Food, reproductive success and multiple breeding in the Great Tit Parus major

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FOOD, REPRODUCTIVE SUCCESS AND MULTIPLE BREEDING IN THE GREAT TIT *PARUS MAJOR*

NANETTE VERBOVEN[1,3], JOOST M. TINBERGEN[2] & SIMON VERHULST[2]

We studied the reproductive success of facultatively double brooded Great Tits *Parus major* in relation to (seasonal) variation in abundance of their main food supply: caterpillars in Oak *Quercus robur*. Data were collected in two mixed woods (Vlieland and Hoge Veluwe, from 1985-1996). The caterpillar food stock is characterised by a strong peak in the breeding season, and height and timing of this peak vary between years. In first broods, nestling survival, number of fledglings and fledging mass were highest at the time of the food peak and lower before and after this time. Clutch size, and success of the first clutch, were positively related to the caterpillar density on individual territories. On the annual level, multiple breeding (defined as the proportion of pairs starting a second clutch after fledging young from the first brood) occurred at increasing frequency as the tits bred earlier relative to the food peak, while there was no additional effect of absolute laying date. As has previously been shown, also within years multiple breeding decreased strongly with time. Early in the season, family-flocks foraged in Oak, and later switched to Pine *Pinus nigra*, and we hypothesise that multiple breeding is more frequent in early breeding pairs, because good feeding conditions for the family flock may reduce the effect of a second clutch on fitness of the first clutch. Time that the family-flocks spent in Oak was longer when breeding was earlier relative to the food peak, and the incidence of multiple breeding increased with increasing time spent in Oak, which provides correlational support for this hypothesis. The actual amount of food present did not affect the occurrence of multiple breeding, although the inter-clutch interval decreased with increasing food supply. The natural patterns were confirmed with a supplementary feeding experiment, which increased nestling growth, and resulted in shorter inter-clutch intervals, but had no effect on the occurrence of multiple breeding. Since success of the first clutch increased as the birds bred closer to the caterpillar peak, while the probability of a second clutch decreased, a trade-off exists between the fitness of the first clutch and the residual reproductive value of the parents, which will affect the optimal time of breeding. This trade-off is likely to be less important in single-brooded populations, where individuals should perhaps simply breed close to the food peak. This contrast is illustrated by the finding that the annual timing of breeding in our two multiple breeding populations was not related to the date of the caterpillar peak, which contrasted significantly with the positive relationship previously reported for two single-brooded populations (Oosterhout, Wytham).

Key words: *Parus major* - caterpillar abundance - food availability –postfledging care - reproductive success - second clutches - timing of breeding - trade-off

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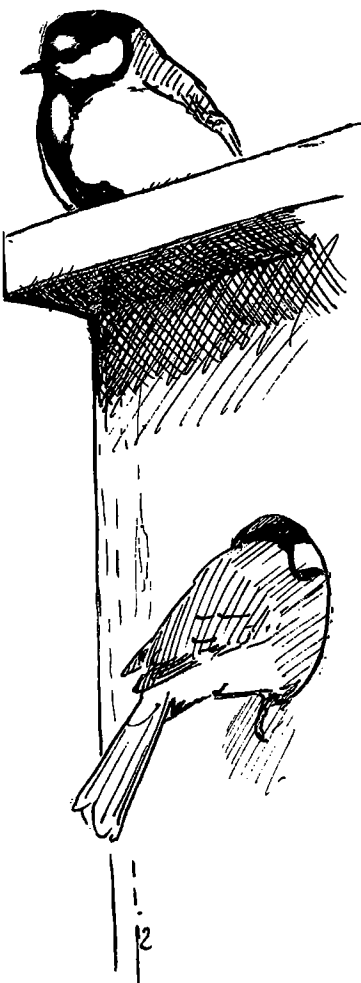
INTRODUCTION

In seasonal environments the timing of breeding is an important life history decision and the breeding time which maximises fitness depends on seasonal changes in the fitness value of the brood and the parents. Lack (1950, 1968) suggested that birds should time reproduction so that the peak demand of the nestlings coincides with the peak in food supply, since this would maximise fledgling production. Perrins (1970) emphasised the proximate role of food in the timing of breeding by suggesting that birds may breed later than the food peak due to food shortage during egg laying. The picture was further modified by Daan et al. (1989) who showed that, when there is a seasonal decline in recruitment probability, parents would maximise fitness by starting reproduction before the food peak. A seasonal decline in the future reproductive prospects of the parents would have the same effect, a pattern found in e.g. facultative multiple breeding species where the frequency of multiple breeding generally declines through the breeding season (Geupel & DeSante 1990; Møller 1990; Stoufer 1991; Hepp & Kennamer 1993; Verboven & Verhulst 1996).

A seasonal decline in reproductive performance may be due to time per se, but may also be caused by differences in individual and/or phenotypic quality between early and late breeders. We have previously shown, using experimental manipulations, that in Great Tits Parus major breeding on Vlieland the seasonal trend in success of the first clutch, as well as the proportion of pairs starting a second clutch was due to seasonal changes in the environment, rather than to quality differences between birds that bred at different dates (Verboven & Verhulst 1996, although this may be different in other populations, Verhulst et al. 1995). However, at present, the environmental factor responsible for the seasonal trends in reproductive performance remains unknown. Seasonal environments are characterised by temporal fluctuations in food availability and food affects several aspects of reproductive success (Martin 1987; Simons & Martin 1990; Richner 1992; Lindholm et al. 1994; Brinkhof & Cavé 1997). In this paper

we describe to what extent (seasonal) patterns in aspects of reproductive success of Great Tits can be related to (seasonal) variation in food availability, with an emphasis on the seasonal decline in the occurrence of second clutches. More in particular, we investigated clutch size and the number and body mass of first brood fledglings in relation to food availability in individual territories, seasonal variation in food availability as a potential factor influencing the occurrence of multiple breeding and interclutch intervals, the effect of food availability on tree choice during post-fledging care (Oak/Pine), and its relation to multiple breeding and we provided extra food during the first breeding attempt to test if food availability was directly related to the probability of a second clutch or the success of the first brood. In this way we describe the effects of food supply on the state of the brood up till fledging (number and quality of offspring), and these parameters can be expected to have strong effects on reproductive value of the brood. Nevertheless, it must be kept in mind that early fledglings probably have a competitive advantage over late fledglings (Verhulst 1992, and references therein), and early fledglings may experience better foraging conditions during post-fledging care (see below). Thus number and quality of fledglings cannot simply be translated in number of recruits.

The diet of Great Tit nestlings consists largely of caterpillars, such as the Winter Moth Operophtera brumata and the Green Tortrix Tortrix viridana (Betts 1955; Gibb & Betts 1963; Royama 1970; Van Balen 1973; Minot 1981; Török 1986; Cowie & Hinsley 1988; Perrins 1991; Bañbura et al. 1994). Thus with respect to measurements of the food supply we restricted ourselves to caterpillars in Oak Quercus robur. The development of the caterpillars is related to the phenology of their host trees (Feeny 1970; Van Dongen et al. 1997) and therefore the food supply of Great Tits shows a strong seasonal peak (Van Balen 1973; Zandt et al. 1990). We investigated the effect of food using caterpillar biomass measured in individual territories, as well as the interval between the time of breeding and the date of the caterpillar peak.

