EFFECT OF EXPERIMENTALLY ALTERED BROOD SIZE ON FREQUENCY AND TIMING OF SECOND CLUTCHES IN THE GREAT TIT

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ABSTRACT.—Brood size in the Great Tit (*Parus major*) was manipulated (increased, decreased, or unchanged) when nestlings were 5 days old. Both the frequency of second clutches and the interbrood interval were affected. The number of nestlings and hatching date, but not nestling and female mass, differed between first broods followed and not followed by second clutches. Hatching date and the number of nestlings in the first brood explained most of the variation in interbrood interval, whereas female mass did not contribute.

Feeding first-brood nestlings and fledglings is an energy-demanding process, and the female may have to allocate resources to brood-feeding at the expense of reproductive development. Furthermore, a larger brood requires a longer period of feeding than a smaller brood. These circumstances probably explain why the size of the first brood affects the timing of the second clutch. Female condition and food depletion of the territory do not seem to be important.

Because late second clutches have a lower probability of fledgling survival than do earlier ones—and consequently are of lower value from the female's standpoint—a large first clutch may delay laying to the point that a second clutch is not worthwhile. We conclude that a female's decision whether to lay a second clutch is a strategic one based on the value of the second clutch; a female that "decides" to lay a second clutch starts as quickly as possible.
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CURRENT life-history theory assumes that reproduction imposes a cost, i.e. that investment in current offspring will decrease future reproductive output (Williams 1966, Charnov and Krebs 1974, Stearns 1976), and that an optimal balance between current and future reproductive output will maximize lifetime reproductive success. Only a few studies on vertebrates have shown a negative correlation between brood size and future reproductive output (Reznick 1985, Nur 1987). This may occur because individuals adjust reproductive effort to their own quality or that of their territory (Perrins and Moss 1975, Högstedt 1980, Smith 1981, Askenmo 1982, Nur 1987). To establish whether reproduction has a cost, it is necessary to manipulate reproductive effort.

Earlier studies on multibrooded species showed that the frequency of second clutches differs between habitats (e.g. Berndt 1938, Kluyver 1951), as does the interval between the first and second clutch (Kluyver et al. 1977). The interval is shorter in optimal habitats (Kluyver et al. 1977), and the frequency of second clutches is lower (Kluyver 1951, Kluyver et al. 1977). Further, the interval between clutches shows no relationship to population density, while the frequency of second clutches does (Kluyver et al. 1977). Brood-size manipulation experiments may help to determine if rearing the first brood influences the probability and timing of a second clutch.

We report the effects of brood-size manipulation on the proportion and timing of second broods in the Great Tit (*Parus major*). The Great Tit breeds readily in nest boxes, is monogamous, and is facultatively double-brooded. Only the female incubates, but the young are fed by both parents.

METHODS

The experiment was carried out between 1982 and 1986 in the Revinge area of southern Sweden (55°41'N, 13°27'E). The area consists of deciduous forests and groves. In 1982 nest boxes in broad-leaf forest at Skarhult (15 km north of Revinge) and Linnebjer (12 km northwest of Revinge) also were used. The nest boxes were set out at low density (<1/ha). About 100 were used during 1982–1985 and about 50 in 1986. All nest boxes were of equal size.

The boxes were inspected weekly. The day of hatching was determined by daily inspections (in 1982 we inferred hatching date from the size of the nestlings when 2–5 days old). Hatching day was designated as day 0, and the young were counted on days 5 and 13.

TABLE 1. Mean number of offspring added or removed for each clutch-size manipulation category and subsequent mean mortality. Only broods where the presence or absence of a second clutch was established are included. Total nest failures are excluded. *n* = the number of broods.

Year	Category	No. added	No. of young that died		*n*
			Day 5–14	Day 5–fledging	
1982	Reduced	−5.3	0.1	—	15
	Enlarged	+5.1	0.8	—	14
1983	Reduced	−4.4	0.1	0.1	19
	Enlarged	+4.4	1.5	3.5	17
	Control	0	0.7	0.9	20
1984	Reduced	−4.0	0.1	0.1	22
	Enlarged	+4.1	1.5	2.8	21
	Control	0	0.6	0.9	28
1986	Reduced	−4.5	0.0	0.1	13
	Enlarged	+4.4	2.0	2.0	10

TABLE 2. Percentage of first broods followed by a second clutch in relation to experimental manipulation of the size of the first brood. Tested with the G-test using Williams' correction. Sample sizes are given in parentheses.

