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Seasonal variation in the incidence of double broods: the date hypothesis fits better than the quality hypothesis

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Summary

1. In three great tit (*Parus major*) populations the probability that a pair starts a second clutch, a clutch produced after a successful first brood, varied between years and areas but generally declined through the breeding season.
2. By exchanging first clutches between early and late breeding pairs during incubation we tested experimentally whether this seasonal decline was related to quality differences between early and late breeding pairs (quality hypothesis) or hatching date of the first clutch (date hypothesis).
3. Body mass of first brood fledglings increased through the season and was only determined by hatching date of the first clutch.
4. Advanced pairs were more likely and delayed pairs less likely to lay a second clutch compared to control pairs. As predicted from the date hypothesis, individual birds did not differ in their ability to produce a second clutch, but only those birds that bred early did so.
5. The interbrood interval and possibly also the probability of a second clutch was related to the number of first brood fledglings and their body mass.

Key-words: fledgling mass, great tit, hatching date, individual quality, second clutch.

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Introduction

In many bird populations reproductive success varies through the breeding season. Often early breeders are more successful than late breeders in terms of the number of recruits they produce (e.g. Perrins 1970; Daan *et al.* 1988; van Noordwijk, McCleery & Perrins 1995). An increasing number of experimental studies have tested whether breeding performance is related to the timing of breeding or to quality differences between early and late breeders (Parsons 1975; Hunt & Hunt 1976; Nilsson 1990; Hatchwell 1991; Verhulst & Tinbergen 1991; Norris 1993; Brinkhof *et al.* 1993; Wiggins, Gustafsson & Pärt 1994; Brouwer, Spaans & de Wit 1995; Verhulst, van Balen & Tinbergen 1995). Many of these studies are concerned with single-brooded species that raise only one clutch per season, and where species could have more than one reproductive attempt per breeding season often only fitness components of the first clutch have been reported.

For many multiple breeders, however, the reproductive output, measured as the number of young fledged, largely depends on the number of clutches raised per season (Smith & Roff 1980; Geupel &

DeSante 1990; Møller 1990; Holmes *et al.* 1992). It is therefore important to include the probability that a second clutch will be laid as one of the fitness components. Moreover, the number of clutches laid may not be independent of the reproductive success of earlier clutches.

The probability that a new clutch will be laid is generally negatively correlated with the initiation date of the previous clutch (e.g. Kluyver 1951; Geupel & DeSante 1990; Smith, Källander & Nilsson 1987; Møller 1990; Stouffer 1991; Hepp & Kennamer 1993). There are two hypotheses explaining why earlier birds lay more second clutches.

1. Individual quality hypothesis: early and late pairs may differ in phenotypic quality (e.g. foraging ability), or environmental quality (e.g. territory quality). These characteristics may be confounded with the ability to produce a second clutch in such a way that early birds are able to rear a second clutch whereas late birds are not.

2. Date hypothesis: there is a (gradual) change in the environment affecting all individuals in the same way. As a result, the balance between costs and benefits of raising an additional clutch changes for all individuals

as the season progresses. All birds are able to produce a second clutch but only those birds that breed early do so.

Here we describe the seasonal variation in the frequency of second clutches in the great tit (*Parus major*), a facultatively multiple brooded passerine. A variable proportion of great tit pairs starts a second clutch after successfully rearing a first clutch (Kluyver 1963; Kluyver, van Balen & Cavé 1977; Den Boer-Hazewinkel 1987; Tinbergen 1987). Exceptionally, some pairs even produce a third clutch (Tinbergen & van Balen 1988). We examine whether the occurrence of second clutches generally declines throughout the season by comparing different breeding populations and different years.