METHODS

Study areas and breeding birds

The data for this study were collected in two woodlands during the years 1985-1996. Both Vlieland (295 ha) and Hoge Veluwe (160 ha) are part of a long-term study of the breeding biology of the Great Tit (Kluyver 1971: Van Balen 1973; Tinbergen *et al.* 1987). The areas are covered with mixed vegetation dominated by Pines *Pinus nigra* and Oaks. During the breeding season nestboxes were inspected once per week. Hatching dates were recorded by checking the nestboxes around the expected day of hatching, or by comparing newly hatched chicks with chicks of known age. Parents were caught at the nest and ringed when the young were 7-10 days old. Chicks were ringed and weighed to the nearest 0.1 gram at the age of 15 days.

Second clutches were defined as clutches produced after a successful first brood (*i.e.* a brood of which at least one chick fledged). Great Tits usually do not switch mates between the first and the second breeding attempt (Kluyver 1951, personal observation). Therefore, first and second clutches were matched on the basis of the identity of the female. The length of the interclutch interval was defined as the number of days between hatching of the first brood and the first egg of the second clutch. Ideally, we would have used the interval between the end of parental care for the first breeding attempt and the start of the second clutch, however we do not have accurate information on fledging date or the end post-fledging for all years and areas included in this study.

In six years (1989-1995, excluding 1992)

family flocks were observed during the post-fledging care period in the largest woodland on Vlieland ('Bos bij Dorp'). The whole area was searched every two days and family flocks were identified by their colour rings (see for details Verhulst & Hut 1996). For each observation we noted the tree species in which the birds were found foraging (Pine, Oak or a deciduous tree other than Oak). Since the majority of observations recorded in deciduous wood occurred in Oak (84%), for simplicity we lumped all observations in deciduous trees into one group which we refer to as Oak. 42-99 different families were observed in each breeding season, and in total there are 1896 observations for which the tree species was known.

Food availability

Caterpillar abundance was measured by collecting caterpillar frass in a cheese cloth net placed under an Oak tree (Tinbergen 1960; Van Balen 1973; Liebhold & Elkinton 1988a; Fischbacher *et al.* 1998). To reduce sampling error (Liebhold & Elkinton 1988b; Zandt 1994) we sampled several trees (range 1-8) in each locality. Frass was collected over an average period of five days (range 2-16). Frass was not collected on days with heavy rain. Frass was air dried, then separated from debris, and weighed to the nearest 0.1 mg. We converted frass mass into caterpillar biomass following Tinbergen & Dietz (1994), using temperatures from the meteorological stations of the KNMI in Den Helder and De Bilt, for Vlieland and the Hoge Veluwe, respectively. Caterpillar biomass was expressed as g m^{-2}, and log-transformed prior to analysis because of the skewed distribution.

Table 1. Number of local caterpillar measurements near nestboxes with 12 day old young on Vlieland and on the Hoge Veluwe in different years. Numbers in brackets indicate the number of broods that did not fledge. Only successful first broods were included in the analyses, because they were potential candidates for a second clutch.

	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	Total
Vlieland	-	-	-	-	11	10	10	8(1)	-	18(3)	-	57(4)
Hoge Veluwe	9(1)	9	10	16(2)	-	-	-	24(1)	-	-	-	68(4)

To obtain a global estimate of seasonal fluctuations in food availability we collected caterpillar frass at Vlieland (eight years, 1988-1995) and the Hoge Veluwe (twelve years 1985-1996) in 10, respectively 6-11 standard localities scattered over the study area. On Vlieland these were the same localities in each year, except 1988, while on the Hoge Veluwe different trees were sampled each year. The frass samples were taken throughout the breeding season. For each year and area we calculated the mean caterpillar biomass per day for every sampling period. The date of the annual caterpillar peak was defined as the midpoint of the interval in which the highest daily caterpillar biomass production was recorded (listed in Appendix). This date was highly synchronised between trees.

To measure local food availability, we selected the 2-3 Oak trees nearest to a nestbox that contained a Great Tit brood. These measurements were conducted in 1989-1992 and 1993 on Vlieland and in 1985-1988, 1992 on the Hoge Veluwe and comprised 117 broods in total (Table 1). In the early years these measurements of local food availability were taken to accompany measurements of daily energy expenditure of parents with 12-day old young (Verhulst & Tinbergen 1997). In order to standardise the measurements over all years we continued to use the same sampling intervals, *i.e.* we chose the sampling period in such a way that the date on which the nestlings were 12 days old fell in the middle of the interval. The age of twelve is a compromise between the age at which the nestlings needed the highest amount of food (9-10 days, Van Balen 1973) and the day at which we determined the fledging mass (day 15).

Relative timing of breeding

Throughout the paper we use the number of days between the date at which the young of the first brood are 12 days old and the date of the annual caterpillar peak in the study area as a measure of the relative timing of breeding. We refer to this value as R_{timing}. Negative values of R_{timing} indicate that the period in which the brood requires large amounts of food occurs before the seasonal peak in caterpillar availability, whereas positive values indicate that this period falls after the food peak.

Supplemental feeding experiment

Supplemental food was offered to 15 and 21 Great Tit broods on the Hoge Veluwe in 1987 and 1990. Mealworms (27.6 kJ g^{-1}, Graveland & Van Gijzen 1994) were provided two times a day in a small container inside the nestbox and the amount of food was adjusted to the number and age of the chicks. Starting with two times 1 g per day, when the chicks were five days old, supplemental feeding gradually increased to two times 2 g per day at day 8, after which the amount was held constant. Feeding continued until the chicks fledged and usually all food was consumed. We compared the success of the first brood, the probability of a second clutch, and the length of the interclutch interval of experimental pairs with 56 and 67 unfed control pairs in 1987 and 1990 respectively.

Data analysis

Data on proportions such as nestling survival and the probability of a second clutch were analysed with simple correlations when comparing different years. When comparing individual pairs or foraging observations in different trees, we used generalised linear models with binomial error distribution and logit link function (Crawley 1993). The data were analysed using backward deletion of the least significant terms in the model. Other variables (laying date, clutch size, interclutch interval, number of fledglings in successful nests and fledging mass) were analysed using normal error distribution and identity link function. Significance was tested by removing a variable from the model, and comparing the change in deviance with the change in degrees of freedom. P-values were calculated with F-tests. The quadratic term of R_{timing} was tested to investigate non-linear seasonal effects. Our aim was to investigate the effect of variation in food availability among pairs within a population, in a particular year, and therefore we controlled for year and area in all analyses.

This was done by including a categorical variable in the model with one level for each year of study in a study area. We collected data in nine years, but only in one year (1992) were data collected in both study areas simultaneously, and hence the categorical variable year/area has ten levels. A further categorical variable was included in the analyses to account for the brood size manipulation experiments which were carried out in both study areas (control and reduced on Vlieland, reduced, control and enlarged on the Hoge Veluwe). The 'manipulation variable' had four levels: control, reduced on Vlieland, reduced on Hoge Veluwe, enlarged on Hoge Veluwe. Since in this paper we concentrate on effects of food supply, little attention will be paid to the experimental effects, which are discussed in detail elsewhere (e.g. Tinbergen & Daan 1990; Verhulst & Tinbergen 1997).

RESULTS

Seasonal variation

In each year and study area the caterpillar biomass showed a distinct seasonal peak (Fig. 1). The date and the height of the caterpillar peak differed between years (date: $F_{11,8} = 5.4$, $P = 0.012$, height: $F_{11,8} = 6.0$, $P = 0.009$). However, there was no overall difference between Vlieland and the Hoge Veluwe either in date ($F_{1,18} = 0.0$, $P > 0.9$) or height ($F_{1,18} = 0.4$, $P = 0.5$) of the annual caterpillar peak.

