EFFECTS OF LOCAL ENVIRONMENTAL CONDITIONS ON NESTLING GROWTH IN THE GREAT TIT Parus major L.

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ABSTRACT Daily weight increments of nestling Great Tits are expressed as ratios of observed increment divided by the increment expected under favourable conditions. We used this ratio to examine the effects of local environmental conditions on nestling growth. We demonstrate a positive relationship between nestling growth and food availability at that time and location. This relationship is stronger with the maximum rather than the median prey availability for the three to five trees sampled at a location. Residuals of the regression of the realized growth ratio on age are used to demonstrate a 10 to 20% reduction of growth on days with some daytime rain above one millimeter per hour, relative to growth in the same brood on dry days. Our trapping of the adults had an effect on nestling growth similar to that of two to three hours of rainfall. Finally, we show significantly later fledging in broods with slow growth.

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INTRODUCTION

Recently variation in avian growth patterns has received considerable attention. Studies have attributed intraspecific variation in growth to a variety of environmental factors (for detailed references see e.g. Ricklefs 1983; O'Connor 1984; Richner et al. 1989) and genetical effects (e.g. Ricklefs 1983; van Noordwijk et al. 1988; Gebhardt-Henrich & van Noordwijk 1991). Growth patterns have been used in particular as a tool to assess the impact of environmental contaminants on populations of birds (e.g. Fendley & Brisbin 1977; Brisbin et al. 1986a; Brisbin et al. 1986b; Brisbin et al. 1987; Williams & Croxall 1990; Zach & Mayoh 1986).

Environmental influences during ontogeny (i.e. growth) may have lasting effects on the phenotype if the growth of the trait is determinate, which is the case for fledging weight in Great Tits. Fledging weights are in turn causally related to subsequent survival in several species (e.g. Tinbergen & Boerlijst 1990; Gebhardt-Henrich & van Noordwijk 1991; Magrath 1991). Since in birds individual differences in offspring survival are one of the most important components of variation in parental lifetime reproductive success (e.g. chapters 8 to 20 in Clutton-Brock 1988; Newton 1989), fledging weight is an easily measurable estimate of the reproductive value of a brood (Tinbergen & Boerlijst 1990). To get more insight into how fledging weights are achieved, we have to study the growth process (i.e. the increase in body weight) and the different factors affecting growth. Despite the many studies demonstrating genetic variation in the growth performance of birds, the genetic component has usually been neglected when investigating environmental effects on growth. However, taking genetic differences into account by removing the variability they cause in the growth measurements will enhance the power to detect environmental effects on growth.

Lack (1968) suggested that the growth rate of a species is an evolutionary compromise between mortality factors selecting for more rapid growth and food limitation selecting for slower growth: when food is scarce, slow growth reduces the dai-
ly energy requirements and enables parents to rear more offspring (e.g. Ricklefs 1979; Drent & Daan 1980; Ricklefs 1983). This may be crucial for the reproductive success of the parents. If we are to evaluate the savings to the daily requirement involved in slowing the growth rate, it is essential to have quantitative measures of the reduction of daily growth rates in response to short-term fluctuations in the environment.

This study quantifies the effects of differences in local environmental conditions — i.e. food availability and weather conditions — on daily growth of nestling Great Tits, while accounting for the estimated genetic component of growth. As a special environmental factor we additionally consider the effects of our interference when trapping the parents.

METHODS

Analysis of growth

To compare the growth performance of nestlings of different ages and to account for the known genetic component of nestling growth in Great Tits, we used the method described by Keller & van Noordwijk (1993). Here we will only give a brief summary of this method. The aim of this method is to quantify the influence of the environment as a parameter of growth which is basically independent of age and actual size. The basic idea is as follows (details are given later): Daily growth of the nestlings under good conditions is modelled while accounting for what is known about genetic variation in fledging weight. Environmental influences on daily growth are then represented as the growth realized under the actual conditions relative to the growth predicted for good environmental conditions. The ratio of the realized over the expected growth — henceforth called $R_t$ — is independent of age and actual size and incorporates the current knowledge about genetic components in growth of nestling Great Tits. $R_t$ is calculated for every day (or any other time period) for each nestling.