	Reduced	Enlarged	Control	*P*
1982	53.3 (15)	0.0 (14)		<0.001
1983	68.4 (19)	29.4 (17)	15.0 (20)	<0.005
1984	36.4 (22)	19.0 (21)	25.0 (28)	>0.1
1986	76.9 (13)	40.0 (10)		<0.1

Adults were sexed according to the criteria of Svensson (1983). Females were captured on the nest early in the night between nestling days 12 and 13, ringed with an aluminum ring (1983–1986), aged (1984–1986), and weighed to the nearest 0.1 g. In 1984–1986 female wing length was measured; in analyses involving female mass, the use of mass corrected for size (wing length) did not change the results. On day 13 the nestlings were ringed and their mass (to the nearest 0.1 g) and wing length (to the nearest 0.5 mm) determined (1983–1986).

In 1984 and 1985 the length of the nestling period was determined for most first broods. All nests were visited daily from day 16 or 17 until the young fledged. Fledglings were assumed to have left the nest on the first day the nest box was found empty. Care was taken not to induce premature nest departure; we often observed boxes from a distance to record feeding visits by adults.

After the young fledged we inspected the nest boxes for aluminum rings to determine nestling survival between ringing and fledging. When the first brood had fledged we continued regular visits to determine whether a second clutch was laid. In 1983–1986 visits were frequent enough to determine the day on which a second clutch was started. An interbrood interval was defined as the number of days between hatching of the first brood and laying of the first egg in the second clutch. The identity of the females that reared second broods was checked during incubation or feeding of the second-brood nestlings. The females were not ringed in 1982, but each second-brood female was assumed to be the same bird that had produced the first brood in a given nest box. The same assumption was made during other years for females that had escaped identification while rearing a second brood (e.g. because of desertion). Only 1 of 22 control females changed nest boxes between broods.

When nestlings were 5 days old some broods were manipulated. In 1983–1985 about one-third of the broods were randomly chosen as controls. The others were either reduced or enlarged. In 1982 and 1986 we manipulated the size of all broods. We tried to increase or decrease brood size by about 50% relative to the original clutch, and clutches were matched by size (Table 1). Hatching date of controls (1983–1985) and experimental broods were distributed equally, and initial brood sizes were the same. Nestlings were transported between nests in a small cloth bag; this normally took less than 10 min. Control nests also were visited 5 days after hatching, and the nestlings were counted, taken from the nest, placed in a small cloth bag for a short time, and replaced.

Because egg production takes 4 days (cf. Schifferli 1980), we excluded female masses taken within 4 days of laying an egg in the second clutch. In 1982 only a relatively few female masses were used.

RESULTS

Frequency of second clutches.—Only 4 second clutches were started in 1985, so we excluded the 1985 data on second-clutch frequency and timing from the analyses. In 1982 and 1983 reduced first-brood size led to an increased frequency of second clutches. The trends were similar but not statistically significant in 1984 and 1986 (Table 2).

First broods followed by a second brood were earlier (2 yr) and had fewer nestlings and fledglings (3 yr) than first broods not followed by a second clutch (Table 3). The only other significant difference found between first broods followed by a second clutch and those not followed was female mass in 1982; the sample size was small, however.

Time in the nest.—First-brood nestlings stayed in the nest for 16–21 days. The length of this period differed significantly between manipulation categories in 1984, and the same tendency

TABLE 3. Differences in selected reproductive parameters in the Great Tit between first broods that were followed by a second clutch and those that were not. Brood size and hatching date were tested with a one-sided Mann-Whitney *U*-test and body size with a one-sided *t*-test.[a] Hatching day was designated as day 0.

Variable	1982	1983	1984	1986
Hatching date	1.11^{NS}	−3.44**	-1.00^{NS}	−2.24*
No. of young				
Day 5	−5.45**	−2.54*	-0.54^{NS}	−3.79*
Day 13	−4.71**	−2.08*	-0.55^{NS}	−4.86**
Fledging		−1.83*	-0.72^{NS}	−4.93**
Female mass	2.86**	0.19^{NS}	-0.03^{NS}	0.12^{NS}
Nestling mass		0.83^{NS}	-0.08^{NS}	-0.42^{NS}
Nestling wing length		-0.40^{NS}	-0.65^{NS}	-1.08^{NS}

[a] * = $P < 0.05$, ** = $P < 0.01$, NS = $P > 0.05$.

was apparent in 1985 (Table 4). Nest time was correlated positively with number of young and negatively with nestling mean wing length (Table 5). A stepwise multiple regression analysis showed time in the nest to depend most strongly on nestling wing length (Table 6). In 1984 it also depended on the number of young fledged (Table 6).