First brood

Before analysing the correlations between food supply and the success of a pair in raising a particular number of offspring, we investigated whether an association existed between clutch size and food supply on the territory at the time of brood rearing. A significant positive relationship emerged between clutch size and caterpillar biomass ($F_{1,106} = 5.4$, $P < 0.025$, controlling for year and study area $F_{9,106} = 8.5$, $P < 0.001$, Fig. 2), indicating that females adjusted their clutch size to the food supply on their territory. This is a sig-

nificant achievement of the tits, since they completed the clutch approximately 26 days before the day on which the caterpillar biomass on their territory was measured. One possible explanation is that caterpillar biomass follows a rather fixed seasonal pattern (there is a strong correlation between caterpillar biomass and the over all effect of timing, $R_{timing} + R_{timing}^2$, $r^2 = 0.25$, $F_{2,114} = 19.9$, $P < 0.001$), which would be relatively easy to predict. However, controlling for R_{timing} and/or R_{timing}^2 enhanced the statistical significance of the correlation between food supply and clutch size ($P < 0.01$).

Nestling survival was quadratically related to the timing of breeding relative to the annual caterpillar peak, being at its maximum 2.5 days after the peak, and differed in level between years/study areas (Table 2A). A quadratic relationship does not necessarily imply that nestling survival first increased, and then decreased, because, for example, an increase followed by a plateau would also yield a significant quadratic term. To test directly whether the curve had a significant positive slope among the early broods and a significant negative slope among the late broods, we split the data set at the date of maximum nestling survival and refitted the model (Table 2A), excluding R_{timing}^2. This was indeed the case (early broods: $F_{1,55} = 21.5$, $n = 68$, $P < 0.001$, late broods: $F_{1,38} = 9.2$, $n = 49$, $P < 0.005$). Thus, up to the caterpillar peak nestling survival increased, and after the peak it decreased, but in contrast there was no additional effect of the amount of food that was actually measured on the territory. However, since caterpillar biomass was strongly correlated with R_{timing} and R_{timing}^2, co-linearity may explain this discrepancy. Indeed, when caterpillar biomass is substituted for R_{timing} and R_{timing}^2 in the model (Table 2A), caterpillar biomass is strongly positively correlated with nestling survival ($F_{1,103} = 7.8$, $P < 0.007$).

The number of fledglings produced showed a similar pattern as nestling survival, with the maximum found at 7.5 days after the caterpillar peak (Fig. 3A). Again we split the data set in broods that occurred before and after the day with maxi-

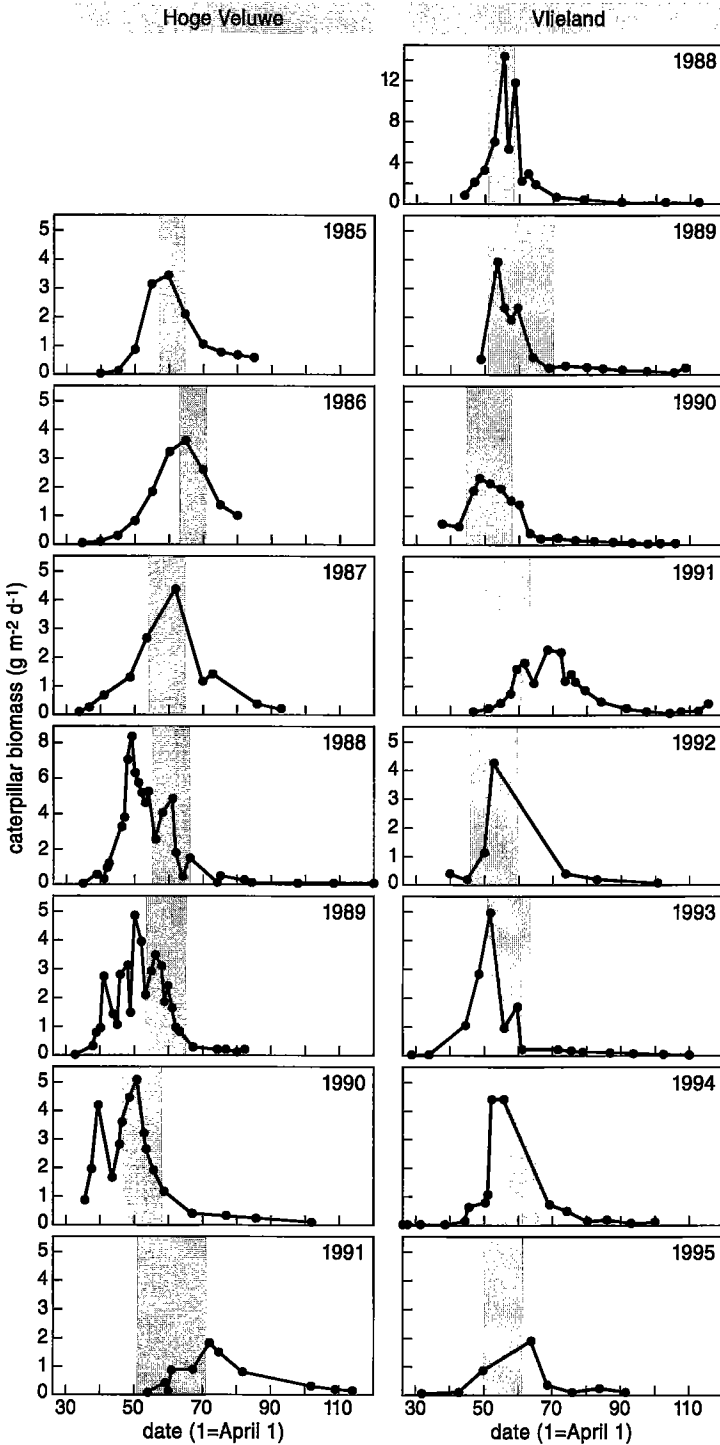**Fig. 1.** Seasonal variation in caterpillar biomass (g d^{-1} m^{-2}) measured in standard localities on the Hoge Veluwe (1985-1991) and on Vlieland (1988-1995). For 80% of the pairs the date on which they had 12-day old nestlings fell within the period indicated by the shaded areas. Dates are given as April-days (*i.e.* 31 = 1 May). Note that the biomass data for 1988 are plotted on a different scale.
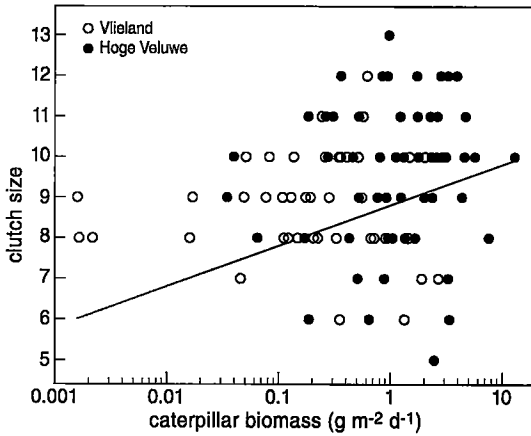
Fig. 2. Clutch size plotted against caterpillar biomass ($g\ d^{-1}\ m^{-2}$) near the nestbox when nestlings were 12 days old on Vlieland, and on the Hoge Veluw. Note that caterpillar biomass is plotted on a logarithmic scale.

