	-0.42±0.19	0.029
Laying date	1	2.96	0.34±0.20	0.085
Clutch size	1	0.04	0.06±0.31	0.835
Year	1	16.60		0.002
Clutch size*Egg size	4	4.07	-0.41±0.20	0.043
Clutch size*Year	4	7.58		0.108
Likelihood ratio	202	189.33		0.729

Table 6. Average egg sizes in nests with and without egg/nestling mortality, compared by t-test. Power of the test $(1-\beta)$ is a probability of rejection of alternative hypothesis (that means are different) given the observed effect. Power is calculated for 5% α-level in two-tailed test according to Kraemer and Thiemann (1987).

	Egg volume: mean±sd (N) if				
Trait	present	absent	t	p	power
Nestling mortality	1.70±0.12 (39)	1.73±0.13 (47)	1.085	0.28	20%>>10%
Eggs with dead embryos	1.71±0.13 (36)	1.71±0.12 (68)	0.087	0.93	<10%
Infertile eggs	1.72±0.12 (48)	1.70±0.13 (83)	-1.054	0.29	20%>>10%

more offspring to the breeding population, independent of clutch size and laying date. Selection on clutch size fluctuated in sign between years and there was a general but weak tendency for early laying to be beneficial.

Our primary interest was in the question, whether the mutually exclusive effects of breeding traits on fitness can be detected in the multiple analysis. Such an effect emerged when selection on laying date and egg size was examined simultaneously. The marginally significant effect of early laying on recruitment rate (Table 1) disappeared when the egg size term was incorporated into the model (Table 2). Our interpretation is that the primary target of selection was not the laying date *per se* but some property of a female which has an effect on

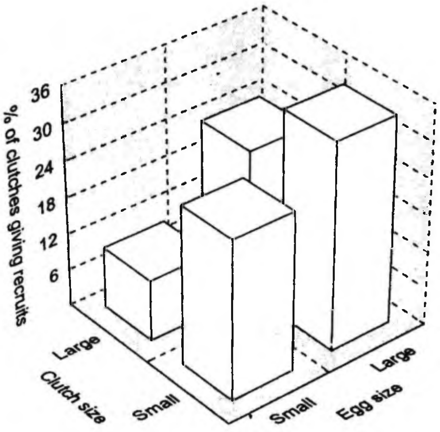

Fig. 2. Visualization of the interaction term between clutch size and egg size. 'Small' clutches and eggs are smaller than yearly average while 'large' ones are greater than average.

both laying date and egg size. This is consistent with the 'quality hypothesis' for explaining the seasonal decline in reproductive success (see Askenmo 1982, Wiggins et al. 1994, Verhulst et al. in press), which states that reproductive success declines seasonally because 'high quality' birds breed earlier than 'low quality' birds.

Selection for clutch size fluctuated in sign during the five year period, the net selection differential (s=-0.04 SD) being close to zero. Unlike selection on laying date, fluctuating selection on clutch size occurred independently of the factors affecting the relationship between egg size and recruitment rate since the 'clutch size*year' interaction term remains significant after the incorporation of the egg size term into the model (Table 3). If the phenotypic quality of a laying female was been correlated with clutch size, we would expect persistent positive selection for large clutches (as found e.g. by Boyce and Perrins (1987), Rockwell et al. (1987), and Gibbs (1988)). Contrary to this expectation, the selection differential for clutch size sometimes even had a relatively large negative value (s=-0.45 SD in 1989) indicating that individuals with large clutches were not always the most efficient in brood rearing.

A possible explanation for the lack of consistent positive selection on clutch size is the gene flow hypothesis (cf. Perrins and Moss 1975, Dhondt et al. 1990). Nestling mortality in our urban great tit population is notably higher than in the neighbouring rural population (Hõrak 1993), while the adaptive brood reduction is unlikely (Hõrak 1995). This suggests that the average clutch size of our urban great tit population is too large and does not match the parental brood-rearing ability. This in turn could be explained by persistent immigration from rural areas where the laying of large clutches is not selected against (Hõrak 1993). In this context the result that, among individuals with large clutches, those with small eggs did worst (Fig. 2) is noteworthy. Since large eggs most likely reflect the good condition of a laying female, our result might indicate that selection against large clutches was mediated through the effects of female condition: a bird in good condition can afford to lay a large clutch while a bird in poor condition would be mistaken in doing so.