To model growth in Great Tits we used Eq. 2 from Keller & van Noordwijk (1993):

$$\frac{dW}{dt} = \frac{2(m+1)}{13(1-m)} (A^{1-m} \cdot W^{m} - W_t) \cdot R_t + e_t \quad (1)$$

where $W_t$ is the weight at time $t$, $A$ is the asymptotic weight towards which the young grow, $m$ is a parameter determining the shape of the growth curve, $R_t$ is the above mentioned ratio of the growth under good conditions that has been realized and $e_t$ is the residual stochastic error term, i.e. the random measurement error which is in the order of 0.1 g (but see Keller & van Noordwijk, 1993). For broods from several different study areas growing under good conditions, i.e. which grew during the period of peak food supply, van Noordwijk (1988) and Keller & van Noordwijk (1993) calculated $m$-values of 1.7.

In their study on the genetical ecology of nestling growth in the Great Tit, Gebhardt-Henrich & van Noordwijk (1991) found considerable genetic variation in fledging weight when conditions were good. No other parameter of the growth curve showed any significant heritability (Henrich 1989). As the genetic component of the model we therefore used the mean parental winter weight as an estimator for the asymptote $A$ of the nestlings.

The expected growth under good conditions can now be calculated for every day given the parameter values mentioned above ($m = 1.7$, $A =$ mean parental winter weight, and $R_t = 1$) and the actual weight $W_t$ of a nestling at time $t$. The measured daily growth of each nestling is then divided by this expected daily growth. This ratio is $R_t$ and is calculated for every day and each nestling. Since the time intervals between two successive measurements could not practicably be maintained at 24 hours the $R_t$-values are corrected for the different time intervals, by multiplying the $R_t$-values with 24 and dividing them by the time interval (in hours) between two consecutive measurements. $R_t = 1$ therefore means that a nestling grew as expected under good conditions. If $R_t < 1$ then some environmental factor limited growth. $R_t > 1$ indicates that a nestling grew more than expected under good conditions, which
could not only arise from environmental variation but also from compensatory growth (van Noordwijk 1988) or measurement errors. To avoid large effects of measurement errors on the estimation of $R_t$-values, all values where the expected growth was less than 0.05 g, i.e. much smaller than the random measurement error, were excluded from the analysis. All tests are two-tailed.

FIELD WORK

Study area

The data used in this study were collected in two different forests near Basel, N.W. Switzerland. The Birsfelder Hard is a flat, predominantly deciduous forest with mainly Oak *Quercus robur*, Beech *Fagus sylvatica* and Hornbeam *Carpinus betulus* trees and contains about 300 nestboxes. The Great Tits had a breeding density of about 1.5 pairs per hectare during our study. The other study area – the Blauen – is situated on a northern slope of the Jura, ranging from 380 to 770 m a.s.l. The Blauen is covered with mixed woodland in which the composition of the tree species varies with altitude and exposure. In contrast to the Birsfelder Hard, Oak trees are only rarely found (usually 0-12% of the trees, with a few single territories up to 50%). About 430 nestboxes are provided at the Blauen, sustaining approximately 0.35 breeding pairs of Great Tits per hectare. Data were collected in 1989 at the Birsfelder Hard and in 1989 and 1990 at the Blauen.

Breeding biology and growth

The general field methods for recording breeding biology and growth were the same in both study areas. The nestboxes were checked at least once a week during the breeding season and daily around the expected day of hatching to record the exact hatching date. Nestlings were marked individually at day 2 (hatching = day 0), first with felt-tip pens, and later with aluminium rings. Each nestling was weighed every day from day 2 onwards with a Pesola spring balance (50 g capacity) to the nearest 0.1 g. To avoid premature fledging due to disturbance the last measurements were taken on day 15 when Great Tits usually reach their maximum weight. Further weight changes until fledging are small and usually no consistent trend is observed (e.g. Gibb 1950; van Balen 1973; Schifferli 1973; van Noordwijk *et al.* 1988). Hence we denote the weights on day 15 as fledging weights. For most broods at the Blauen study area fledging date was also recorded by checking the nestbox daily from day 16 onwards until the nestlings had left the box. Since all nestlings of a brood usually fledge within one day, the day the nestlings were last seen in the nestbox was recorded as the fledging date.

