

Breeding time, food supply and fitness components of Blue Tits *Parus caeruleus* in Mediterranean habitats

PAULA C. DIAS^{1,2} & JACQUES BLONDEL^{1,2}

¹ Centre National de la Recherche Scientifique, CEFE, BP5051, F-34033 Montpellier cedex 1, France

² Department of Zoology, Uppsala University, Sweden

We analysed the relationship between the timing of food availability and within-season variation of both reproductive success and nestling body size of Blue Tits *Parus caeruleus* in Mediterranean habitats. Synchronization between food supply and reproduction was expected to be positively related to fitness components. We measured deviation from maximum food supply using a parameter that we called "time-lag", which quantifies the degree of synchronization between the date of maximum food requirements by the nestlings and the date of maximum caterpillar supply in the habitat. This parameter was expected to be related to reproductive success as measured by the number and body-condition of fledglings. The predictions were that time-lag should be negatively correlated with the proportion of nestlings raised to fledging and the size of the fledglings. These predictions have been tested in different types of habitat. The results demonstrate that caterpillar supply during a critical nestling period can have a strong influence on fitness components. As predicted, synchronization with caterpillar supply is positively related to the number and body size of fledglings. Since there is large between-habitat variation in the timing of food supply, the key issue seems to be the adjustment to local patterns of food availability.

Several factors influence reproductive success in birds, but the most important is the amount of food available to raise the young (Lack 1968, Drent & Daan 1980, Martin 1987 and references therein). In species whose nestlings are mainly fed a prey which is markedly seasonal, food availability during the nestling period varies largely according to the hatching date of the nestlings and thus to laying date.

In tits (*Parus* spp.), caterpillars are the preferred food during the nestling period (Perrins 1965, van Balen 1973, Blondel *et al.* 1991, Banbura *et al.* 1994). The greatest food requirements in these species occur when nestlings are about 9–10 days old (Perrins 1991, van Balen 1973). Food abundance at this time is known to affect the growth of nestlings (Garnett 1981, Gebhardt-Henrich 1990).

Caterpillars on trees feed mainly on the young leaves and become available for tits after bud burst. They reach their peak abundance (in both number and size) when the leaves are partly developed (Blondel *et al.* 1993). Therefore, the timing of caterpillar development is determined by bud burst and leaf development, which in turn (although influenced by environmental factors) vary strongly according to tree phenology. Consequently, food availability largely depends on the dominant tree species in the habitat. Mediterranean landscapes are mosaics of habitats with deciduous and evergreen trees. Deciduous trees renew their whole foliage annually, whereas evergreen trees renew only c. 30% of their foliage every year, and leaf growth starts several weeks later (Floret *et al.* 1989, Blondel *et al.* 1992, Blondel & Dias

1994). Therefore, caterpillars are expected to be more abundant and available earlier in deciduous than in evergreen habitats (Blondel *et al.* 1992). Such features must have important consequences for the breeding of tits, especially for the local timing of reproduction. A common feature in most Mediterranean ecosystems is a large diversity of arthropod species, of which few are abundant (Owen 1977, Blondel *et al.* 1991). Zandt *et al.* (1990) have shown that in the Mediterranean region deciduous oaks produce much lower densities of caterpillars than in the Netherlands and that evergreen oaks may produce even fewer caterpillars. Therefore, food constraints on the reproduction of tits are likely to be much stronger than in northern Europe (Blondel *et al.* 1991).