To disentangle the effects of date and individual quality on the probability of a second clutch it is necessary to change the timing of breeding experimentally and evaluate whether the probability of laying a second clutch remains the same (individual quality hypothesis) or changes according to the seasonal trend (date hypothesis). We manipulated the timing of breeding by exchanging first clutches between early and late breeding pairs (Hunt & Hunt 1976; Norris 1993; Brinkhof *et al.* 1993), so that the nestling care of early pairs was delayed and that of late pairs was advanced. If the quality hypothesis is true then the probability of an individual pair producing a second clutch will not change. On the other hand, if the date hypothesis is valid we would expect advanced pairs to be more likely and delayed pairs to be less likely to have a second clutch than pairs that were not manipulated. The two hypotheses are not mutually exclusive and it is possible that both individual quality and date explain part of the seasonal variation. If this is the case then we would expect an intermediate effect: the probability of a second clutch would change as a result of the experiment, but the change would be smaller than predicted from the natural seasonal trend.

Methods

DESCRIPTIVE DATA

We analysed the occurrence of second clutches recorded in three great tit populations in the Netherlands: Vlieland, Hoge Veluwe and Oosterhout. For a description of the study areas see Kluyver (1971) and van Balen (1973). During the breeding season, nestboxes were visited at least once a week to determine laying date, clutch size, hatching date, number of eggs hatched and the number of young fledged. Laying date was calculated by assuming that one egg is laid per day. Hatching date was recorded by inspection of the nestbox around the expected day of hatching or by estimating the age of newly hatched chicks. Parents were caught in the nestbox for ringing 7–10 days after

hatching. The young were ringed 7 (Hoge Veluwe and Oosterhout) or 15 (Vlieland) days after hatching.

We reserve the term 'second clutch' for clutches following a successful first brood. Therefore, only pairs that produced at least one fledgling in their first brood were used in the analysis on second clutches; replacement clutches that were produced after nest failure were not included in the analysis. In great tits mate switching between first and second breeding attempt is rare (Kluyver 1951; personal observation). Therefore, first and second clutches were matched on the basis of identification of the female only.

The analysis involved data on non-experimental clutches from Vlieland and Hoge Veluwe in 1982–91 and from Oosterhout in 1983–91.

EXCHANGE EXPERIMENT

In 1992 we manipulated the timing of parental care of great tit pairs that bred on Vlieland. Breeding variables were recorded as described above. In addition, we measured the length and breadth of the eggs in 79 out of 84 nests to the nearest 0.1 mm with sliding callipers. Egg volume was estimated as $0.5 \times \text{length} \times (\text{breadth})^2$ (van Noordwijk *et al.* 1981a). Body mass of chicks at fledging was estimated by recording body mass 15 days after hatching, approximately 4 days before fledging. For each nest the mean fledgling weight was calculated by averaging the mass using only chicks known to have fledged. Fledging date was established by visiting the nestbox around the expected day of fledging.

We selected 28 pairs of two clutches that had the same clutch size but differed by approximately 6 days in laying date. During incubation we swapped clutches between these two nests so that the hatching date of the early pair was delayed and that of the late pair was advanced. For each group of experimental clutches we selected a third clutch that served as a control. This clutch was of the same size as the two experimental clutches (± 1 egg) and the laying date was equal (± 1 day) to that of either the early pair or the late pair (alternating between the early and the late pair).

To prevent clutch desertion during egg transfer, the eggs were temporarily replaced with warmed dummy eggs. The females readily accepted the artificial eggs. The eggs were carried in a warmed insulated box for an average of 18 (range 5–45) min. Control clutches were not exchanged between nests. They were also replaced with a clutch of dummy eggs and transported for approximately the same amount of time (Table 1).

Advanced, delayed and control clutches did not differ in clutch size, mean egg volume and period over which the eggs were transported (Table 1). Furthermore, the probability that a clutch hatched was not influenced by the duration of egg transport (logistic regression, $\chi^2_{1,80} = 0.12$, $P = 0.73$).