If possible both parents were caught, ringed and weighed while feeding their young, when nestlings were between 7 and 12 days old. If we were not successful in catching both parents within two hours we made another attempt the next day. Only data from first broods are used in the analyses. Some of the first broods at the Blauen in 1989 were used for experiments. The experimental design is described in van Noordwijk (1991) and included brood size manipulations and artificial delaying of hatching of some eggs in a brood. These experimental broods were excluded from all analyses with the exception of the analysis of the influence of local food availability on growth and on duration of nestling period. Since these analyses were restricted to broods around the eight locations where food availability was measured (see below) and since experimental broods did not differ from natural broods in their reaction to food availability (see Fig. 3, open circles) they were included in these analyses to increase sample size.

Local food availability

At the Blauen study area local food availability was measured weekly at 8 different locations, starting one to two weeks before bud burst and continued as long as there were nestlings of first broods. These sites differed in elevation, exposure and composition of the tree species and were chosen to represent the different habitat types at the Blauen. Two branch samples were taken with
a skylift of 16 m maximal height from each of three to five individual trees every week at each location. The sampled trees were chosen to be representative for the composition of tree species at that location. Since deciduous trees support roughly 50 times more caterpillar biomass than coniferous trees (van Balen 1973) and since caterpillars are the predominant prey item of Great Tits (e.g. van Balen 1973; Perrins 1979; Török 1986) branches were collected only from deciduous trees (Oak, Hornbeam and Beech). Food availability was estimated as the fresh weight (in mg) of the caterpillars per 10 m branch. Zandt (1994) gives a detailed description of the methods used. At the Birsfelder Hard food supply was measured in a similar manner. In contrast to the Blauen area elevation and exposure are the same all over the Birsfelder Hard so that 46 trees (Oak, Beech, Hornbeam and Ash *Fraxinus excelsior*) distributed over the whole study area were sampled.

For each location and sampling date at the Blauen study area two different measures of food supply were calculated: the median food availability of all six to ten samples of a given location; and the maximum food availability, that is the mean of the two samples from that tree at every location with the highest caterpillar biomass on that particular date. To achieve normality, a $\log_{10}$-transformation was applied to the data. In the case of the Blauen 1990 data, a few data points were strong outliers (Fig. 4). Therefore, we used robust regressions based on the least median of squares method (Rousseeuw & Leroy 1987) to analyse the effect of food availability on growth in 1990. The food availability measured for each location and sampling date was assumed to be representative for all broods recorded at that time within approximately 200m of the sampled trees. As shown elsewhere (Keller & van Noordwijk 1993) $R_t$-values are rather sensitive to measurement errors. Particularly in broods that are growing well variation in $R_t$ due to measurement errors becomes large when the expected growth is less than 0.05 g, that is from about day 13 onwards. Since food is likely to be limiting only after the age of about 5 days we only used data from broods which were between 6 and 12 days old to investigate the effect of local food availability on growth. To further reduce the influence of measurement errors in single $R_t$-values on our analysis we calculated the median of $R_t$ of every brood over a period of three days around the sampling date. Thus we assumed that the food availability did not change considerably over this three day period.

For the time when first brood nestlings were present at the Blauen we also calculated the average maximum food availability for each location, defined as the mean of all maximum food availabilities during this period per location. This measure was used to obtain an estimate of the overall food availability at each location over the whole breeding period. Due to the different sampling scheme in the Birsfelder Hard no local food availability could be estimated. Instead, the average food availability on individual trees over the whole sampling period was calculated. These values were used to compare food availability between the Blauen and the Birsfelder Hard.