Blue Tits *Parus caeruleus* breeding in the Mediterranean region show a large between-habitat variation in the timing of reproduction, reproductive success and degree of synchronization between the period of maximum food requirements of the nestlings and the peak date of food abundance (Cramm 1982, Isenmann *et al.* 1987, Clamens 1990, Blondel *et al.* 1992, 1993, Lambrechts & Dias 1993, Blondel & Dias 1994, Dias *et al.* 1994). In tits, the degree of synchronization between the timing of breeding and food supply can be quantified by determining both the date of maximum food demand (by monitoring reproduction) and the food peak date (by monitoring caterpillar abundance) (van Balen 1973, Perrins 1991, Blondel *et al.* 1993). We can calculate the difference between these dates, the so-called "time-lag",

Table 1. Mean values \pm s.e. of breeding traits of Blue Tits in each of the three study sites for 1991–1993 combined. Only first clutches and broods with at least one fledgling were considered

| Study site | <i>n</i> | Laying date | Clutch size | Number of fledglings | Breeding success | Fledging success | MFD–CPD (days) |
|------------|----------|-----------------|----------------|----------------------|------------------|------------------|-----------------|
| MD | 118 | 41.8 \pm 0.60 | 9.7 \pm 0.15 | 7.2 \pm 0.24 | 0.74 \pm 0.02 | 0.82 \pm 0.02 | 7.10 \pm 0.67 |
| ME | 25 | 55.3 \pm 3.5 | 8.4 \pm 0.26 | 6.0 \pm 0.42 | 0.73 \pm 0.05 | 0.79 \pm 0.05 | –20.1 \pm 1.6 |
| IE | 84 | 71.5 \pm 1.1 | 6.6 \pm 0.15 | 5.2 \pm 0.23 | 0.78 \pm 0.03 | 0.89 \pm 0.03 | 5.95 \pm 0.79 |

n = sample size (number of broods); MFD = maximal food demand; CPD = caterpillar peak date; MD = mainland deciduous; ME = mainland evergreen; IE = island evergreen.

which can be used to quantify the match or mismatch between breeding and the period of maximum food supply (Dias *et al.* 1994, Dias 1995).

We assume that (1) the amount of food available for raising young determines their number and quality; (2) the number and quality of fledglings are important components of fitness; (3) in altricial birds, final body size depends on food availability during growth (Boag 1987, van Noordwijk *et al.* 1988); and (4) nestling body size is a good estimate of survival (Garnett 1981, Nur 1984a, Smith *et al.* 1989). In particular, nestling mass reflects the fitness of a brood (Nur 1984b, 1987, Tinbergen *et al.* 1987) because it is related to recapture rate (Nur 1984a), to survival (Perrins 1965, Gebhardt-Henrich & van Noordwijk 1991), and, for males, to the probability of getting a territory (P.J. Drent, pers. comm.). Body-mass is a measure of both body size and body-condition (Garnett 1981, Lindén 1990), and fledging mass reflects the overall feeding conditions during the growth period (Perrins 1979, Zach 1988).

Since time-lag measures deviation from optimality in food supply for the nestlings, its value should have consequences for some fitness components. We predict that this time-lag should be negatively related to the proportion of nestlings fledged and their size and mass, which depend strongly on the food conditions. The aim of this study was to test these predictions in different habitats.

STUDY AREAS AND METHODS

Study plots

The study was carried out in three study plots. Two of them are located near Montpellier, southern France; one was an evergreen habitat dominated by the Holm Oak *Quercus ilex* (the site hereafter referred to as ME for “mainland evergreen”), and the other was a deciduous forest dominated by the Downy Oak *Q. pubescens* (hereafter called MD for “mainland deciduous”). The third study plot was located on the island of Corsica and is dominated by the evergreen Holm Oak (hereafter referred to as IE for “island evergreen”). Details of the study plots can be found in Blondel *et al.* (1993). In each study plot, 100 to 150 nest-boxes were erected at a density of c. 2 nest-boxes per ha. The nest-boxes were visited

at least once a week for routine inspection throughout the breeding seasons of 1991, 1992 and 1993.

Breeding traits and reproductive success

For each breeding pair we recorded laying date, clutch size, number of fledglings, breeding success (number of young fledged/number of eggs laid) and fledging success (fledged/hatched young). Nests where nestling mortality was due to factors other than food shortage (e.g. predation) were not used to estimate reproductive success. Hatching date was recorded as day 0, and this date was used as a reference to determine the tenth nestling day, which is the period of maximum food requirements by the young (hereafter called MFD for “maximum food demand”). Dates are numbered with 1 March = 1.