Interval between first and second clutches.—The interbrood interval ranged from 13 to 29 days. In a few instances the first egg of the second clutch was laid while first-brood nestlings were still in the nest. The interbrood interval differed significantly between manipulation categories in 1983 and 1986, and nearly so in 1984 (Table 7). The interval was correlated positively with the number of young in the first brood and negatively with hatching date and with first-brood nestling mass and wing length (Table 8, Fig. 1). The mass of the female when rearing the first brood was not correlated with interbrood interval (Table 8). A stepwise multiple regression analysis showed the interbrood interval to be positively associated with the number of young in the first brood 5 days after hatching in 1983 and 1986 and negatively associated with mean nestling mass in the first brood in 1984 (Table 9, Fig. 1). The number of first-brood nestlings on day 5 and their mass were highly correlated ($P < 0.001$ for 1983–1985, $P < 0.02$ for 1986). The effect of one extra young on day 5 was a delay of 0.43 (1983), 0.73 (1984), and 0.71 days (1986) (1984: regression with number of young on day 5 as the independent variable, $R = 0.62$).

DISCUSSION

Kluyver (1963) found that the frequency of second clutches in the Great Tit increased as the success of the first brood decreased. We found that the frequency of second clutches was affected by manipulation of first-brood size. A similar response was reported for the Great Tit in Holland (Tinbergen and Albers 1984) but not for the American House Wren (*Troglodytes aedon;* Finke et al. 1987). Contrary to Tinbergen and Albers (1984) but like Finke et al. (1987) and Kluyver et al. (1977), who also studied the Great Tit, we found that brood-size manipulation affected the interval between first and second broods. Using natural variation in brood size, Kluyver et al. (1977) reported no effect of brood size on interbrood interval in an optimal habitat and obtained inconsistent results in a suboptimal habitat. In the Song Sparrow (*Melospiza melodia*) and the House Sparrow (*Passer domesticus*), however, a positive correlation exists between natural brood size and interbrood interval (Smith and Roff 1980, McGillivray 1983). Our results support the hypothesis that rearing a first brood imposes a significant cost, which affects the probability of laying and the timing of a second clutch.

The size of the first brood might affect the timing of second clutches in three ways. First, the energy expended when feeding first-brood young may affect the female's condition. This seems not to have been the case, however, because the timing of second clutches was not related to female mass.

Second, resources in the territory might be depleted in relation to the size of the first brood. There is evidence to support this alternative. Slagsvold (1984) reported a longer renesting interval for female Great Tits with enlarged first broods than for those with reduced first broods when he removed all the first-brood nestlings on day 15. This might be due either to an effect on female condition or to depletion of the territory. Local food depletion due to feeding nestlings was reported for Stonechats (*Saxicola tor-*

TABLE 4. Mean number of days Great Tit first-brood young stayed in the nest for reduced, enlarged, and control broods. Differences between means were tested with Kruskal-Wallis one-way analysis of variance. Sample sizes are given in parentheses.

Category	1984	1985
Reduced	18.6 (22)	18.2 (13)
Enlarged	19.7 (21)	19.1 (12)
Control	19.0 (24)	18.4 (17)
P	<0.05	<0.1

TABLE 6. Regression coefficients in a stepwise multiple regression analysis (b) for different variables explaining the number of days first-brood young stayed in the nest box. NS = $P > 0.05$.

	1984		1985	
Variable	b	*P*	b	*P*
Hatching date	—	NS	—	NS
No. of young				
Day 5	—	NS	—	NS
Day 13	—	NS	—	NS
Fledging	0.12	<0.01	—	NS
Nestling mass	—	NS	—	NS
Nestling wing length	−0.21	<0.001	−0.21	<0.001
Female mass	—	NS	—	NS
Multiple *R*	0.61		0.57	

quata; Greig-Smith 1982). In Slagsvold's (1984) study, however, neither incubation time (which reflects resource abundance; Nilsson and Smith in prep.) nor nestling mass of second broods differed between treatments. Furthermore, in Slagsvold's experiment, all birds renested and the mean difference in the interbrood interval between treatments was small (<1 day).