One advanced clutch was deserted following the manipulation and two advanced clutches were

Table 1. Comparison of breeding parameters of four experimental groups: advanced, delayed, early control and late control pairs. Sample sizes are given between brackets

	Advanced	Delayed	Early control	Late control	
Laying date (April)	23.0 (<i>n</i> = 28)	16.9 (<i>n</i> = 28)	17.8 (<i>n</i> = 14)	22.6 (<i>n</i> = 14)	<i>F</i> = 7.43 <i>P</i> < 0.001
Clutch size	9.54 (<i>n</i> = 28)	9.43 (<i>n</i> = 28)	9.07 (<i>n</i> = 14)	9.86 (<i>n</i> = 14)	<i>F</i> = 1.32 <i>P</i> = 0.27
Egg volume (cm ³)	1.52 (<i>n</i> = 26)	1.51 (<i>n</i> = 26)	1.52 (<i>n</i> = 14)	1.53 (<i>n</i> = 13)	<i>F</i> = 0.13 <i>P</i> = 0.94
Transport period (min)	17.0 (<i>n</i> = 28)	20.0 (<i>n</i> = 28)	18.4 (<i>n</i> = 14)	19.6 (<i>n</i> = 14)	<i>F</i> = 0.46 <i>P</i> = 0.72
Proportion clutches hatched	0.96 (25/26)	0.86 (24/28)	0.93 (13/14)	0.93 (13/14)	<i>G</i> = 1.90 <i>P</i> = 0.59
Proportion broods fledged	0.78 (18/23)	0.86 (21/24)	0.67 (8/12)	1.0 (12/12)	<i>G</i> = 5.82 <i>P</i> < 0.001
Proportion second clutches	0.89 (16/18)	0.71 (15/21)	1.0 (8/8)	0.50 (6/12)	<i>G</i> = 71.3 <i>P</i> < 0.001

deserted just before or just after hatching, probably because we weighed the females at the end of the incubation period. One clutch that served as an early control was destroyed by people before the chicks were 15 days old and another two clutches (one advanced and one late control) were destroyed after the chicks were weighed. These clutches were not included in subsequent analyses.

The manipulation period was defined as the number of days between the actual hatching date and the original hatching date. Since the original clutch did not always hatch, and birds may incubate with different intensity, the original hatching date was estimated from the formula: hatching date = $16.01 + 0.87 \times$ laying date + $0.92 \times$ clutch size (multiple regression, $r = 0.97$, $n = 26$ control clutches). With original hatching date we refer to the estimated original hatching date throughout this paper. The average manipulation period was -5.8 days ($SD = 1.79$, $n = 25$) for advanced pairs, $+5.4$ days ($SD = 1.27$, $n = 24$) for delayed pairs, and 0 days for control pairs.

The probability that a second clutch will be produced might depend on the outcome of the first clutch as well as on the time at which a second clutch could be started. Therefore, we first describe the effect of the experiment on the breeding success of the first clutch and the length of the interbrood interval before looking at the probability of a second clutch.

Calendar dates were expressed as the number of days after 31 March (i.e. 1 = 1 April).

DATA ANALYSIS

Data were analysed using linear regression techniques available in the GLIM statistical package (version 4.0, Numerical Algorithms Group, Oxford 1993). For data on proportions such as hatching success, fledging success and the probability of a second clutch, error terms are binomially distributed and the appropriate analysis for such data is logistic regression. Logistic

regression assumes that the 'log odds' of the response variable or the 'logit' is a linear function of the explanatory variables. (Sokal & Rohlf 1995). A full model was fitted to the data (including two-way interactions and quadratic terms). Variables were then sequentially dropped from the model until all remaining variables were significant. We used the change in deviance and the degrees of freedom to test whether the contribution of a variable was significant. If the deviance was high compared to the number of degrees of freedom we applied William's correction for overdispersion (Crawley 1993) in combination with an *F*-test.