**Weather conditions**

Several bird species are known to reduce their feeding frequency during rain (see e.g. Kluijver 1950; Perrins 1979; O'Connor 1984) and the reduction is larger when the rain is stronger. Great Tits show a considerable reduction in foraging effort only when rain intensity exceeds about one millimeter per hour (pers. obs.). The important factor in connection with growth performance is therefore likely to be a combination of duration and quantity of rainfall. Hence, we only considered daylight hours with more than one millimeter precipitation per hour as rainy hours. A rainy day was defined as a day with at least one hour with more than one millimeter precipitation. Mean as well as maximum and minimum daily temperatures were used to investigate the influence of temperature on growth. Data on hourly weather conditions and daily mean values were provided by the Schweizerische Meteorologische Anstalt from their measuring station Binningen Sternwarte near Basel, about 7 km North of the Blauen study area and about 7 km WSW of the Birsfelder Hard.
Due to the fact that food does not usually limit the growth performance during the first few days of the growth period, broods growing when food is limited show a negative correlation between $R_t$ and age (see Keller & van Noordwijk 1993). To correct for this general relation when analysing the influence of short-term environmental fluctuations such as rain, we used the residuals of a weighted linear regression of $R_t$ versus age per brood instead of the absolute $R_t$-values. To calculate the regression line the weights of all $R_t$-values larger than ±3 were set to zero thus providing a robust estimate of the regression line (Rousseeuw & Leroy 1987). Residuals of all observations were included in the data set used in the subsequent analysis. We then calculated the difference for each brood between the median residual $R_t$ of all days without rainfall and the median residual $R_t$ of all rainy days. If this difference is positive then the nestlings of a brood grew less on rainy days compared to all other days. The $R_t$-values from days when we caught the parents were excluded from these calculations.

RESULTS

Local food availability

The two study areas differed considerably with respect to the overall food availability of the different tree species. Figure 1 shows the average food availability in the course of the breeding season 1989 of oak and beech at the two study areas. Oak as well as beech clearly supported more caterpillars (in terms of biomass) at the Birsfelder Hard than at the Blauen (Median 2-sample Test using the median caterpillar biomass per individual tree, oak: $z = -2.854, p = 0.0043, n = 14$ for the Hard 1989 and $n = 6$ for the Blauen 1989, beech: $z = 2.828, p = 0.0047, n = 6$ for the Hard 1989 and $n = 21$ for the Blauen 1989). A comparison of the data from the Blauen in 1989 and 1990 shows that the median food availability during the nestling period was higher in 1990 than in 1989 (Median 2-sample Test, $z = -2.48, p = 0.013, n = 32$ trees in both 1989 and 1990), both in absolute values and

![Fig. 1. Median ± SE food availability (in log mg caterpillar biomass per 10 m branch) on oak (a) and beech (b) in the course of the breeding season 1989 at the Birsfelder Hard and the Blauen. Sample sizes are 14 oaks and 6 beeches in the Hard and 6 oaks and 21 beeches at the Blauen. Two branch samples were taken per tree.](attachment:fig1.png)

![Fig. 2. Median food availability (in mg caterpillar biomass per 10 m branch) at the Blauen in the course of the breeding season 1989 and 1990. Sample sizes are 32 individual trees in 1989 and in 1990. The horizontal bars indicate the mean hatching date ± 1 standard deviation in 1989 and 1990, respectively. Mean hatching date was April 40 and April 37 in 1989 and 1990 respectively. In both years almost all broods hatched between April 30 and April 49.](attachment:fig2.png)
due to a better synchronization of the Great Tits with their main food source in 1990 (see Fig. 2).

No relation between the median of $R_t$ and the median food availability was found at the Blauen study area in 1989 (Fig. 3a). However, there was a significant positive relation with the maximum food availability (Fig. 3b). A five times higher maximum food availability resulted in about 11% better growth of the nestlings. The relationship between median $R_t$ and maximum food availability in the 1990 data was also significant (Fig. 4b), although the increase in $R_t$ per unit caterpillar biomass was only a little more than one third of that in 1989. As in 1989 the relation between the average $R_t$ and the median food availability was not significant in 1990 (Fig. 4a).