mum fledgling production. The number of fledglings increased in the early group ($F_{1,79} = 15.5$, $P < 0.001$, $n = 94$), but there were only 23 broods in the descending part of the curve, and the decrease was not significant ($F_{1,14} = 0.1$, $P = 0.7$). Independent of the effect of R_{timing}, the number of fledglings increased with increasing caterpillar biomass (Table 2B, Fig. 3B).
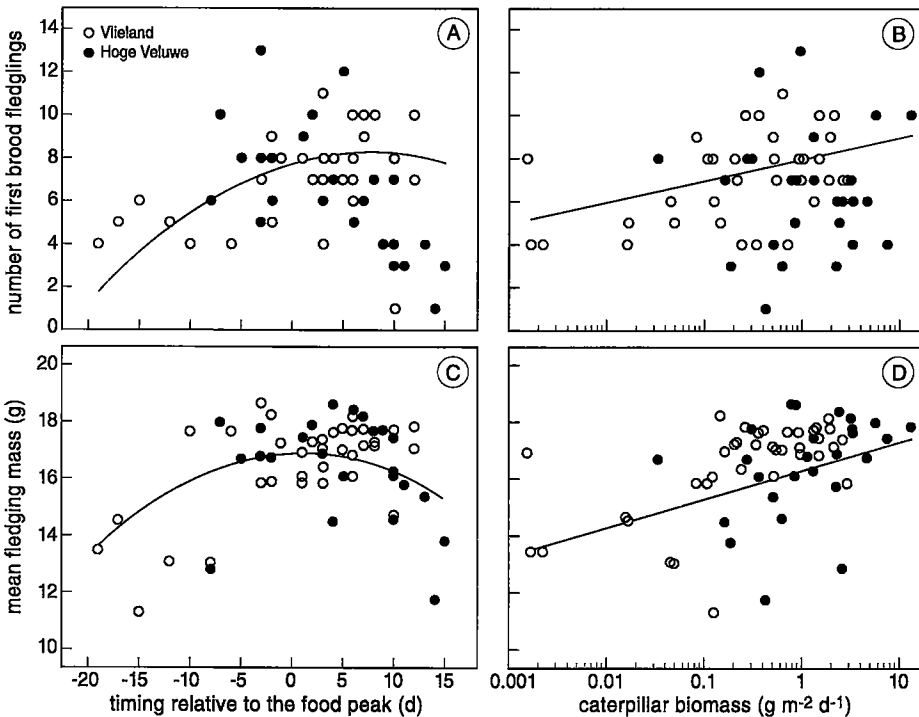
Fig. 3. Number of first brood fledglings plotted against the timing of breeding relative to the annual caterpillar peak (A) and the caterpillar biomass on day 12 of the nestling period (B). Similarly, the body mass of first brood fledglings plotted against the relative timing of breeding (C) and against the local caterpillar biomass measured on day 12 (D). For clarity, only data from unmanipulated broods are plotted, but all broods were included in the analyses (see Table 2). Note that caterpillar biomass is plotted on a logarithmic scale. Vlieland and Hoge Veluwe.

Table 2. Logistic regression model of nestling survival (A), and multiple regression models of the number of first brood fledglings (B) and fledging mass (C). Estimates of coefficients are averaged over different years and areas.

	(change in) Deviance	(change in) df	P	Estimates Coefficients ± SE
A. Nestling survival				
Null model	270.0	116		
Final model	159.2	102		
Constant		1		3.74
Year/area	38.8	9	< 0.007	
Brood size manipulation	16.1	3	< 0.02	
R_{timing}	4.3	1	0.1	+ 0.069 ± 0.029
R_{timing}^2	30.6	1	< 0.001	- 0.011 ± 0.002
Rejected terms:				
Log caterpillar biomass (g d^{-1} m^{-2})	0.5	1	0.5	
B. Number of fledglings				
Null model	889.8	116		
Final model	436.8	103		
Constant		1		8.025
Year/area	139.8	9	< 0.001	
Brood size manipulation	128.0	3	< 0.001	
Log caterpillar biomass (g d^{-1} m^{-2})	22.6	1	< 0.025	+ 0.427 ± 0.187
R_{timing}	33.8	1	< 0.006	+ 0.141 ± 0.050
R_{timing}^2	19.7	1	< 0.04	- 0.009 ± 0.004
C. Fledging mass (g)				
Null model	302.1	116		
Final model				
	176.4	101		
Constant		1		16.83
Year/area	24.1		90.1	
Brood size manipulation	35.9	3	< 0.001	
R_{timing}	0.4	1	0.6	+ 0.0161 ± 0.0319
R_{timing}^2	16.5	1	< 0.003	- 0.0081 ± 0.0026
Rejected terms:				
Log caterpillar biomass (g d^{-1} m^{-2})	5.1	1	0.08	

Seasonal variation in fledging mass also showed a convex pattern, with maximum mass at 1.0 day after the caterpillar peak (Table 2C). Fledging mass increased among early broods (R_{timing} < 1.0, $F_{1,40}$ = 5.4, P = 0.025, n = 52), and tended to decrease among late broods (R_{timing} > 1.0, $F_{1,53}$ = 3.3, P = 0.07, n = 65, Fig. 3C). Controlled for R_{timing}, fledging mass tended to increase with increasing caterpillar biomass in the territory (Fig. 3D). The effect of caterpillar biomass on fledging mass was significant when R_{timing} and R_{timing}^2 were omitted from the model ($F_{1,103}$ = 7.0, P < 0.01) and when the term year/area (P = 0.1) was not controlled for ($F_{1,110}$ = 4.4, P = 0.04).
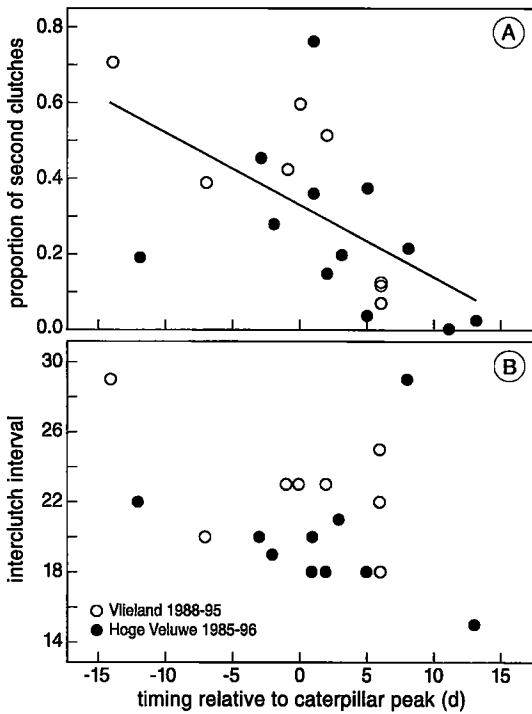
Fig. 4. A. The annual proportion of second clutches plotted against the timing of breeding, *i.e.* number of days between the average date at which the nestlings were 12 days old and the date of the caterpillar peak in that year ($r = -0.59$, $n = 20$, $P < 0.007$). Only broods of which at least one young fledged are included. B. Mean length of the interclutch interval plotted against the annual timing of breeding ($r = -0.34$, $n = 19$, $P = 0.2$). Vlieland 1988-1995 and Hoge Veluwe 1985-1996.

