

ORIGINAL PAPER

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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 11×11×30 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 nes-

ting 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 added 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 pre-fledging 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

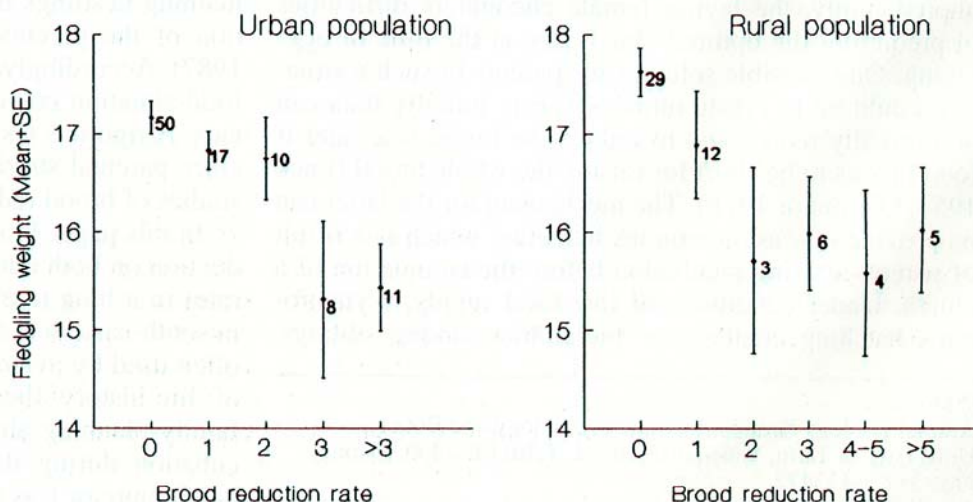


Fig. 2 Relationship between local recruitment rate and brood reduction rate. Totally failed broods are excluded. Pooled data from 1987–1994. Trend is significant for urban population: $\pi = 1/[1+\exp\{0.83+0.37(\pm 0.18) \text{ brood reduction rate}\}]$, $P = 0.038$, $N = 152$ broods, but not for rural population: $\pi = 1/[1+\exp\{0.73+0.51(\pm 0.32) \text{ brood reduction rate}\}]$, $P = 0.108$, $N = 131$ broods

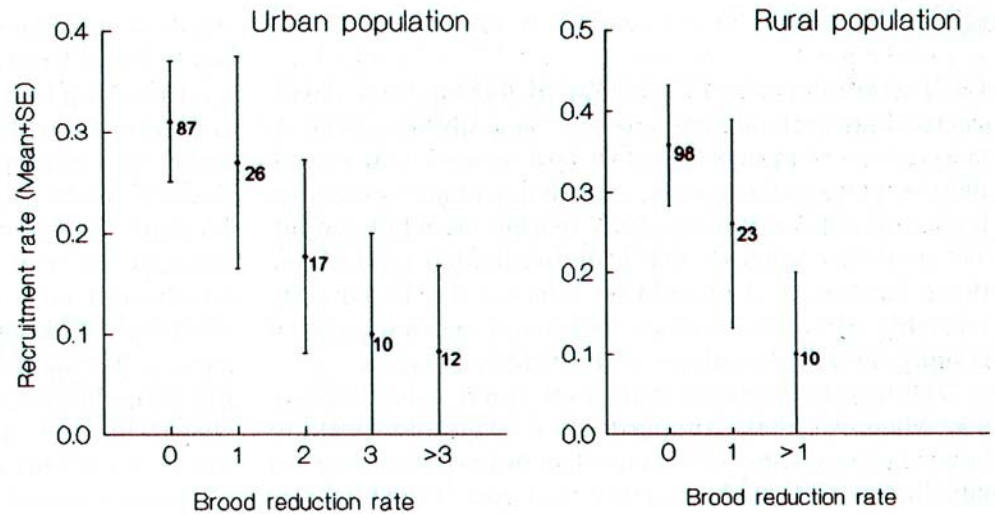


Fig. 3 Relationship between proportion of recruited fledglings and brood reduction rate. Pooled data from 1987–1994. Totally failed broods are excluded