**Weather conditions**

At the Blauen area nestlings grew on average 20.2% less in 1989 and 10.5% less in 1990 during rainy days (Wilcoxon’s matched-pairs signed-
ranks test, 1989: \( S = 62, p = 0.011, n = 19 \), 1990: \( S = 163, p = 0.009, n = 36 \), Fig. 5a&b). The reduction in \( R_t \) at the Blauen in 1990 was only about half of that at the Blauen in 1989. Most broods were between four and eleven days old when it rained in 1989 (Fig. 5d). In 1990 the age distribution is almost the same (Fig. 5e). At the Birsfelder Hard no reduction in growth performance on rainy days was observed in 1989 (mean reduction = -10\%, Wilcoxon’s matched-pairs signed-ranks test, \( S = 63.5, p > 0.1, n = 26 \); Fig. 5c). In contrast to the Blauen in 1989 most of the broods were between 10 and 15 days old when it rained (Fig. 5f). No significant correlation between the number of rainy hours per day and the amount of reduction in growth was found in any of the study areas and years (\( p > 0.19 \) in all cases). Residual \( R_t \) did not show any correlation with mean, maximum or minimum temperature of that day in either study area or year after the effect of rain was removed using partial correlations (partial Spearman correlation coefficients, \( p > 0.19 \) in all cases, sample sizes are 25, 32 and 37 for the Hard 1989, Blauen 1989 and the Blauen 1990, respectively).

Trapping the parents

Our study gives us the opportunity to test how our manipulations, particularly our trapping of the parents, affected the daily growth of nestlings. The data were analysed in a way analogous to that used in the analysis of the influence of rain. For each brood we calculated the difference in the median residual of \( R_t \) between all days when we did not trap a parent, and those days when we did. Again, positive differences represent a reduction in daily growth due to trapping. A significant reduction in residual \( R_t \) due to trapping the adults was found in 1989 at the Blauen (Table 1). The
Table 1. Influence of trapping the breeding birds on the daily growth performance of their nestlings. Differences per brood in median residual $R_t$ between all days when we did not trap an adult and those days when we trapped a parent, sample sizes and standard errors are given. Significance levels refer to the Wilcoxon's signed-rank test. A positive difference in residual $R_t$ indicates a reduction in growth. A difference in residual $R_t$ of 0.1 represents a 10% reduction in daily growth due to trapping.

<table>
<thead>
<tr>
<th></th>
<th>One parent caught per attempt</th>
<th>Two parents caught per attempt</th>
<th>All trapping attempts combined</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blauen 1989</td>
<td>$\Delta R_t (\pm SE)$</td>
<td>$n$</td>
<td>$p$</td>
</tr>
<tr>
<td></td>
<td>0.023(0.080)</td>
<td>14</td>
<td>1.0</td>
</tr>
<tr>
<td>Blauen 1990</td>
<td>$\Delta R_t (\pm SE)$</td>
<td>$n$</td>
<td>$p$</td>
</tr>
<tr>
<td></td>
<td>-0.040(0.066)</td>
<td>13</td>
<td>0.636</td>
</tr>
<tr>
<td>Hard 1989</td>
<td>$\Delta R_t (\pm SE)$</td>
<td>$n$</td>
<td>$p$</td>
</tr>
<tr>
<td></td>
<td>-0.012(0.051)</td>
<td>9</td>
<td>0.82</td>
</tr>
<tr>
<td>Blauen both years</td>
<td>$\Delta R_t (\pm SE)$</td>
<td>$n$</td>
<td>$p$</td>
</tr>
<tr>
<td>combined</td>
<td>-0.007(0.052)</td>
<td>27</td>
<td>0.744</td>
</tr>
</tbody>
</table>

nestlings grew about 12.5% less on the day(s) when we trapped one or both parents. In 1990 the 8% reduction in residual $R_t$ due to trapping is not significant. In the Birsfelder Hard in 1989 reduction in growth through trapping is just significant (Table 1). In both years and study areas, however, the reduction in residual $R_t$ is much larger when both parents were trapped at the same time (mean reduction at the Blauen in both years = 19%, mean reduction in the Hard 1989 = 13%) compared to the case when we caught just one parent at each trapping attempt (mean reduction at the Blauen, both years combined = -0.7%; Hard 1989 = -1%; see Table 1). In other words, catching just one parent per day does not reduce the growth of the nestlings whereas trapping both parents simultaneously has a severe influence on daily growth. Due to the relatively small sample sizes resulting from this kind of analysis, this difference is not statistically significant within each single year (Mann-Whitney-U-Test: Blauen 1989, $p = 0.16$; Blauen 1990, $p = 0.08$; Hard 1989, $p = 0.10$). An analysis combining the data from both years at the Blauen study area, however, showed that the difference between the effects of trapping both parents at once versus the effects of trapping just one adult bird per attempt is significant (Mann-Whitney-U-Test, $z = -2.23$, $n = 35$ for the Blauen 1989 and $n = 27$ for the Blauen 1990, $p = 0.026$; Table 1). Both years could be combined since there were no differences at the Blauen between years with respect to the reduction in growth due to trapping one or two parents per trapping attempt (Nonparametric Two-Factor Analysis of Variance, $p > 0.34$ for year effect and $p > 0.75$ for the interaction with the number of parents caught per attempt).