Persistent positive selection differential for clutch' mean egg size is perhaps the most striking of our results. How did this effect emerge? Like most other studies, we found no relationship between egg size and hatching success (e.g. Schifferly 1973, Moss et al. 1981, Briskie and Sealy 1990, Reid and Boersma 1990, Bolton 1991, Smith et al. 1995, but see Järvinen and Väisanen 1983, Ojanen 1983, Nilsson and Svensson 1993). In our study, eggs were not significantly smaller in the nests where nestling mortality occurred. In two great tit studies, however, some evidence for the higher mortality of nestlings in broods hatched from small eggs has been found: Schifferly (1973) in late broods and Ojanen (1983) in two of five years. In general to date there is only little unequivocal evidence in support of a positive relationship between egg size and offspring fitness in birds (Williams 1994). Most studies have not controlled for the possible effect of parental quality on both egg size and breeding success which is likely to confound the interpretation of results, especially if data are based on the mean egg size of the clutch (Williams 1994).

We have a good reason to expect that in our study the relationship between the mean egg size of a clutch and local recruitment rate was also due to the effects of female quality rather than due to the long-term effect of egg size on postfledging survival of young.

First, if the egg size *per se* did affected offspring fitness, then this effect had to be hidden during the embryonal and nestling period and influence only the postfledging survival of young. The mechanism behind such a phenomenon would be difficult to explain since the majority of studies have found that the effect of egg size on nestling growth and survival decreases rapidly with nestling age (see e.g. Ricklefs 1984, Greig-Smith et al. 1988, Williams 1994, Smith et al. 1995 and references in these).

Second, the results of a previous study in the same population (Hõrak et al. 1995) indicate that interclutch variation in egg size reflects a component of an individual's condition which is persistent during breeding, since females laying large eggs were heavier than other females about one month after the onset of laying. A positive relationship between egg size and female condition has also been found in numerous other studies, demonstrating that females' average egg size is correlated to their body weight (irrespective of body size) during the later phases of breeding (e.g. Ojanen et al. 1979, Järvinen and Väisanen 1983, Mänd 1988, Järvinen and Pryl 1989, Leblanc 1989, Nilsson and Svensson 1993, Smith et al. 1993, Nager and Zandt 1994).

Thus, the most likely explanation for the persistent positive selection for large mean egg size is that individuals laying large eggs were for some reason able to provide better parental care, resulting in the production of fledglings with better survival/establishing perspectives. At present we do not have an explanation for the mechanisms behind the positive correlation between egg size and parental brood-rearing ability. A possible explanation could be the effect of blood parasites on reproducing females. Infection with some haematozoan taxa has been shown to have a negative effect on egg size in the great tit and the pied flycatcher (Dufa 1994), probably because parasites compete with the female for energy and nutrients during egg formation (Korpimäki et al. 1993, Allander and Bennett in press). If the same parasites have a negative effect on parental brood-rearing ability, a positive correlation between egg size and recruitment rate would result. To test for this possibility, parasitological studies of our great tit population are in progress.

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References

Alatalo, R. V., Gustafsson, L. and Lundberg, A. 1990. Phenotypic selection on heritable size traits: Environmental variance and genetic response. - Am. Nat. 135: 464-471.

Allander, K. and Bennett, G. F. in press. Retardation of breeding onset in great tits (*Parus major*) by blood parasites. - Funct. Ecol.

Askenmo, C. 1982. Clutch size flexibility in the pied flycatcher. - Ardea 70: 189-196.

Bolton, M. 1991. Determinants of chick survival in the lesser back-backed gull: Relative contributions of egg size and parental quality. - J. Anim. Ecol. 60: 949-960.

Boyce, M. S. and Perrins, C. M. 1987. Optimizing great tit clutch size in a fluctuating environment. - Ecology 68: 142-153.

Briskie, J. V. and Sealy, S. G. 1990. Variation in size and shape of least flycatcher eggs. - J. Field Ornithol. 61: 180-191.

Dhondt, A. A., Adriaensen, F., Matthysen, E. and Kempenaers, B. 1990. Nonadaptive clutch sizes in tits. - Nature. 348: 723-725.

Dufva, R. 1994. Effects of blood parasites on egg size in two bird species. - J. Ornithol. 135: 10.

Falconer, D. S. 1989. Introduction to quantitative genetics, 3rd ed. - Longman, New York.

Gibbs, H. L. 1988. Heritability and selection on clutch size in Darwins medium ground finches (*Geospiza fortis*). - Evolution 42: 750-762.

Greig-Smith, P. W., Feare, C. J., Freeman, E. M. and Spencer, P. L. 1988. Causes and consequences of egg-size variation in the european starling *Sturnus vulgaris*. - Ibis 130: 1-10.

Hõrak, P. 1993. Low fledging success of urban great tits. - Ornis Fennica 70: 168-172.

Hõrak, P. 1995. Brood reduction facilitates female but not offspring survival in the great tit. - Oecologia: 102: 515-518.