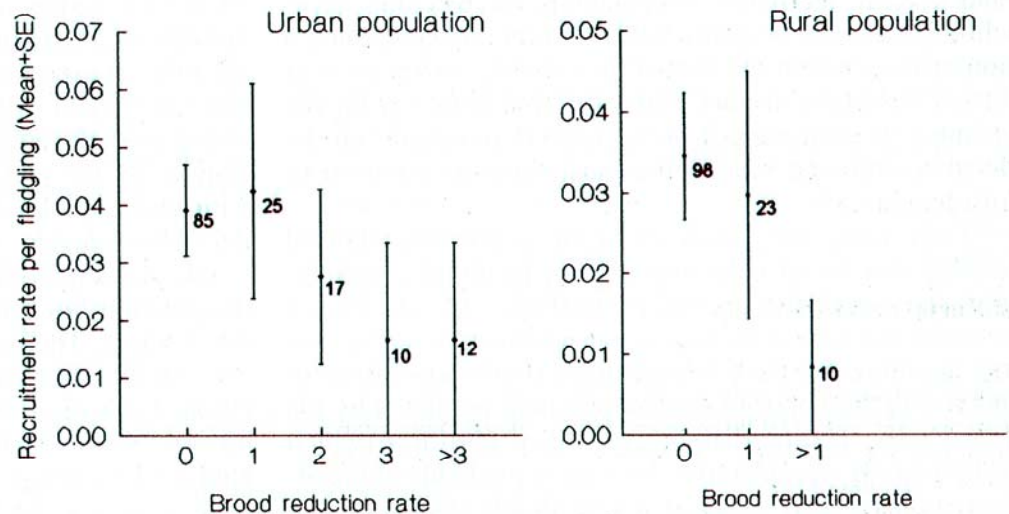
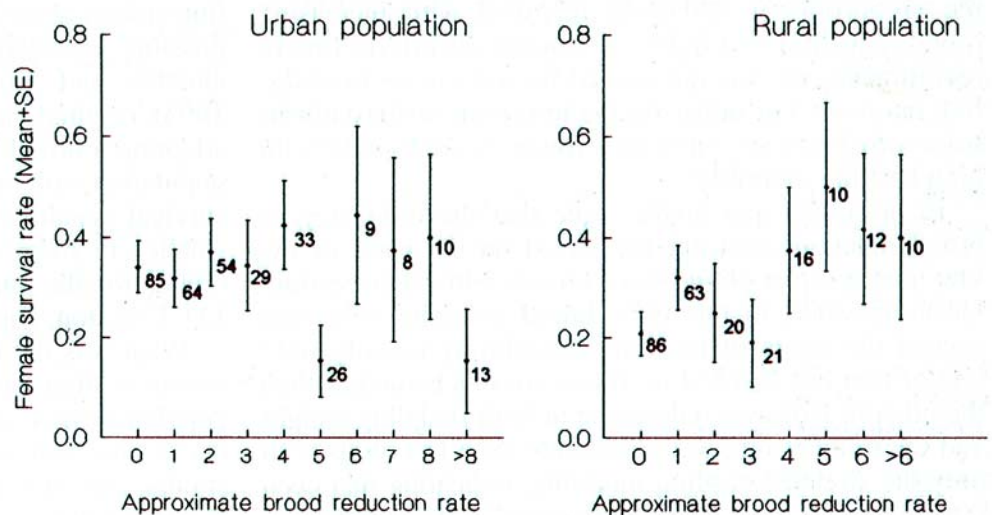


Fig. 4 Relationship between female survival rate and approximate (see methods) brood reduction rate. Pooled data from 1987–1994. Trend is significant for rural population: $\pi = 1/[1+\exp\{1.21-0.13(\pm 0.06) \text{ brood reduction rate}\}]$, one-tailed $P = 0.014$, $N = 228$, but not for urban population: $\pi = 1/[1+\exp\{0.61-0.03(\pm 0.05) \text{ brood reduction rate}\}]$, one-tailed $P = 0.238$, $N = 331$



The probability of female survival increased with brood reduction rate in the rural population: $\pi = 1/[1+\exp\{1.34-0.24(\pm 0.15) \text{ brood reduction rate}\}]$, 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 $\times$ "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 (Hörak 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. Hörak 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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