Duration of nesting period

By recording fledging date at the Blauen study area we could determine the length of the nesting period for most of the broods. An analysis of covariance revealed a significant decrease in the time spent in the nest with increasing median of
Table 2. Effects of growth performance on nestling period. Results are from an ANCOVA including data from the Blauen study area 1989 and 1990 with year as the effect and median $R_t$ as the covariate. Median $R_t$ refers to the median of all $R_t$-values per brood over the whole growth period until day 15. Nestling period is the difference in days between fledging and hatching date.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Sums of squares</th>
<th>df</th>
<th>$F$</th>
<th>$P$</th>
<th>$b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>median $R_t$ (covariate)</td>
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<tr>
<td>year</td>
<td>0.342</td>
<td>1</td>
<td>0.31</td>
<td>0.581</td>
<td>-</td>
</tr>
<tr>
<td>median $R_t \times$ year</td>
<td>0.354</td>
<td>1</td>
<td>0.32</td>
<td>0.575</td>
<td>-</td>
</tr>
<tr>
<td>error</td>
<td>62.343</td>
<td>56</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 6. Mean length of the nestling period at a location in relation to the average maximum food availability. Closed circles represent data from the Blauen 1989, open circles data from the Blauen 1990. No data on fledging date were available for one location in 1989, reducing sample size to seven.

In the present study we quantify the effects of several environmental factors on daily growth of nestling Great Tits. The potential to reduce the energy requirements of the nestling by slowing the growth rate during short periods of poor environmental conditions is therefore present. The energy savings for the nestlings as well as their parents resulting from the slower growth may be rather small (Ricklefs 1979, 1983; see also Weathers 1992), but the amount may be crucial when the environmental conditions are harsh anyway. The method, however, does not take into consideration any pre-hatching factors that may affect growth, e.g. egg size or quality of the egg. Although such effects have been found in the Great Tit (e.g. Schifferli 1973) their influence is usually small compared with post-hatching factors, particularly if feeding conditions are good (e.g. Schifferli 1973; Bryant 1978; Ricklefs & Peters 1981).

Local food availability
Several studies have demonstrated the influence of differences in direct measures of food availability between, as well as within, populations on nestling growth (e.g. van Balen 1973;
Bryant 1975, 1978; Moss 1979; Quinney et al. 1986; Blancher & Robertson 1987; Bortolotti 1989; Gebhardt-Henrich 1990). Experimentally providing supplemental food has also been shown to increase growth performance of nestlings (e.g. Högstedt 1981; Smith & Arcese 1988; Simons & Martin 1990). In this study we found a significant positive correlation of average daily growth of a brood with the maximum food availability in both years at the Blauen, but not with the average food availability. Thus, daily growth of nestlings was better at those locations where maximum food availability was higher, irrespective of the influence of any other environmental factor during this three day period (e.g. rain, human disturbance). This relationship is found in both years despite the large standard errors in the maximum food availability estimates which result from the fact that the mean of only two branch samples was used to calculate maximum food availability.

The fact that this relationship is found in both years implies that food was at least temporally and/or locally limiting daily growth of the nestlings at the Blauen. In 1990, however, the relationship between median $R_t$ and maximum food availability was much weaker than in 1989. In both years there was no relationship between median $R_t$ and average local food availability. The fact that daily growth is correlated with maximum food availability at a location is in good accordance with findings of a radio-telemetry study of Great Tits at the Birsfelder Hard (Naef-Daenzer pers. comm.). Their results suggest that Great Tits preferentially feed on those trees in their territory which provide the highest caterpillar abundance (Naef-Daenzer, pers. comm.). This fact is further corroborated through findings by Smith & Dawkins (1971) who showed, that in the laboratory, too, Great Tits concentrate their search in the areas with the highest prey densities.