We checked for seasonal variation in the various breeding parameters by fitting a model with hatching date as independent variable on control clutches only. To distinguish between the date hypothesis and the individual quality hypothesis we combined experimental and control clutches and fitted a model with original hatching date and manipulation period as independent variables. If the date hypothesis were true we would expect that removal of manipulation period from the model would significantly increase the deviance. Furthermore, if the date hypothesis was valid in the pure form (i.e. the effect of the experiment was completely independent of the individual quality of the birds, no intermediate effect), the regression coefficients of original hatching date and manipulation period should be identical. In addition, a model with only actual hatching date should explain the data as well as a model with original hatching date and manipulation period combined.

If seasonal variation in the incidence of second clutches was caused by variation in quality between early and late breeding pairs, experimentally delayed pairs would produce second clutches more often as compared with pairs breeding late spontaneously, while experimentally advanced pairs would produce second clutches less often as compared with pairs breeding early spontaneously. Under this hypothesis,

manipulation period should significantly decrease the deviance in a model including the actual hatching date.

Results

DESCRIPTIVE DATA

Great tit pairs with a first clutch hatching early in the season were more likely to produce a second clutch than pairs that hatched their first clutch late (Fig. 1). In each of the three woods the proportion of pairs that produced a second clutch varied among years (interaction term year $\times$ area, $F_{2,17} = 43.4$, $P < 0.001$). The steepness of the seasonal decline differed among areas (interaction term hatching date $\times$ area, $F_{2,2} = 14.1$, $P < 0.001$), but not among years (interaction term hatching date $\times$ year, $F_{2,9} = 14.6$, $P = 0.10$). We examined the regression coefficients of hatching date on the probability of a second clutch in 24 combinations of years and areas in which more than one second clutch was found. All 24 coefficients were negative and 16 significantly so (two-tailed Student's t -test, $P < 0.05$).

EXCHANGE EXPERIMENT

Breeding success of first broods

Hatching success in control clutches (defined as the proportion of eggs hatched from clutches in which at least one egg hatched), increased throughout the breeding season ($F_{1,24} = 11.96$, $P = 0.002$, William's

correction). This correlation remained significant when experimental and control clutches were pooled (using the actual hatching date; Table 2(1)a). However, if the actual hatching date in this model is replaced by a combination of original hatching date and manipulation period (which together form the actual hatching date), neither was significant (Table 2(1)b). Original hatching date by itself ($F_{1,73} = 0.63$, $P = 0.43$), or the manipulation period in addition to actual hatching date ($F_{1,72} = 0.30$, $P = 0.59$) did not explain a significant part of the variation in hatching success. Thus, no definite conclusion could be made regarding the importance of date and quality in the seasonal trend in hatching success, although date appears more important than quality.

Fledging success was defined as the proportion of chicks that fledged from successful broods (i.e. nests that produced at least one fledgling). In control pairs fledging success of first broods did not vary throughout the season ($F_{1,22} = 2.86$, $P = 0.11$, William's correction). The absolute number of fledglings from successful nests was not correlated with actual hatching date ($r = 0.38$, $n = 20$, $P = 0.10$). Although the proportion of broods that fledged differed among advanced, delayed and control pairs (Table 1), fledging success was not significantly different among these groups ($F_{2,68} = 1.20$, $P = 0.31$).

In control clutches the mean body mass of fledglings increased throughout the breeding season ($F_{1,18} = 10.6$, $P = 0.004$). To establish whether fledging mass in experimental pairs followed this seasonal trend we added manipulation period to a regression

Fig. 1. Results of a logistic regression analysis of the proportion of pairs that produced a second clutch (p) in relation to hatching date of the first clutch (HD). Data were collected during a long-term study in three great tit populations in the Netherlands: Vlieland and Hoge Veluwe (1982–91) and Oosterhout (1983–91). Deviance of the null model was 1642.7, d.f. = 1439. The following variables were included in the model: hatching date of the first clutch, area, year, hatching date $\times$ area and year $\times$ area (stepwise backwards procedure). Deviance of the final model was 1283.6, d.f. = 1407. Fitted logistic regression lines are shown for the three woodlands, regression coefficients were averaged over all years. (Vlieland: $\ln(p) = 7.27 - 0.17 HD$, Hoge Veluwe: $\ln(p) = 3.86 - 0.12 HD$, Oosterhout: $\ln(p) = 15.0 - 0.48 HD$). The lines are shown over the range where clutches actually hatched. For graphical presentation all breeding pairs of each area were divided into five equally sized groups according to the hatching date of the first clutch. The proportion of second clutches is plotted against mean hatching date of each group (Vlieland $\blacktriangle$, Hoge Veluwe $+$, Oosterhout $\bullet$).