Proportion of second clutches

The effect of food on the proportion of pairs starting a second clutch was first analysed on the level of annual variation. There was a strong negative correlation between the proportion of pairs starting a second clutch and R_{timing}: fewer pairs started a second clutch each year as the mean timing of breeding was later relative to the caterpillar peak (Fig. 4A). Obviously, R_{timing} and absolute date of reproduction will be correlated to some extent, but R_{timing} remained significant in a partial correlation analysis when absolute calendar date was controlled for (partial $r = -0.57$, $n = 20$, $P < 0.009$), while conversely there was no significant effect of the absolute time of breeding when R_{timing} was controlled for (partial $r = -0.36$, $n = 20$, $P = 0.1$). Although the time of breeding relative to the caterpillar peak indicates that food supply has a strong effect on the occurrence of multiple breeding, there was no detectable effect of the height of the caterpillar peak on the propor-

Fig. 5. The probability of a second clutch of individual pairs plotted against the timing of breeding relative to the caterpillar peak (A). The line represents a fitted logistic regression line (see Table 3A). For graphical reasons the broods are grouped according to the relative timing of breeding. Sample sizes and 95% confidence intervals are shown. The length of the interclutch interval plotted against the relative timing of breeding (B) and the caterpillar biomass measured near the nestbox on day 12 of the nestling period (C, see Table 2B). Note that caterpillar biomass is plotted on a logarithmic scale.
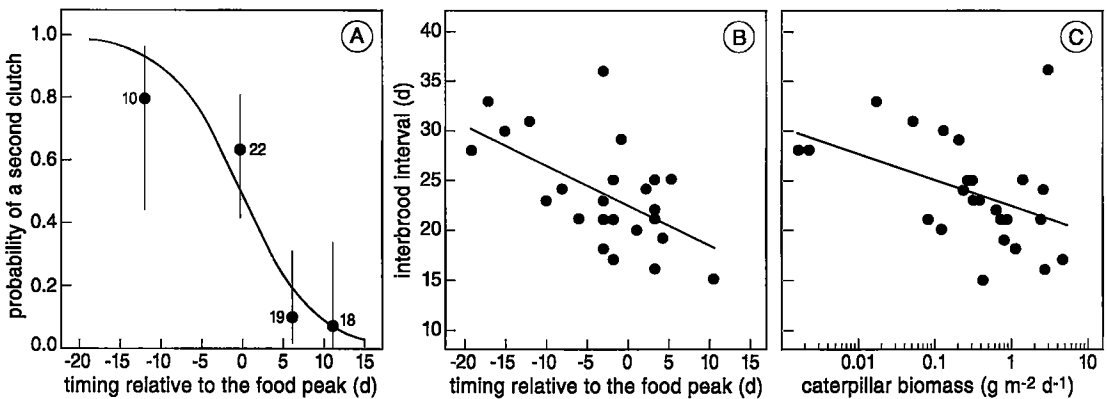
Table 3. Logistic regression model of the probability of a second clutch (A) and a multiple regression model of interclutch interval (B). Estimates of coefficients are averaged over different years and areas.

	(change in) Deviance	(change in) df	P	Estimates Coefficients ± SE
A. Probability of a second clutch				
Null model	158.4	116		
Final model	88.7	103		
Constant		1		-0.838
Year/area	25.4	9	< 0.002	
Brood size manipulation	13.0	3	< 0.003	
R_{timing}	17.9	1	< 0.001	-0.316 ± 0.090
Rejected terms:				
R_{timing}^2	0.1	1	0.8	
Log caterpillar biomass (g d^{-1} m^{-2})	0.2	1	0.7	
B. Interclutch interval				
Null model	1098.8	47		
Final model	610.5	42		
Constant	9470.5	1	< 0.001	21.92±0.86
Brood size manipulation	72.4	3	0.2	
Log caterpillar biomass (g d^{-1} m^{-2})	46.8	1	0.08	-0.70 ± 0.39
R_{timing}	151.7	1	< 0.003	-0.28 ± 0.09
Rejected terms:				
Year/area	113.0	8	0.5	
R_{timing}^2	13.6	1	0.4	

tion of pairs starting a second clutch, neither when analysed in isolation, nor when calculating the partial correlation coefficient controlling for R_{timing} (both $P > 0.4$). On the annual level the length of the interbrood interval was also not related to R_{timing} (Fig. 4B) or height of the caterpillar peak ($r = -0.15$, $n = 19$. $P = 0.6$).

Analysis of the variation within years confirmed the results on the annual level, in the sense that the probability of a second clutch declined with R_{timing} (Table 3A, Fig. 5A). This is a common result for many bird species, that has previously also been described for the Great Tit populations on Vlieland and the Hoge Veluwe (Verboven & Verhulst 1996). However, the finding that year was retained in the model indicates that yearly differences in the probability of a second clutch

existed over and above differences due to annual variation in the timing of breeding relative to the caterpillar peak (Fig. 4A). Possible causes of this variation are e.g. breeding density of Great and Blue Tits *Parus caeruleus* (Kluyver 1951, Den Boer-Hazenwinkel 1987). There was no effect of the actual amount of food present on day 12 of the nestling period, and removing R_{timing} from the model did not change this result.

Within years the length of the interclutch interval declined with increasing R_{timing} (Table 3B, Fig. 5B), and tended to decrease with increasing caterpillar biomass on the territory (Fig. 5C). In this model we did not control for year/area ($P = 0.5$), because the sample size was considerably reduced by taking only those broods which were followed by a second clutch. Brood size

manipulation was not significant in this analysis, but was nevertheless retained in the model, since previous analyses of all experimental data showed clear manipulation effects on interclutch interval (Tinbergen 1987; Verhulst 1995). Brood size manipulation can be replaced by the actual number of young that fledged ($F_{1,44} = 7.6$, $P < 0.01$), and in this model the correlation with caterpillar biomass was significant ($F_{1,44} = 4.8$, $P < 0.04$) over and above the effect of R_{timing}.

Thus we conclude that more second clutches are produced by Great Tits breeding early relative to the date of the caterpillar peak, and this is true between years as well as within years, and within years late breeding and high caterpillar biomass are independently associated with short interclutch intervals. Caterpillar biomass had no effect on the occurrence of multiple breeding, whether considered within or between years.