Weather conditions

Great Tits may reduce their feeding frequency when it is raining partly because the young may need more brooding in cold weather (Perrins 1979). Additionally, caterpillars may be harder to find when it is raining; movements of the leaves and reduced activity of the caterpillars may make searching more difficult. One therefore expects a reduced daily growth of nestlings during periods of rain. Although this has been shown in several other species (e.g. Lack & Lack 1951; Dunn 1975; Moss 1979) an earlier attempt to relate variation in daily growth of nestling Great Tits to rainfall and maximum and minimum temperatures did not reveal any significant results (Schifferli 1973). However, the measurement used by Schifferli (1973), i.e. the deviation of a brood’s daily weight increment from the mean increment of all broods for each age, is not independent of actual size. With our approach we were able to show that at the Blauen study area nestlings grew about 20% less in 1989 and 10% less in 1990 during days with at least one hour with more than one millimeter rain. The lack of any correlation between the amount of reduction in residual $R_t$ and the number of rainy hours per day may be because there were only a few days with more than three hours with more than one millimeter rain. The reason might be that most broods were already quite old when it rained. Nestling Great Tits older than about eight days are likely to be less sensitive to the effects of rain since they have developed the ability to thermoregulate (Perrins 1979) and thus both parents are free to forage. Additionally, at the end of the growth period energy is allocated mainly to feather growth and no longer to the growth of bones or body weight (e.g. O’Connor 1977). Thus the reduction in daily growth may no longer be detectable with the available sample size. An alternative to this explanation is that the linear regression of $R_t$ on age per brood was biased by this accumulation of rainy days at the end of the growth period at the Birsfelder Hard in 1989. Such a bias would lead to too steep regression lines and thus mask the effects of rain during the last days of the growth period on daily growth. Two factors may have caused the difference in the reaction of the nest-
lings between the Hard and the two years at the Blauen. First, there is generally much more food available at the Birsfelder Hard than at the Blauen (Fig. 1). Thus, parents may be able to compensate for the reduced food delivery to the nestlings during rainy hours with an increased foraging effort later on during the day at the Birsfelder Hard but not at the Blauen study area. According to Kluijver (1950) Great Tits do increase their feeding rate immediately following a shower. Second, the weather data from the meteorological measuring station near Basel may be more representative of the Birsfelder Hard than for the Blauen as it is situated in the same plain as the Birsfelder Hard. Since the Blauen study area is located on the northernmost chain of the Jura it may rain more at the Blauen than our data suggest. The difference between 1989 and 1990 at the Blauen study area may not only be caused by the richer food supply but also by the fact that there were fewer rainy hours per day in 1990 than in 1989. Whereas there were on average 3.1 rainy hours per rainy day in 1989, only 1.8 rainy hours per rainy day were recorded in 1990.

No influence of mean, minimum or maximum temperature on daily growth was found. This agrees with van Balen (1973) and Schifferli (1973) who also did not detect any influence of air temperature on daily growth of nestling Great Tits. The reduced feeding frequency of the female resulting from brooding the nestlings is usually compensated by the male (Kluijver 1950). For approximately the first six to seven days the male may be capable of bringing enough food to the nest. After this period the young need less brooding leaving the female more time to collect food. This may lead to the fact that no effects of air temperature on nestling growth could be detected.

Trapping the parents

Although frequently referred to (e.g. Perrins 1979), effects of the interferences of the observer on the measurements recorded have rarely been quantified. Trapping the parents is likely to be our most disturbing activity although daily weighing of the nestlings by itself may also influence their growth performance (Keller & Keller, own obs.). Kania (1988) has analysed the effect of catching Great Tits at the nest during different stages of the breeding cycle on the frequency of brood desertion. He found that broods where the parents were caught when the young were older than 6 days and air temperature higher than 12 °C were hardly ever deserted. Since our trapping procedure followed these rules brood desertions were very rare and hardly related to our trapping attempts. However, trapping significantly reduced the growth of the nestlings during that day at the Blauen area and at the Birsfelder Hard (Table 1) but did so only when both parents were trapped at once.