Food abundance

Food availability was studied in five sites within each study plot by monitoring caterpillar frass weight through time. The abundance of caterpillars was estimated by collecting their droppings twice a week during the breeding season using 0.25-m² trays randomly erected under the canopy of the oaks (15 trays per plot). Droppings of the Gypsy Moth *Lymantria dispar* (identified by their very distinctive large size, egg-shape and sharply ridged surface) were discarded because this caterpillar is not eaten by tits (Zandt *et al.* 1990). Data were averaged for each study plot; the “caterpillar peak date” for a plot is the day when the average value of caterpillar frass weight in that plot is highest, which probably approximates the maximum biomass.

We defined time-lag for each nest as the absolute value of the difference between the date of maximum food demand in that nest and the caterpillar peak date in the corresponding study plot (Dias *et al.* 1994).

Morphometry of adults and nestlings

Adults were captured when the nestlings were around 10 days old. We recorded the following morphometric measurements of the breeding adults: mass to the nearest 0.1 g (using a Pesola spring balance), wing-length to the nearest

0.5 mm and tarsus-length and culmen-length to the nearest 0.1 mm. When recaptures occurred, each individual was considered only once (randomly chosen).

Body size of 15-day-old young was measured by mass (to the nearest 0.1 g) and tarsus-length (to the nearest 0.1 mm); values were averaged per brood for the analysis. Since nestling tits usually reach their final body-mass by 15 days old (van Balen 1973, Schifferli 1973), mass on day 15 was called fledging mass.

Statistical analysis

The effect of time-lag and hatching date on various parameters was tested using general linear modelling (McCullagh & Nelder 1989) using GLIM (Baker & Nelder 1985).

To test for the effect of time-lag and hatching date on morphological measurements of nestlings, a model incorporating the year (YEAR) and site (SITE) factors, plus the variables describing the time-lag (TL), clutch size (CS) and hatching date (HD) was constructed (YEAR*SITE + TL + CS + HD in GLIM terminology) in order to take into account the various correlations among variables. The effect of time-lag (and, respectively, hatching date) was estimated by removing it from the model, and an index, F , was calculated from the corresponding change in deviance and in degrees of freedom according to Crawley (1993).

The same model was used to test for the effect of time-lag and hatching date on measures of reproductive success. When breeding success or fledging success was considered, the model was established on a logit scale (binomial logit-linear model). When the absolute number of fledglings was considered, the model was established on a log scale (Poisson log-linear model). Effect of time-lag (and, respectively, hatching date) was estimated by removing it from the model, and the resulting changes in deviance and in degrees of freedom were used as an approximate chi-squared test (Crawley 1993).

Because body size is partly heritable (Dhondt 1982, van Noordwijk *et al.* 1980, 1988), a relationship between offspring morphometric traits and time-lag could be due to a correlation between parent morphometric traits and laying date. To avoid these confounding effects, we tested the effect of laying date on morphological measurements of breeding adults (wing-size, culmen-size, tarsus-length or body-mass) using a model incorporating the year and site factors plus the variables describing the laying date (LD) (YEAR*SITE + LD in GLIM terminology). The effect of the laying date was estimated by removing the variable LD from the model, and an index, F , was calculated from the corresponding change in deviance and in degrees of freedom (Crawley 1993). This procedure was performed separately for males and females.