Table 2. The effect of the experimental manipulation on the first broods: (1) logistic regression of hatching success of the first clutch, and (2) multiple regression of the body mass of first brood fledglings. Two models are shown: (a) actual hatching date (*HD*), and (b) original hatching date (*OHD*) in combination with the number of days advanced or delayed or the manipulation period (*MP*)

	(1) Hatching success				(2) Body mass at fledging			
	(Increase in) deviance	d.f.	<i>P</i>	Estimates of coefficients $\pm$ SE	(Increase in) deviance	d.f.	<i>P</i>	Estimates of coefficients $\pm$ SE
Null model	81.75*	74			51.55	58		
(a) Actual hatching date								
Final model	77.42	73			41.08	57		
Constant		1		1.08 ± 1.16		1		13.8 ± 0.86
<i>HD</i>	4.33	1	0.05	0.06 ± 0.03	10.47	1	< 0.001	0.08 ± 0.02
(b) Original hatching date								
Final model	76.78	72			41.05	56		
Constant		1		-0.71 ± 1.33		1		13.91 ± 1.00
<i>OHD</i>	2.37	1	0.14	0.05 ± 0.03	7.35	1	0.003	0.07 ± 0.02
<i>MP</i>	3.96	1	0.06	0.07 ± 0.04	6.75	1	0.004	0.08 ± 0.03

*After William's correction for overdispersion (original deviance = 213.1, d.f. = 74).

model with fledgling mass as dependent and original hatching date as independent variable. This significantly decreased the deviance. Fledgling mass could thus be explained by either actual hatching date or by original hatching date in combination with the number of days advanced or delayed (Table 2.2). The two models were not significantly different from each other ($F_{1,72} = 0.64$, $P = 0.43$). Furthermore, the difference between the regression coefficients of original hatching date (0.07 ± 0.02 SE) and manipulation period (0.08 ± 0.03 SE) in model 2(2)b was only one standard error and therefore not significantly different. This means that an experimental change in hatching date is followed by a change in fledgling mass, exactly as predicted from the seasonal trend observed in control clutches. We tested whether the experiment affected fledgling mass in another way than through a change in hatching date by introducing manipulation period to a model with actual hatching date as independent variable. This did not have a significant effect on mean body mass at fledging ($F_{1,56} = 0.04$, $P = 0.84$). Therefore, we conclude that there were no side-effects of the experimental manipulation.

Interbrood interval

The interbrood interval was defined as the number of days between hatching of the first clutch and laying

of the first egg of the second clutch. On average, it took the birds 24.6 ± 0.73 SE ($n = 45$) days to start a subsequent clutch. In 27 out of 45 cases (10 control, 9 advanced and 8 delayed pairs) the fledging date was known to within 1 day. In seven of these nests the first eggs of the second clutch were laid before the fledging of the first brood, the extreme being 1 week before fledging. In all these cases the eggs were laid among the first brood young.

In control clutches the length of the interbrood interval was not correlated with the hatching date of the first clutch ($r = -0.22$, $n = 14$, $P = 0.44$). Neither did the length of the interbrood interval differ among the three experimental groups (one-way ANOVA, $F_{2,42} = 0.28$, $P = 0.76$). But the number of days between the first brood and the start of the second clutch was related to both the number of first brood fledglings and their body mass (Table 3). Parents that fledged a few or heavy chicks renested sooner than pairs that produced many or light fledglings.