Food, multiple breeding and post-fledging care

The occurrence of multiple breeding was strongly related to the timing of breeding relative to the date of the caterpillar peak (Fig. 4A, 5A). However, when the young of the second brood are in the nest, the caterpillar biomass in Oak trees has become very low, and previous studies have shown that the parents feed other prey species, such as Pine-feeding caterpillars (Gibb & Betts 1963). This raises the question why the occurrence of multiple breeding is correlated with timing relative to the caterpillar peak in Oak. When a second clutch is started, parental care of the first and second clutch overlap, and this has a detrimental effect on the fledglings from the first clutch (Verhulst & Hut 1996; Verhulst et al. 1997). We hypothesise that this detrimental effect may be weaker when foraging conditions are good, i.e. when there is sufficient food to forage in Oak, and therefore we investigated the relationship between relative timing and tree choice (Oak / Pine) during post-fledging care (data collected on Vlieland only). Unfortunately, we have no data on food availability in Pine, which forces us to assume that feeding conditions in Pine change slowly relative to the changes in Oak, which seems reas-
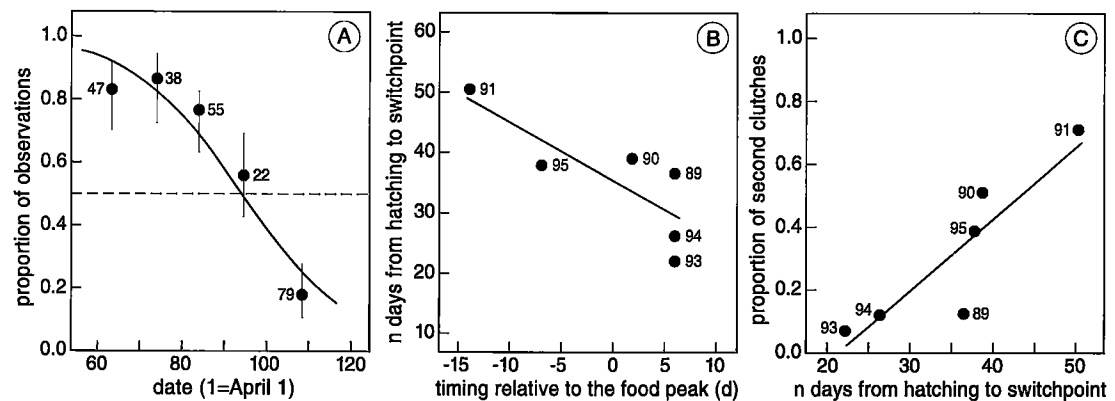

Fig. 6.   The proportion of family flocks foraging in Oak throughout the post-fledging care period in 1991. The curve represents a fitted logistic regression line ($y = 1 / e^{-(7.2 - 0.08 \times date)}$). For graphical reasons the observations are put together in groups for which the sample sizes and 95% confidence intervals are shown. The dotted line indicates the point where 50% of the observations occurred in Oak (switchpoint). Dates are given as April days (i.e. 31 = 1st of May). B. Number of days between the mean annual hatching date of the first clutch and the date at which the birds no longer showed preference for Oak trees (switchpoint) plotted against the relative timing of breeding ($r = -0.82$, $n = 6$, $P = 0.05$). C. The proportion of pairs with a second clutch plotted against the number of days between mean annual hatching date and the switchpoint ($r = 0.89$, $n = 6$, $P = 0.02$). The different years are indicated in B and C.

Table 4. Reproductive success and occurrence and timing of second clutches of pairs with and without supplementary feeding in the nestling period.

Year	Category	Hatching date (April)		No. hatchlings		Fledging mass (g)		Nestling survival	Second clutches		Interclutch interval (d)		
		mean	SD	mean	SD	mean	SD	mean	mean	n	mean	SD	n
1987	Control	45.5	3.8	8.8	2.3	17.4	1.4	0.91	0.34	58	23.9	4.1	20
	Fed	46.2	1.4	9.5	1.1	18.5	0.7	0.89	0.33	15	20.4	1.7	5
1990	Control	41.6	5.5	8.4	2.0	17.0	1.5	0.87	0.12	67	22.5	8.2	8
	Fed	39.8	3.5	8.3	1.4	17.6	1.0	0.96	0.24	21	17.0	1.0	5

onable given the data available in the literature (Van Balen 1973).

In all years of the study, Great Tit family flocks gradually changed from feeding almost exclusively in Oak to feeding almost exclusively in Pine (for example 1991, Fig. 6A). We constructed a logistic regression equation for each year of study with tree species (Oak / Pine) as dependent variable and absolute date as independent variable, and estimated the date at which half of the observations occurred in Oak. The mean time spent in Oak (defined as the number of days between mean fledging date, and the date that 50% of observations were in Oak) increased as the tits bred earlier relative to the caterpillar peak (Fig. 6B). In accordance with our hypothesis, the proportion of pairs starting a second clutch was positively correlated with the time spent in Oak (Fig. 6C), suggesting that food availability during the post-fledging care period was important for the decision whether or not to start a second clutch.

Supplemental feeding experiment

Previous analyses of the effects of food availability (Tables 2, 3) are correlational, preventing us to identify food as a causal factor in the patterns observed. Hence a supplementary feeding experiment was carried out in two years (1987, 1990) on the Hoge Veluwe study area (Table 4). As in previous analyses, broods were reduced, enlarged or unmanipulated, and manipulation and year are controlled for in the analyses. Supplemental food

had no effect on nestling survival ($F_{1,156} = 2.0$, $P = 0.2$), or the number of first brood fledglings ($F_{1,156} = 0.7$, $P = 0.4$), but resulted in increased fledging mass ($+0.9$ g, $F_{1,156} = 13.4$, $P < 0.001$). Controlled for year, hatching date, and brood size manipulation, the probability of having a second clutch was not significantly increased in fed pairs ($F_{1,155} = 0.8$, $P = 0.4$), but the interclutch interval was 4.5 days (SE = 1.8) shorter in pairs that received supplementary food ($F_{1,33} = 6.1$, $P < 0.02$).

The supplementary feeding experiment can also be used to examine to what extent the seasonal trend in reproductive success can be attributed to seasonal variation in feeding conditions. When a seasonal pattern in food availability is causally involved in this pattern, it should disappear when food is presented (at least when it is presented *ad libitum*). We restricted this test to nestling mass. The critical test is whether there is an interaction between R_{timing} and/or R_{timing}^2 and food supplementation, in such a way that the coefficients of R_{timing} and/or R_{timing}^2 are effectively zero for the fed group (Brinkhof & Cavé 1997). As in the larger sample (Table 2), a quadratic effect of R_{timing} on nestling mass was found in the two years of food supplementation (R_{timing}: $F_{1,154} = 3.6$, $P < 0.06$, R_{timing}^2: $F_{1,154} = 4.1$, $P < 0.04$, controlling for year: $F_{1,154} = 4.40$, $P < 0.04$, and brood size manipulation: $F_{2,154} = 9.9$, $P < 0.001$). Food supplementation (FS) significantly enhanced nestling mass ($F_{1,154} = 9.1$, $P < 0.004$), but this effect is apparently independent of R_{timing}, as indicated by the non-significant interactions with food supple-

mentation (FS * R_{timing}^2: $F_{1,152} = 1.3$, $P = 0.3$, FS * R_{timing}: $F_{1,153} = 1.4$, $P = 0.2$). This suggests that food supplementation enhanced fledging weight independent of timing relative to the food peak.

DISCUSSION

Success of the first brood

Nestling survival, fledgling number, and fledging mass increased with increasing caterpillar biomass on the territory (see Table 5 for an overview), despite the fact that females reduce their effort when the amount of caterpillars is high (Tinbergen & Dietz 1994). These correlational effects of food availability were partly confirmed with a supplemental feeding experiment, which enhanced nestling growth (Table 4). A correlation between local caterpillar biomass and growth was also observed by Gebhardt-Henrich (1990), Keller & Van Noordwijk (1994) and Naef-Daenzer & Keller (1999). Independent of the caterpillar biomass on the territory, there were strong effects of timing of breeding relative to the caterpillar peak (Fig. 3), success being highest when the day that the chicks were 13-20 days old coincided with the peak (slightly later than reported for another Great Tit population, Van Balen 1973). Nestling survival and fledging mass of Blue Tits were also related to the timing of breeding relative to the caterpillar peak (Dias & Blondel 1996).