Hõrak, P., Mänd, R., Ots, I. and Leivits, A. 1995. Egg size variation in the Great Tit: individual, habitat and geographic differences. - Ornis Fennica 72: in press.

Järvinen, A. and Pryl, M. 1989. Egg dimensions of the great tit parus major in southern Finland. - Ornis Fennica 66: 69-74.

Järvinen, A. and Väisanen, R. A. 1983. Egg size and related reproductive traits in a southern passerine *Ficedula hypoleuca* breeding in an extreme northern environment. - Ornis Scand. 14: 253-262.

Korpimäki, E., Hakkarainen, H. and Bennett, G. F. 1993. Blood parasites and reproductive success of Tengmalm owls: Detrimental effects on females but not on males. - Funct. Ecol. 7: 420-426.

Kraemer, H. C. and Thiemann, S. (eds.). 1987. How many subjects? - SAGE Publications Inc., Newbury Park, California.

Lande, R. and Arnold, S. J. 1983. The measurement of selection on correlated characters. - Evolution 37: 1210-1226.

Leblanc, Y. 1989. Variation in size of eggs of captive and wild canada geese. - Ornis Scand. 20: 93-98.

Lindén, M., Gustafsson, L. and Pärt, T. 1992. Selection on fledging mass in the collared flycatcher and the great tit. - Ecology 73: 336-343.

Mitchell-Olds, T. and Shaw, R. G. 1987. Regression analysis of natural selection: Statistical inference and biological interpretation. - Evolution 41: 1149-1161.

Moss, R., Watson, A., Rothery, P. and Glennie, W. W. 1981. Clutch size, egg size, hatch weight and laying date in relation to early mortality in red grouse, *Lagopus lagopus scoticus*. - Ibis 123: 450-462.

Murphy, M. T. 1986. Body size and condition, timing of breeding, and aspects of egg production in eastern kingbirds. - Auk 103: 465-476.

Møller, A. P. 1994. Parasites as an environmental component of reproduction in birds as exemplified by the swallow *Hirundo rustica*. - Ardea 82: 161-172.

Mänd, R. 1988. Intrapopulational variation of avian eggs (In Russian with English summary). - Valgus, Tallinn.

Mänd, R., Nigul, A. and Sein, E. 1986. Oomorphology: a new method. - Auk 103: 613-617.

Nager, R. G. and Zandt, H. G. 1994. Variation in egg size in great tits. - Ardea 82: 315-328.

Nilsson, J.-Å. and Svensson, E. 1993. Causes and consequences of egg mass variation between and within blue tit clutches. - J. Zool., Lond. 230: 469-481.

van Noordwijk, A. J., van Balen, J. H. and Scharloo, W. 1988. Heritability of body size in a natural population of the great tit *Parus major* and its relation to age and environmental conditions during growth. - Genet. Res. 51: 149-162.

Ojanen, M. 1983. Significance of variation in egg traits in birds, with special reference to passerines. - Ph. D. Thesis, Dept. of Anatomy and Dept. of Zoology, Univ. Oulu.

Ojanen, M., Orell, M. and Väisanen, R. A. 1979. Role of heredity in egg size variation in the great tit *Parus major* and the pied flycatcher *Ficedula hypoleuca*. - Ornis Scand. 10: 22-28.

Perrins, C. M. and Moss, D. 1975. Reproductive rates in the great tit. - J. Anim. Ecol. 44: 695-706.

Price, T. and Liou, L. 1989. Selection on clutch size in birds. - Am. Nat. 134: 950-959.

Price, T., Kirkpatrick, M. and Arnold, J. 1988. Directional selection and evolution of breeding date in birds. - Science 240: 798-799.

Reid, W. V. and Boersma, P. D. 1990. Parental quality and selection on egg size in the magellanic penguin. - Evolution 44: 1780-1786.

Ricklefs, R. 1984. Components of variance in measurements of nestling european starlings (*Sturnus vulgaris*) in southern Pennsylvania. - Auk 101: 319-333.

Rockwell, R. F., Findlay, C. S. and Cooke, F. 1987. Is there an optimal clutch size in snow geese. - Am. Nat. 130: 839-863.

SAS Institute 1985. SAS User's Guide, Version 6 Edition. - SAS Institute Inc., Cary, NC.

Schifferly, L. 1973. The effect of egg weight on the subsequent growth of nestling great tits. - Ibis 115: 549-558.

Schluter, D. and Gustafsson, L. 1993. Maternal inheritance of condition and clutch size in the collared flycatcher. - Evolution 47: 658-667.

Smith, H. G., Ottosson, U. and Ohlsson, T. 1993. Interclutch variation in egg mass among starlings *Sturnus vulgaris* reflects female condition. - Ornis Scand. 24: 311-316.