At the Birsfelder Hard in 1989, the reduction in growth due to trapping both parents is less than at the Blauen. This may again be due to the greater possibility at the Birsfelder Hard of compensating for the effects of trapping by an increased foraging effort later in the day. At the Blauen the reduction in growth due to trapping both parents simultaneously is very similar in the two years. The difference between the two years at the Blauen with respect to the reduction in growth when all trapping attempts were combined in the analysis, is therefore likely to be the result of our higher trapping success in 1989.

Duration of nestling period

Broods growing under poor conditions fledged significantly later (Table 2). The prolongation of the nestling period can be rather long as shown by the range of nestling periods at the Blauen between 16 and 21 days. Prolonged nestling periods caused by slow growth extend the period over which the young are vulnerable to predators (e.g. Lack 1968) and parasites (e.g. Möller 1990). Even in nestboxes total or partial predation of Great Tit broods can occur quite often: about 12% of the first broods in 1989 and 11% in 1990 at the Blauen could be attributed to predation with certainty. Perrins (1979) reported an average predation rate of 7.6% for Great Tits broods in Wytham Wood during the nestling period. The vast majority of predation at the Blauen occurred after
the nestlings were ten days old. Thus in nestboxes too, a prolongation of the nestling period can increase the risk of predation. Hence, fast growth should be at a selective advantage. The higher the average maximum food availability at a location the shorter was the average nestling period in 1989 but not in 1990 (Fig. 6). Brood size, however, did not influence the duration of the nestling period as reported by Bryant (1975) for House Martins and Soler (1988) for Jackdaws Corvus monedula. Thus, differences in local food availability between different parts of the Blauen study area were more important in 1989 in determining the length of the nestling period than differences in food supply mediated by different brood sizes. We do not know why there is no such relationship in 1990. As pointed out by several authors (e.g. Perrins 1979), broods growing poorly may partly compensate for the reduced growth by fledging later. We do not know whether the nestlings at the Blauen in 1989 really did catch up during the elongated nestling period since we did not measure the nestlings after day 15.

CONCLUSION

The method we used (Keller & van Noordwijk 1993) has proved to be a useful approach in quantifying environmental effects on growth while accounting for differences due to different actual size, age and genetic influences. In particular, it allows daily growth increments to be related to the environmental conditions on particular days. It thereby bridges the gap between measures of fledging condition and the physiology of growth. The detected influence of trapping the parents on daily growth is experimental evidence that our method has the power to detect the effects of short-term fluctuations in environmental conditions. The reduction in median residual $R_t$ due to trapping both adults at once at the Blauen in 1989 is about the same as the one caused by rain. Since usually not more than two hours elapsed between installation of the trap and its removal, and adults may resume feeding and brooding up to about 30 minutes after release, the average reductions in foraging time due to either trapping or rain (which lasted about three hours in 1989) was similar. This and the fact that the reduction in growth after trapping both breeding birds is almost equal at the Blauen in 1989 and 1990 suggests that our method makes rather accurate estimates of environmental influences on daily growth.

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**SAMENVATTING**

De dagelijkse groei van jonge Koolmezen werd weer-gegeven als een breuk: de teller is de waargenomen groei (in grammen) en de verwachte groei onder gun-stige omstandigheden staat in de noemer. Deze maat werd gebruikt om de effecten na te gaan van lokale om-gevingsinvloeden.

Er blijkt een positieve relatie te bestaan tussen groei en de beschikbaarheid van voedsel op het betreffende tijdstip en de betreffende plaats, maar dan vooral met de hoogste beschikbaarheid die ter plekke kon worden gemeten en niet of nauwelijks met de mediaan van de gemeten waarden (Figs 3, 4).

Kennelijk zoeken de mezen vooral op de beste plekken naar voedsel. Verder kon worden aangetoond dat op dagen met regen (waarbij gedurende één uur minstens één mm regen viel) een vermindering in de groei optrad van 10-20% (Fig. 5). Dat zou te maken kunnen hebben met de behoefte van de jongen aan meer warmte onder dergelijke omstandigheden, maar ook met verslechterde fourageercondities.

Het vangen van de ouders had een effect dat verge-lijkbaar was met twee tot drie uur regen (Tabel 1). Ten-slotte bleek dat in nesten met een trage groei het mo-ment van uitvliegen significant later was (Fig. 6, Tabel 2).

JvR