When R_{timing} was controlled for statistically, only the number of fledglings was significantly correlated with local caterpillar biomass (Table 2). This is surprising, since one would expect that a local value of food availability would be more informative than a global value such as R_{timing}. However, tits forage in the trees with the highest caterpillar biomass (Naef-Daenzer 1994), and those are not necessarily the trees that we sampled. Thus R_{timing} may be a more general predictor of food supply in the places where the tits actually foraged. In addition, the abundance of other prey species may have varied in parallel with the caterpillars (due to the phenology of the Oak), which will not be reflected in our measure of caterpillar biomass.

Given that several aspects of reproductive success were correlated with local food availability, it makes sense that the tits adjusted their clutch size to caterpillar biomass (Fig. 2). Such a correlation was previously reported by Perrins (1991) on the level of annual variation, but has to our knowledge not previously been demonstrated on the level of individual territories. This is an interesting finding, because there is an interval of approximately 26 days between completion of the clutch, and the time of our caterpillar measurements. Apparently the tits are able to predict the caterpillar density, and we can only speculate on the cues the tits could use to achieve this. The tits could either sample the caterpillars (or their eggs) directly at the time of laying, or use environmental cues that predict caterpillar biomass. The most simple of

Table 5. Summary of the relationships found between the fitness components studied and different aspects of food availability: local amount of food present on day 12 of the nestling period, timing of breeding relative to the annual caterpillar peak (R_{timing}) and supplemental food. The relationships are positive (+), negative (-) or quadratic (∩).

Fitness component	Local food availability	R_{timing}	Local food availability controlled for R_{timing}	Supplemental food
Clutch size	+		+	
Nestling survival	+	∩		
Number of fledglings	+	∩	+	
Fledging mass	+	∩		+
Proportion of second clutches		-	-	
Interclutch interval	-	-		-

these would be that high caterpillar biomass m^{-2} simply reflects the size of the Oak which was sampled, which the tits can of course assess well before laying.

Food and multiple breeding

The caterpillar abundance in Oak had no effect on the proportion of pairs starting a second clutch, when comparing either years or individual territories (Table 3), and this was confirmed with a supplementary feeding experiment (Table 4). Perhaps this is not surprising, since caterpillars in Pine have replaced caterpillars in Oak as a staple food when rearing the second brood (Gibb & Betts 1963, Fig. 6A). This is related to the fact that development of caterpillars in Pine is much slower than in Oak, and hence the peak is substantially later (Van Balen 1973). In accordance with this seasonal change, Tinbergen & Van Balen (1989) found a positive correlation between caterpillar biomass in Pine and proportion of pairs starting a second clutch.

The interclutch interval was shorter when food on individual territories was more abundant (Fig. 5C), in agreement with the results of Kluyver *et al.* (1977), who reported the same relationship on the level of annual means. The relationship between interclutch interval and food availability was confirmed with a supplementary feeding experiment (Table 4), indicating a causal effect of food availability on interclutch intervals. A similar result was reported for Moorhens *Gallinula chloropus* (Eden *et al.* 1989). It is a puzzle why food availability affected interclutch intervals, but not the frequency of multiple breeding, since shorter interclutch intervals result in more profitable second clutches (Kluyver *et al.* 1977; Smith *et al.* 1989), and hence an increase in frequency is expected (Verhulst *et al.* 1997). Supplementary feeding did in fact double the frequency of second clutches in one out of two years (although this was not statistically significant). This suggests that it is perhaps premature to conclude that food supplementation does not affect the occurrence of multiple breeding. Both experimental and non-experimental studies are needed for further investigations.

Although the caterpillar abundance in Oak had no discernible effect on the occurrence of multiple breeding, timing of breeding relative to the caterpillar peak in Oak was extremely important (Fig. 4A, 5A), the proportion of pairs starting a second clutch decreasing as the tits bred later relative to the caterpillar peak. The interclutch interval also declined with time of breeding relative to the caterpillar peak (Fig. 5B). As mentioned above, it is unlikely that this can be explained by the importance of caterpillars as a food source when rearing the second brood. Different factors, not mutually exclusive, may explain this correlation. Firstly, the timing of the caterpillar peak in Oak and Pine are correlated (data Hoge Veluwe and Oosterhout from Van Balen 1973, Table 4, $r = 0.75$, $n = 9$, $P = 0.02$). Thus when the tits bred early relative to the caterpillar peak in Oak, they were probably also early relative to the peak in Pine. Secondly, as mentioned in the results section, the trade-off between successive broods could be involved, when high food availability during post-fledging care reduces the effect of a second clutch on the first brood fledglings (Verhulst *et al.* 1997). This is in agreement with Seki & Takano (1998) who found that the duration of post-fledging care was negatively related with the frass density in the territory. Also our finding that post-fledging care takes place in Oak for longer as the tits breed earlier relative to the caterpillar peak (Fig. 6B), and that time spent in Oak was positively correlated with multiple breeding (Fig. 6C) are in agreement with this hypothesis.

Optimal timing of breeding

As mentioned in the introduction, the optimal timing of breeding relative to the seasonal variation in food availability depends on the effect of breeding time on the clutch and the residual reproductive value of the parents. Our results indicate that relative time of breeding had opposite effects on the fitness of the clutch and the parents: early breeding resulted in fewer fledglings with lower mass, but enhanced the proportion of pairs starting a second clutch. However, there may be a seasonal decline in fledgling survival, indepen-

dent of their mass (Tinbergen & Boerlijst 1990; Verhulst & Tinbergen 1991; Lindén *et al.* 1992; Verboven & Visser 1998), and state of the brood at fledging is therefore not sufficient to evaluate the fitness consequences of breeding time. Previous studies investigated the effect of timing of breeding beyond fledging in our study populations (Hoge Veluwe: Tinbergen & Daan 1990, Vlieland: Verhulst 1995). For the Hoge Veluwe a shallow seasonal decline was found for the fitness contribution of the first clutch, and a slightly steeper decline in the future reproductive output of the parents. When the first clutch and later reproductive output were combined, there was a shallow seasonal decline in reproductive value. For Vlieland a slightly different picture emerged. The number of recruits from the first clutch was highest for clutches started close to the mean laying date, and declined for earlier as well as for later clutches. There was a strong seasonal decline in reproductive output from second clutches, and when the first and second clutches were combined a shallow decline in reproductive output over the whole season emerged. Thus for Vlieland there is evidence on the level of recruitment rates that a trade-off exists between first and second clutches with respect to breeding date, while this is less clear for the Hoge Veluwe.