Probability of a second clutch

The proportion of control pairs that started a second clutch declined throughout the breeding season ($F_{1,18} = 18.0$, $P < 0.001$) (Fig. 2a). Advanced pairs were more likely to produce a second clutch than

Table 3. Multiple regression of interbrood interval (i.e. number of days between hatching of the first clutch and laying of the first egg of the second clutch). Mean (SD) number of chicks fledged was 7.00 (2.15) and mean body mass at fledging was 17.03 g (0.89)

	(Increase in) deviance	d.f.	<i>P</i>	Estimates of coefficients
Null model	1064.8	44		
Final model	822.1	42		
Constant				53.35
Number of chicks fledged	124.4	1	0.02	0.79
Body mass at fledging	141.4	1	0.01	-2.01

Fig. 2. The proportion of pairs that produced a second clutch (p) in Vlieland in 1992 plotted against hatching date of the first clutch (HD) for (a) control pairs, (b) advanced pairs and (c) delayed pairs. The line (shown over the range where clutches actually hatched) is a fitted logistic regression line based on control clutches and represents the natural seasonal trend ($\ln(p) = 27.94 - 0.61 \text{ HD}$, deviance of the null model = 24.43, deviance of the final model = 12.22, $n = (20)$). In each experimental category the birds were divided into two equally sized groups (markers indicate means) according to hatching date for graphical presentation only (individual points were used in the analysis, see Table 4). The arrows show the direction and effect of the experimental manipulation. They connect the expected proportion on the original hatching date with the actual proportion found.

control pairs that hatched their first clutch at the original hatching date of the experimental pairs (Fig. 2b). Similarly, delayed pairs were less likely to start a second clutch (Fig. 2c). Therefore, the probability of a second clutch is best explained by actual hatching date. Addition of manipulation period to a model with the probability of a second clutch as dependent variable and original hatching date as independent variable decreased the deviance significantly (Table 4b).

Moreover, this model in which the original hatching date was decreased or increased with the number of days the hatching date was advanced or delayed did

not differ significantly from a model with actual hatching date (comparison of models in Table 4a and b, $F_{1,56} = 0.41$, $P = 0.52$). The difference between the regression coefficients for original hatching date and manipulation period in Table 4b was only one SE and therefore not significant (original hatching date: $-0.31 \pm 0.095 \text{ SE}$ and manipulation period $-0.25 \pm 0.10 \text{ SE}$). This indicates that the effect of experimentally changing the hatching date is in the same order of magnitude as the natural variation in hatching date.

To test if, in addition to the date effect described above, quality effects also played a role in the seasonal decline in the occurrence of second clutches we added manipulation period to a model containing only the actual hatching date. This did not result in a significant change in the deviance ($F_{1,56} = 0.41$, $P = 0.52$). This implies there was no additional effect of quality differences between early and late breeding pairs on the decision to start a second clutch, over and above the effect of time of breeding itself.

Breeding success of the first broods and the probability of a second clutch

Controlling for date we found a negative, non-significant, correlation between the number of chicks fledged and the probability of producing a second clutch: parents that fledged many chicks seemed to be less likely to lay a second clutch. On the other hand, parents that fledged heavy young seemed to be more likely to produce a second clutch than pairs that produced chicks with low body mass. This effect was also not significant (Table 4).

Breeding success of second clutches

Second clutches from control pairs were on average 1.9 egg smaller than first clutches (paired t -test, $n = 14$, $P < 0.001$). There was no seasonal decline in the number of eggs in the second clutches produced by control pairs (regressed against laying date of the second clutch: $r = -0.21$, $n = 13$, $P = 0.83$). Among second clutches we found no significant effect of hatching date of the second clutch on breeding variables such as hatching success ($\chi^2_{1,11} = 1.01$, $P = 0.99$), fledging success ($\chi^2_{1,11} = 0.02$, $P = 1.00$) and body mass of chicks at fledging ($r = -0.26$, $n = 12$, $P = 0.42$). Neither did we find any effect of the experimental manipulation.