Finally, females may have to allocate resources to feed nestlings and fledglings at the expense of egg production. A second clutch may not be started until the daily surplus exceeds a certain level. Whereas the first hypothesis assumed that rearing first-brood young affected the "capital" in the form of stored energy, the third hypothesis relates to daily "income." Even if less energy is required to produce eggs than to feed nestlings, resources must be allocated to the development of reproductive organs for egg production to proceed (e.g. Krementz and Ankney 1986). In the absence of nestlings or fledglings this may cause no problem. In fact, after nestlings were removed in Slagsvold's experiment, the interbrood interval was just long enough to allow follicle maturation (see Schifferli 1980). When the number of fledglings is large, a second clutch probably cannot be initiated until the fledglings are able to forage for themselves. This eases the energy demand on the female.

TABLE 5. Relation between number of days first-brood young spent in nest boxes and selected reproductive parameters. Spearman rank correlation coefficients and significance levels are given.[a]

Variable	1984	1985
Hatching date	0.16^{NS}	-0.09^{NS}
No. of young		
Day 5	0.38***	0.38**
Day 13	0.37***	0.36**
Fledging	0.38***	0.36**
Female mass	0.06^{NS}	-0.04^{NS}
Nestling mass	−0.42***	−0.29*
Nestling wing length	−0.49***	−0.47***

[a] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = $P > 0.05$.

Brood size may affect the female's allocation of resources to the second clutch in two ways. First, the growth rate of nestlings is affected by brood size (Källander, Nilsson, and Smith in prep.) and may influence how long they remain dependent. Brood-size enlargement prolonged the nestling period of the first brood, presumably because of the slower growth rate of the wings (1 mm of growth corresponded to a delay of 0.2 days). The length of time fledglings depend on their parents may also be affected by brood size (but see Nilsson and Smith 1985). Second, the food demands of a large brood are greater than those of a small brood. Consequently, nestlings in large broods must forage more than nestlings in small broods if the food demands on the parents are to be equal for both groups.

The reason the frequency and timing of second clutches depended more strongly on the

TABLE 7. Mean interval between hatching of the first clutch and laying of the first egg in the second clutch for Great Tits rearing a first brood of reduced, normal, or enlarged size. Tested with Kruskal-Wallis one-way analysis of variance (1983 and 1984) or Mann-Whitney *U*-test (1986). Sample sizes are given in parentheses.

Category	1983	1984	1986
Reduced	19.83 (12)	20.63 (8)	19.80 (10)
Enlarged	24.40 (5)	26.38 (4)	25.25 (4)
Control	21.00 (3)	23.42 (6)	
P	<0.05	= 0.06	<0.02