Previous studies of single brooded Great Tit populations have shown that on the annual level the timing of breeding is highly synchronised with the caterpillar peak (Perrins 1965; Van Balen 1973). However a difference in timing-strategy between single- and multiple breeding species may exist, as is illustrated by the finding that multiple breeders advance their laying date more in response to experimental food supplementation before breeding than single breeders (Svensson 1995). Such a difference between single and multiple breeders could potentially also exist between populations of a species, or even between single and multiple brooded individuals within a population. To test this hypothesis, we compared the relationship between laying date and the date of the caterpillar peak in the two (facultatively) double brooded populations of Vlieland and the Hoge
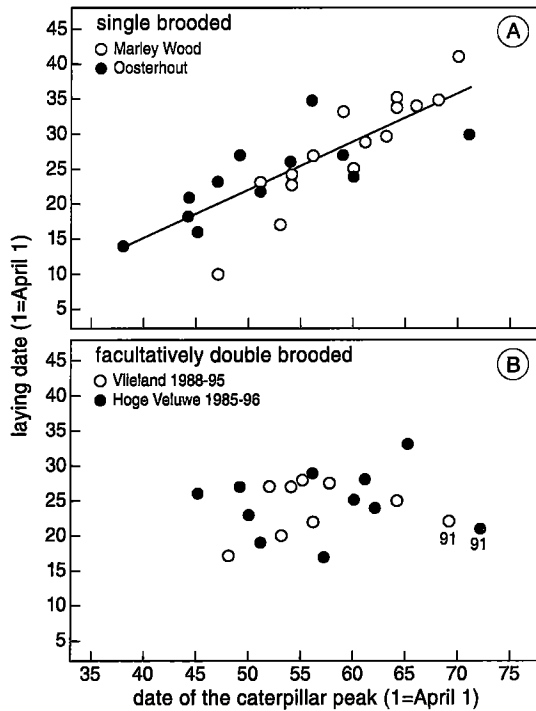

Fig. 7. The mean laying date of Great Tits plotted against the date of the annual caterpillar peak. Data of four populations are shown: (A) Oosterhout (1957-1967, Van Balen 1973 and 1996; M.E. Visser, unpublished) and Marley Wood 1948-1963 (Perrins 1965), both single brooded, and (B) Vlieland (1988-1995) and Hoge Veluwe (1985-1996), both facultatively double brooded. Caterpillar peak dates were determined by collecting caterpillar droppings, except for Marley Wood where half fall dates were used. In 1991 extremely low temperatures occurred at the time incubation had started on Vlieland and Hoge Veluwe. This resulted in a delay in the caterpillars, but not in the birds. Removing 1991 from the data set did not change the results ($F_{1,42}$ = 4.4, P = 0.042). Dates are given as April days (*i.e.* 31 = 1 May).

Veluwe with those of Oosterhout (Van Balen 1973) and Marley Wood (Perrins 1965; Perrins & McCleery 1989) where second clutches are comparatively rare. Following the results of Svensson (1995) we expected that the multiple brooded populations would lay eggs earlier relative to the food peak. This was not the case: the interval between

the first egg and the date of the caterpillar peak did not differ between single and multiple brooded populations ($F_{1,45}$ = 2.5, P = 0.1). However, in the analysis of laying date we found a significant interaction between caterpillar peak date and whether the population was multiple brooded or not (ANCOVA, $F_{1,44}$ = 14.7, P < 0.001, Fig. 7). Single brooded populations showed a positive relationship between laying date and caterpillar peak date (slope 0.69 ± 0.09 SE), whereas in facultatively double brooded populations the slope of the regression line did not differ from zero (slope 0.07 ± 0.13 SE). Two long-term studies support these findings. Great tits in a single brooded population in the UK advanced the timing of egg laying in response to higher spring temperatures and advancement of the caterpillar food supply (McCleery & Perrins 1998). In contrast, no such advancement was found in the facultatively multiple brooded population of the Hoge Veluwe (Visser et al. 1998). Although our findings are not in agreement with our expectation that multiple breeders start egg laying earlier in relation to the caterpillar peak, the results clearly suggests that the optimal timing of breeding differs between single and multiple breeders.

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SAMENVATTING

Tijdens het broedseizoen bestaat het voedsel van Koolmezen *Parus major* voornamelijk uit rupsen. De beschikbaarheid van rupsen vertoont een duidelijke piek, waarvan de datum van jaar tot jaar verschilt. Het succes van het eerste broedsel, gemeten als overleving, aantal en gewicht van de jongen, was het hoogst wanneer de jongenperiode samenviel met de top van de rupsenpiek. Koolmezen die voor of na de top van de voedselpiek broedden, hadden een lager succes. Er was ook een positief verband tussen het succes van het eerste broedsel en de absolute hoeveelheid voedsel gemeten in het territorium. Nadat de jongen van het eerste broedsel zijn uitgevlogen, kunnen Koolmezen aan een tweede legsel beginnen. De kans op zo'n tweede legsel was groter naarmate het eerste broedsel vroeger was ten opzichte van de rupsenpiek. Dit effect werd gevonden onafhankelijk van de absolute datum in het seizoen. Gezinnen met uitgevlogen jongen foerageerden aanvankelijk in eiken. Wanneer de voedselbeschikbaarheid in de eiken afnam, verhuisden ze naar dennen. Er werd langer in eiken gefoerageerd als de timing van het eerste broedsel vroeg was ten opzichte van de rupsenpiek, en de kans op een tweede broedsel was hoger naarmate de gezinnen meer tijd in eiken doorbrachten. Dit geeft indirect aan dat seizoensvariatie in voedselbeschikbaarheid een belangrijke rol speelt in de beslissing voor een tweede legsel. De absolute hoeveelheid voedsel in het territorium had geen effect op de kans op een tweede legsel, maar het interval tussen het eerste broedsel en het tweede legsel was korter naarmate er meer voedsel beschikbaar was. De beschreven patronen werden bevestigd door een bijvoerexperiment. Paren die werden bijgevoerd, produceerden zwaardere jongen in het eerste broedsel en hadden een korter interval tussen de twee broedsels. De kans op een tweede legsel leek echter niet toe te nemen. Als Koolmezen dichter bij de voedselpiek broedden, nam het succes van het eerste broedsel toe, maar tegelijkertijd nam de kans op een

tweede legsel af. Er bestaat dus een *trade-off* tussen het broedsucces van het eerste broedsel en de toekomstige reproductieve waarde van de ouders. Deze *trade-off* heeft gevolgen voor de optimale legdatum. Dit werd geïllustreerd door een vergelijking van Koolmeespopulaties met en zonder tweede broedsels. Alleen in populaties zonder tweede broedsels was de datum van broeden gecorreleerd met de datum van de rupsenpiek.

Appendix. Seasonal measurements of caterpillar abundance on Vlieland (VL) and on the Hoge Veluwe (HV) in different years. The table shows the peak date, the maximum caterpillar biomass, the average hatching date of unmanipulated first broods that fledged, the average timing relative to the annual caterpillar peak and the proportion of second clutches.

Year	Area	Peak date (April)	Maximum biomass (g d^{-1} m^{-2})	Hatching date (April)	Relative timing (days)	Proportion second clutches	Source
1985	HV	60	3.40	49	1	0.76	this study
1986	HV	65	3.53	56	3	0.19	this study
1987	HV	62	4.40	48	-2	0.28	this study
1988	HV	49	8.32	48	11	0.00	this study
	VL	56	14.32	43	-1	0.42	this study
1989	HV	50	4.88	46	8	0.21	this study
	VL	54	3.90	48	6	0.12	this study
1990	HV	51	5.05	41	2	0.15	this study
	VL	48	2.32	38	2	0.51	this study
1991	HV	72	1.81	48	-12	0.19	this study
	VL	69	2.29	43	-14	0.71	this study
1992	HV	57	4.25	42	-3	0.45	C. Both unpubl.
	VL	53	4.27	41	0	0.60	this study
1993	HV	45	9.48	46	13	0.02	M.E. Visser unpubl.
	VL	52	4.94	46	6	0.07	this study
1994	HV	50	5.50	43	5	0.37	M.E. Visser unpubl.
	VL	55	4.39	49	6	0.12	this study
1995	HV	56	3.35	49	5	0.04	M.E. Visser unpubl.
	VL	64	1.89	45	-7	0.39	this study
1996	HV	61	17.60	50	1	0.36	M.E. Visser unpubl.