Smith, H. G., Ohlsson, T. and Wettermark, K.-J. 1995. Adaptive significance of egg size in the european starling: Experimental tests. - Ecology 76: 1-7.

Turner, D. L., Ralphs, M. H. and Evans, J. O. 1992. Logistic analysis for monitoring and assessing herbicide efficiency. - Weed Technology 6: 424-430.

Verhulst, S., Van Balen, J. H. and Tinbergen, J. M. in press. Seasonal decline in reproductive success in the great tit: variation in time or quality? - Ecology.

Wiggins, D. A., Pärt, T. and Gustafsson, L. 1994. Seasonal decline in collared flycatcher *Ficedula albicollis* reproductive success: an experimental approach. - Oikos 70: 359-364.

Williams, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: Effects on offspring fitness. - Biol. Rev. Cambridge Phil. Soc. 69: 35-59.

CURRICULUM VITAE

I was born on December 11, 1963 in Tartu, Estonia. In 1982 I finished secondary school in Tartu and entered Tartu University to study biology. In 1983–1985 I passed military service. I graduated from Tartu University in 1989 with a diploma degree in zoology. The title of my diploma thesis was "Effect of environmental conditions on the breeding biology of the Great Tit in urban and agricultural habitats".

In December 1989, I took up postgraduate studies for the degree of Cand. Sci. in the Laboratory of Ornithology in the Institute of Zoology and Botany, Estonian Academy of Sciences. Since September 1991, I have continued my studies (now for Ph.D.) in the Animal Ecology Section, Department of Zoology and Hydrobiology, Tartu University. During 1993 I worked in the Laboratory of Ecological Zoology, University of Turku, Finland. My stay at Turku was financed by the Kone Foundation (Helsinki).

My current research concentrates on the evolution of optimal reproductive behaviour in birds. It bases on the long-term population study of the Great Tit, started in 1987. Besides the breeding ecology of the Great Tit, I have dealt with problems concerning its wintering biology and examined possible effects of heavy metal pollution in respect of the breeding habitat (in cooperation with Tallinn Technical University). I have presented the results of my study at international conferences in Haapsalu, Kaunas, Pruchten, Korpilahti, Montpellier and Edinburgh. My research has benefitted a lot by grants from the Estonian Foundation in Finland (Viro-Säätiö), Rudolf Sõmermaa Stipendiary Fund within the fraternity Ugala in Sweden, European Science Foundation, and Estonian Science Foundation.

ELULOOKIRJELDUS

Sündisin 11. detsembril 1963. a. Tartus. 1982. a. lõpetasin Tartu V Keskkooli ning samal aastal astusin Tartu Ülikooli õppima bioloogiat. 1983–1985 veetsin armeeteenistuses. Lõpetasin Tartu Ülikooli 1989. a. diplomeeritud bioloogina (diplomitöö: "Keskkonnatingimuste mõjust rasvatihase pesitsusbioloogiale linnas ja põllumajandusmaastikus").

1989. a. detsembris astusin aspirantuuri bioloogiakandidaadi kraadi omandamiseks Eesti TA Zooloogia ja Botaanika Instituudi Ornitoloogia Laboratooriumis. Alates 1991. a. jätkasin oma õpinguid doktorantuuris Tartu Ülikooli Zooloogia ja Hüdrobioloogia Instituudis, Loomaökoloogia Õppetooli juures. 1993. a. töötasin Turu Ülikoolis Ökoloogilise Zooloogia Laboratooriumis finantseerituna Kone Fondi poolt.

Minu uurimistöö teemaks on optimaalse sigimiskäitumise evolutsioon lindudel. Töö baseerub pikaajalisel rasvatihase populatsiooniuuringul (alustatud 1987). Lisaks rasvatihase pesitsusökoloogiale olen uurinud ka sama liigi talvitusbioloogiat ning võimalikku raskemetallide saaste mõju erinevates elupaikades (koostöös Tallinna Tehnikaülikooli teadlastega). Olen esitanud oma uurimistöö tulemusi rahvusvahelistel konverentsidel Haapsalus, Kaunases, Pruchtenis, Korpilahtis, Montpellier's ja Edinburghis. Minu tööle on oluliselt kaasa aidanud stipendiumid Eesti Sihtasutuselt Soomes, samuti Rudolf Sõmermaa nimeliselt fondilt Korporatsioon Ugala Vilistlaskogu juures Rootsis, Euroopa Teadusfondilt (ESF) ning Eesti Teaduse Sihtasutuselt.

Olen Eesti Looduseuurijate Seltsi tegevliige 1982. aastast. Akadeemiliselt kuulun korporatsioon Ugalasse (*coetus* 1988).

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