RESULTS

Breeding traits

Average breeding parameters and time-lag for each study plot are summarized in Table 1, and details for each year

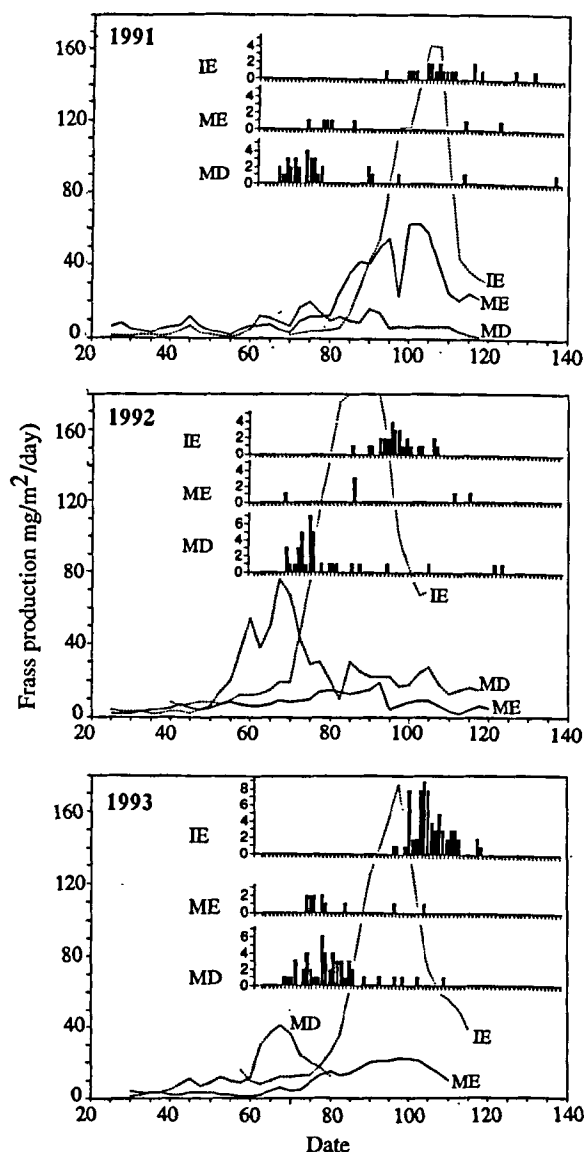


Figure 1. Seasonal variation in the frass production for each habitat and for each year (for date, 1 March = 1). The distribution of the maximum food demand (MFD) for each nest in each habitat and on the same time scale is shown in the histograms. MD = mainland deciduous; ME = mainland evergreen; IE = island evergreen.

are shown in Figure 1. Plot IE showed the latest laying date and the smallest clutch size but the highest breeding and fledging success; MD had the earliest laying date, the highest clutch size, the smallest time-lag and intermediate values of reproductive success; ME showed intermediate laying date and clutch size but the largest time-lag and the smallest reproductive success.

Reproductive success and time-lag

The absolute difference between the caterpillar food peak and the maximal food requirements of the nestlings, or

Table 2. Effect of hatching date and time-lag on measures of reproductive success. For each measure (breeding success, fledging success and number of fledglings) a linear model incorporating several factors (year, site) and variables (clutch-size, time-lag, hatching date) was fitted to the data. See text for details. The change in deviance observed when one variable was removed was tested (P-value). "Effects" are all negative

| Removing one variable | n | Breeding success | | Fledging success | | No. of fledglings | |
|-----------------------|-----|--------------------|-------|--------------------|-------|--------------------|------|
| | | Change in deviance | P | Change in deviance | P | Change in deviance | P |
| Hatching date | 210 | 1.3 | n.s. | 0.21 | n.s. | 0.55 | n.s. |
| Time-lag | 210 | 5.5 | <0.02 | 7.2 | <0.01 | 2.24 | n.s. |

time-lag, significantly explained the variation in fledging and breeding success but not in number of fledglings (Table 2). All effects were negative, suggesting that higher reproductive success is associated with lower time-lag. Possible confounding variables such as study plot, year, clutch-size and hatching date were controlled. The effect of the hatching date did not explain the variability in breeding traits (Table 2).

Adult body size and laying date

No significant effect was found between laying date and morphometric parameters for males or females (results not shown), and no clear pattern emerged. We can thus exclude heritability of body size as a confounding effect in the seasonal variation of nestling body size.