Discussion

Probability of a second clutch

Our analysis suggested that a seasonal decline in the occurrence of second clutches in the great tit is common in all the three areas studied. Although the percentage of second clutches differed among years and

Table 4. Logistic regression analysis of the probability that a second clutch was laid (advanced, delayed and control pairs combined). Two models are shown: (a) actual hatching date (*HD*), and (b) original hatching date (*OHD*) in combination the number of days advanced or delayed or the manipulation period (*MP*)

	(Increase in deviance)	d.f.	<i>P</i>	Estimates of coefficients $\pm$ SE
Null model	64.66	58		
(a) Actual hatching date				
Final model	47.59	57		
Constant		1		13.76 $\pm$ 3.89
<i>HD</i>	17.07	1	< 0.001	-0.28 $\pm$ 0.085
(b) Original hatching date				
Final model	47.24	56		
Constant		1		14.72 $\pm$ 4.29
<i>OHD</i>	15.28	1	< 0.001	-0.31 $\pm$ 0.095
<i>MP</i>	8.12	1	0.004	-0.25 $\pm$ 0.10
Rejected terms				
Body mass of fledglings	-2.94	1	0.09	0.86 $\pm$ 0.53
Number of fledglings	-3.36	1	0.07	-0.37 $\pm$ 0.22

woodlands, in all of the combinations of years and areas we observed a negative seasonal trend.

The manipulation of hatching date had a significant effect on the proportion of pairs that started a second clutch. For example, most late birds which would not normally have laid a second clutch were induced to do so by experimentally advancing the hatching date of their first clutch. Furthermore, the experimental effect was in accordance with the natural seasonal trend in the occurrence of second clutches. We conclude therefore that the results are in agreement with the date hypothesis: the observed seasonal decline in the occurrence of second clutches was the result of seasonal variation in breeding opportunities rather than quality differences between early and late breeding birds. However, variation in quality may still be important to explain why some birds initially laid earlier than others.

There are, however, two alternative explanations for the observed shift in the occurrence of second clutches. First, as a consequence of the experimental design, the duration of the incubation period was changed by an average of 5–6 days (which is approximately half of its usual length). Advanced pairs experienced a shorter incubation period and delayed pairs a prolonged incubation period. We would draw the same conclusion from the experiment if the costs of incubation were high and had a negative effect on future reproductive behaviour (i.e. a second clutch). A number of studies demonstrate an energetic cost to incubation (Biebach 1979; Mertens 1980, 1987; Vleck 1981; Haftorn & Reinertsen 1985). Although Gaston & Perin (1993) found no effect of a prolonged incubation period on body mass of incubating Brunnich's guillemots (*Uria lomvia*). In our study, pairs with a prolonged incubation period performed better in their first brood because body mass of fledglings was higher. Further, a prolonged incubation period did not affect the production of second clutches by delayed pairs

early in the season (Fig. 2c). Although experimental biases can never be ruled out entirely, it is unlikely that the manipulation of the length of the incubation period played an important role in future reproductive behaviour.

The second potential problem is that the number of eggs in first clutches was negatively correlated with laying date ($r = -0.30$, $n = 84$, $P < 0.001$). As a consequence, advanced birds must have had a relatively large clutch size for their original hatching date. Similarly delayed birds had a relatively small clutch. By matching experimental groups on the basis of clutch size we might thus have removed quality differences between early and late birds. However, the effect of hatching date on the probability of producing a second clutch was still present when we controlled for clutch size ($F_{1,56} = 20.0$, $P < 0.001$). Therefore, it is unlikely that this selection effect caused the experimental effects observed.

Breeding success of first broods and the probability of a second clutch

In the year in which the experiment was performed breeding success of the first clutch (i.e. hatching success and body mass of fledglings) was positively related to the timing of breeding. Van Noordwijk, van Balen & Scharloo (1981b) reported positive selection differentials for laying date on Vlieland in some years and Verhulst (1995) found that the number of local recruits was positively correlated with laying date, at least in the first part of the breeding season. This indicates that the results obtained in the experimental year are within the normal range on Vlieland.