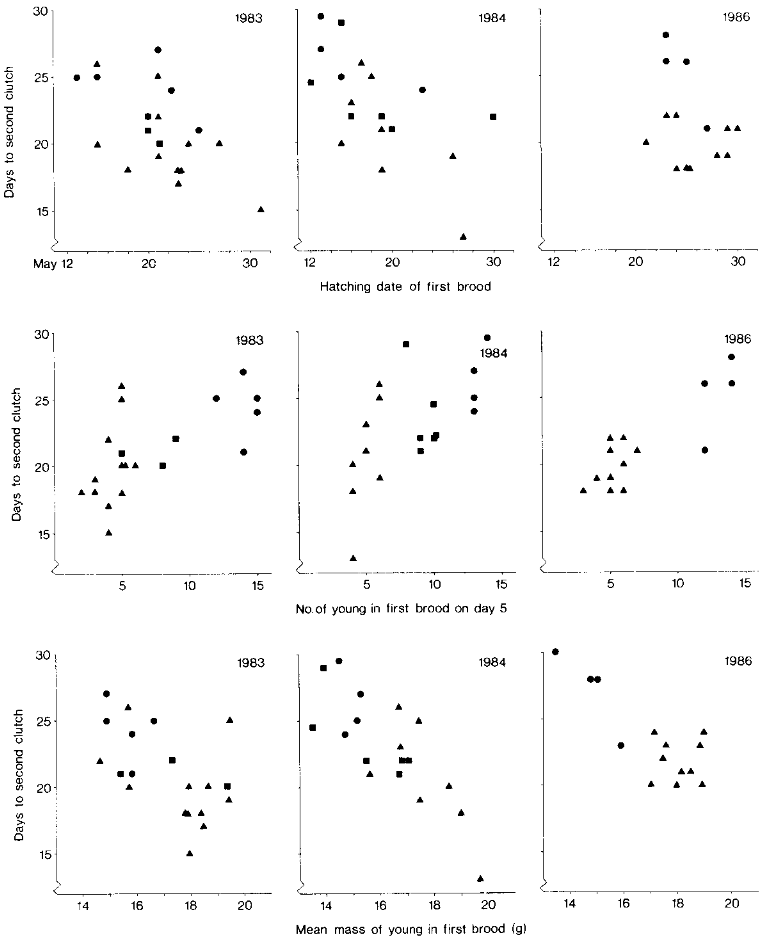

Fig. 1. Relationship between interbrood interval and hatching date, size of the first brood, and mean mass of nestlings in the first brood in the Great Tit. ▲ = experimentally reduced broods, ■ = control broods, ● = experimentally enlarged broods.

TABLE 8. Spearman rank correlation coefficients between interbrood interval and selected reproductive parameters of Great Tit first clutches.[a]

Variable	1983	1984	1986
Hatching date	−0.50*	−0.65**	−0.32^{NS}
No. of young			
Day 5	0.67***	0.65**	0.71**
Day 13	0.62**	0.61**	0.59*
Fledging	0.45*	0.53*	0.60*
Female mass	0.03^{NS}	0.05^{NS}	0.22^{NS}
Nestling mass	−0.55**	−0.74***	−0.53*
Nestling wing length	−0.46*	−0.40*	−0.51*

[a] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = $P > 0.05$.

number of nestlings than on the number of fledglings in the first brood may be that the highest mortality in first broods took place where the quality of territories or parents was lowest. For a second clutch to be started, it may be necessary for the female to be relieved of parental duties by the male. Thus, we predict that males should take a proportionally larger share of the responsibility for feeding fledglings from small, than from large, first broods.

The second clutch is probably initiated when the potential cost of a reduction in feeding the first-brood fledglings is outweighed by the potential survival cost, in terms of their survival probabilities, of a delay in the second clutch. The survival probabilities of second-brood

TABLE 9. Regression coefficients (b) in a stepwise multiple regression analysis for selected reproductive parameters explaining the number of days between hatching of the first clutch and laying of the first egg in the second clutch for female Great Tits. NS = $P > 0.05$.

	1983		1984		1986	
Variable	b	*P*	b	*P*	b	*P*
Hatching date	—	NS	—	NS	—	NS
No. of young						
Day 5	0.43	<0.01	—	NS	0.71	<0.001
Day 13	—	NS	—	NS	—	NS
Fledging	—	NS	—	NS	—	NS
Female mass	—	NS	—	NS	—	NS
Nestling mass	—	NS	−1.49	<0.01	—	NS
Nestling wing length	—	NS	—	NS	—	NS
Multiple *R*	0.630		0.708		0.833	

fledglings will decrease over the season (Kluyver et al. 1977). Thus, the cost-benefit balance may also change. If the pressure to commence a second brood is stronger later in the season, then the interbrood interval should decrease. We found some evidence for this (also see Kluyver et al. 1977). Alternatively, late in the season only females with the capacity to renest quickly may actually do so (cf. Kluyver et al. 1977).

The number of nestlings in the first brood predicted the interbrood interval remarkably well. In contrast, the frequency of second clutches was not affected as clearly by the brood-size manipulation. Life-history theory predicts that fecundity should be adjusted to predictable variation in the survival probabilities of offspring (Kluyver et al. 1977, Drent and Daan 1980, Ekman and Askenmo 1986). A bird that "decides" to lay a second clutch starts it as fast as possible, but not all birds capable of laying a second clutch will do so. The frequency of second clutches decreases with later hatching date of the first clutch (Kluyver et al. 1977, this study). This might depend on the decreased fledgling survival that occurs as the season progresses (Perrins 1965, Kluyver et al. 1977, Dhondt and Olaerts 1981). If so, brood-size manipulation should affect the frequency of second clutches indirectly, through the interbrood interval. This reasoning is strengthened by our observation that the frequency and timing of second clutches were correlated to the same factors, although to hatching date with opposite sign. The delay might seem too small to affect the probability of laying second clutches. The decline in fledgling survival with season is sometimes steep, however (cf. Perrins 1965). Furthermore, the magnitude of the effect of brood-size manipulation on the interbrood interval was almost certainly underestimated because the larger the effect on potential interbrood interval, the lower the probability that a second clutch will be laid.

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