Nestling body size and time-lag

Nestling tarsus-length was significantly longer when hatching date was late and when the time-lag was shorter, i.e. when the maximal food demand was closer to the caterpillar food peak but preferably on the later rather than the earlier side of the food peak (Table 3). Possible confounding variables (hatching date, year, site, clutch size) were controlled. The same tendencies and significant effects were also found for nestling mass (Table 3).

Table 3. Effect of time-lag and hatching date on tarsus-length and mass of nestlings. "Effect" indicates in which way the variable influences the morphometric parameters. *F* is computed from the change in scaled deviance when the considered variable is removed from the linear model (see text for details). All "effects" were significant

| Variable | Tarsus-length | | | Mass | | |
|---------------|---------------|---------------------------|-------|--------|---------------------------|--------|
| | Effect | <i>F</i> _{1,135} | P | Effect | <i>F</i> _{1,160} | P |
| Hatching date | + | 5.58 | <0.02 | + | 5.05 | <0.03 |
| Time-lag | - | 7.52 | <0.01 | - | 10.6 | <0.002 |

DISCUSSION

This study demonstrated an effect of the time-lag between the date on which caterpillar biomass peaked and the day when nestling demand was greatest on the reproductive success of Blue Tits expressed by the number and quality of the young produced.

Because the aim of the study was to evaluate the influence of food availability on the number and quality of offspring, we excluded from the analyses nests where nestling mortality was obviously due to factors other than food shortage (e.g. predation or nest desertion following manipulation), and we included only broods in which at least one young fledged. Therefore, the estimates of reproductive success presented here are overestimates and do not correspond exactly to the natural average reproductive success of the habitats (the latter would have to be used if we wanted to analyse for instance the demographic functioning of the study populations).

Previous results (Dias *et al.* 1994) predicted that the larger the time-lag, the lower the Blue Tit's reproductive success. In all cases, global tests (taking into account year and plots plus other possible confounding variables like clutch-size and hatching date) for breeding success and fledging success resulted in significant probabilities, and this supports the predictions. The effect was not significant, however, for the number of fledglings.

If adult body size and laying date were correlated, seasonal variation of nestling body size might be explained by heritability of body size alone. However, since no systematic relationship was found between adult body size and laying date (results not shown), we assume that the observed within-season variation of nestling body size is mainly due to environmental factors, namely food supply.

Although hatching date determines the time delay between maximal food requirements and the food peak date, there is not a linear relationship between hatching date and time-lag. The fact that hatching date has no significant effect by itself indicates that the important cue to take into account is the size of the deviation of the mismatch, irrespective of being early or late.

According to life-history theory, the larger the time-lag

the smaller the size of the young. All effects of the time-lag on both nestling weight and nestling tarsus-length fit this prediction (Table 3) and were significant. It is worth emphasizing that the effect of hatching date and the effect of time-lag on nestling body size have opposite signs (Table 3); this means that it is advantageous for the nestlings to have their maximal food requirements as close as possible to the food peak, but it is better to be late than early. In other words, the advantages of matching the food peak are asymmetrical: if food shortage is unavoidable, it has less influence on fledgling morphometry if it occurs after the age of 10 days than at an earlier age.

Although some differences in reproductive success and/or nestling mass among our study sites may be explained by differences in caterpillar abundance between deciduous and evergreen habitats, they seem to be better explained by the degree of synchronization between reproduction and local caterpillar peak date. At both MD and IE the breeding time matches the caterpillar peak date (Table 1, Fig. 1; see also Blondel *et al.* 1992, 1993). In spite of a year-to-year variation within each plot, the significant negative effect between time-lag and nestling mass indicates that Blue Tits are strongly dependent on the caterpillar supply for raising their young.

The amount of food during a critical period of the nestling stage is strongly related to fitness components, such as the number and quality (i.e. body size and/or condition) of young produced. Deviations from optimal time of breeding relative to food supply result in lower reproductive success and lower nestling body mass. Since there is large between-habitat variation in the timing of food supply, the key issue seems to be how tits adjust to the local timing of food availability.

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