Hatching success increased in the course of the season (Table 2.1), but no clear conclusion could be drawn regarding the importance of date and quality. Fledging success was independent of time of breeding, but seasonal variation in body mass of fledglings

clearly resulted from differences in timing of the first clutch (date-hypothesis) and not from quality differences between early and late breeders.

We observed no seasonal variation in the length of the interbrood interval, but the interbrood interval was affected by the reproductive success of the first clutch (number and body mass of young). The probability of starting a second clutch seemed also to be affected by the outcome of the first clutch. These effects bordered on significance, possibly because parents that produced many young of low body mass were unable to realize a short interval and they refrained from laying a second clutch altogether (Tinbergen & van Balen 1988). Some studies on brood size manipulations report similar effects of the number and body mass offspring on the percentage of second clutches (Stouffer 1991), the length of the interval (Hegner & Wingfield 1987; Smith *et al.* 1989; Ten Cate & Hilbers 1991) or both (Smith *et al.* 1987; Tinbergen 1987; Lindén 1988; Verhulst 1995).

Seasonal variation in breeding opportunities

We have shown that the hatching date of the first clutch is related to two important fitness components: fledgling mass and the probability of a second clutch. The next logical question to ask is which environmental variables are responsible for the observed seasonal variation. It seems likely that food availability plays a role in both these effects (Tinbergen & van Balen 1988), and it is therefore somewhat confusing that fledgling mass increases in the course of the season, while the proportion of pairs starting a second clutch decreases. However, the abundance of caterpillars, the main prey of great tits, typically increases and then decreases in the course of the season. This pattern was also observed on Vlieland in the experimental year (N. Verboven & S. Verhulst, unpublished). It seems possible therefore that the seasonal increase in fledgling mass was caused by the increase in caterpillar abundance in the first part of the season, while the seasonal decrease in the occurrence in second clutches was caused by the decrease in caterpillar abundance in the last part of the season. We measured caterpillar abundance in the experimental year and the relationship between food supply and reproductive success will be presented elsewhere.

In years with many caterpillars more great tits produced a second clutch (Tinbergen & van Balen 1988) and renesting intervals were shorter in these years (Kluyver *et al.* 1977). Supplemental food increased the proportion of pairs that started a second clutch in cactus wrens (*Campylorhynchus brunneicapillus*) (Simons & Martin 1990), decreased the interbrood interval (Eden, Horn & Leonard 1989), or both (Arcese & Smith 1988).

Late-hatched juveniles were less likely to become established in a winter flock and as a consequence experienced lower survival rates (Nilsson & Smith

1988). Removal of first-brood fledglings enhanced survival of second-brood fledglings (Kluyver 1971; Tinbergen, van Balen & van Eck 1985; Verhulst 1992), probably because of reduced competition with older, dominant juveniles. Thus, competition between early and late-hatched fledglings may reduce the reproductive value of late second clutches and this could also potentially explain why late breeders refrain from starting a second clutch.

Timing of breeding in multiple brooded species

In this study we found that body mass of fledglings increased with hatching date. Body mass at fledging is an important determinant of recruitment rate, and hatching date did not correlate significantly with recruitment rate when nestling weight was controlled for (Tinbergen & Boerlijst 1990). This suggests that in our study the fitness contribution of the first reproductive attempt increased the later the eggs of the first clutch hatched (in agreement with the results of van Noordwijk, van Balen & Scharloo 1981b and Verhulst 1995). At the same time, however, the proportion of pairs that started a second clutch decreased in the course of the season. Therefore, this study demonstrates that a trade-off may exist between the reproductive value of the first clutch (later breeding resulted in higher fledgling mass) and the reproductive value of the second clutch (early breeding leaves more time to start a second clutch), as was suggested by Humphrey, Wingfield Gibbons, & Magrath (1993). It seems likely that this trade-off generally plays a role in the optimization of timing of breeding in multiple brooded species.

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