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Weight loss of the female during the first brood as a factor influencing second brood initiation in Great Tits *Parus major* and Blue Tits *P. caeruleus*

JENNY F. DE LAET & ANDRÉ A. DHONDT
Laboratorium voor Oecologie der Dieren, University of Ghent, Ledeganckstraat 35, B-9000 Ghent, Belgium and Department of Biology, University of Antwerp, U.I.A., B-2610 Wilrijk, Belgium

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We tested the hypothesis that the weight lost by female Great and Blue Tits *Parus major* and *P. caeruleus* while raising their first brood influences their ability to start a second brood. The evening weight of female parents was recorded when the nestlings were 5 and 13 days old, in different years and habitats. Several predictions were tested: (1) both species lose weight while raising nestlings and Great Tit females which start a second brood lose less weight than females which do not; (2) differences in the average weight lost between years and areas correlate with differences in the proportion of second broods; (3) the relative weight loss in Blue Tits, which only rarely undertake second broods, is higher than in Great Tits in which second broods are more common. Other factors also are related to the probability of undertaking a second brood: more second broods are undertaken by more successful females, adult females and females that lay earlier.

The comparison of Great and Blue Tits suggests that the two species use different reproductive strategies.

A variable proportion of female continental Great Tits *Parus major* proceed to a second clutch after completing their first brood. More second broods are undertaken in coniferous compared with deciduous habitats and when populations are at lower densities (Kluyver 1951, Dhondt 1971). Kluyver (1963) also found that a slightly lower proportion of yearling females proceed to a second clutch, but a more important influence was the degree of success obtained with the first brood: 'the rearing of a large number of nestlings exhausts the endocrine secretion so markedly that a second clutch is omitted' (p. 715).

Tinbergen (1987) showed that the number of fledglings in the first brood strongly affected the likelihood of starting a second clutch, but the effect was only apparent when enlarged broods were compared with broods of normal size. It was expected that differences in parental condition would result in a differential allocation of energy to parents and nestlings, but no differences were found in body weight between females that did or did not produce a second clutch. Van Balen (1973) showed a positive relationship between the availability of food and the percentage of second broods started. Dhondt (1977) found that Blue Tit *Parus caeruleus* numbers adversely affected the percentage of Great Tits undertaking a second brood. He suggested that when Blue Tit density was higher it would be more difficult for Great Tit females to make up for the weight loss he assumed they incurred while raising their first brood, resulting in a lower proportion of them undertaking second broods. That female weight decreases while raising first brood young has been found by

Kluyver (1952) in Great Tits, by Nur (1984) in Blue Tits and has been explicitly stated in Drent & Daan (1980).

If it is correct that weight loss influences the probability of a female starting a second brood, several predictions can be tested: (1) females which start a second brood should lose less weight while raising their first brood than females which do not start a second brood; (2) differences in the proportion of second broods between areas and years should be correlated with weight loss while raising a first brood; (3) in regions where Blue Tit second broods are rare and Great Tit broods more frequent (as in Belgium), relative weight loss in Blue Tits should be higher.

In this paper these predictions will be tested. In addition some other factors that determine whether or not females proceed to a second brood will also be investigated.

Materials and methods

In the course of a long-term study of titmice, data on female weight loss were collected in three study areas near Ghent: a mature beech wood 'Hutsepot' at Zwijnaarde, a suburban park 'Maria Middelares' at Ghent and a coniferous plantation with a rich undergrowth 'COO' at Nazareth. Wooden nestboxes were available at high densities (> 8/ha) in all areas. More information on these study areas is given in Dhondt & Eyckerman (1980).

From the end of March onwards all nestboxes were inspected routinely once a week and their contents noted. Laying date is the date on which the first egg of a clutch is laid, assuming females lay one egg per day until the clutch is completed (Dhondt *et al.* 1984). The number of eggs laid in complete clutches were counted and nestlings were ringed at 15 days. From 1976 onwards all adults were systematically trapped on nestlings in Hutsepot. To eliminate year effects (Dhondt 1970) laying date, clutch size and number of young fledged were standardized to zero mean and unit variance. Female weight loss is the difference in evening weights between the initial weight (nestling day *5*) and the final weight (nestling day *13*). Handling females with younger nestlings sometimes resulted in brood desertion, while females often discontinued roosting in the nest when nestlings were older than 13 days. All measurements were made with a field balance accurate to 0·05 g. For the Great Tit, 12 (1977), 16 (1978) and 14 (1979) pairs of weights were obtained in 'Hutsepot', 9 (1977) and 4 (1978) pairs in 'Maria Middelares', and 8 (1977) pairs in 'COO'. Weight changes in Blue Tit females were only obtained in 'Hutsepot' (17 females) in 1977. Weight change was expressed as the percentage of the female weight when pulli were 5 days old (see also Nur 1984).

For each year and habitat the percentage of second broods was calculated and compared with the average percent female weight change. The proportion of second broods was determined by dividing the number of second broods initiated by the number of pairs that could have undertaken a second brood. Pairs whose first brood failed and which started a repeat clutch were therefore excluded.

Results

The initiation of second broods in Hutsepot Great Tits

The proportion of Great Tits that started a second clutch over the period 1976–86 in Hutsepot varied between years with a minimum of 10% in 1982 and a maximum of 50% in 1976. Rather than trying to correlate these different percentages with factors such as density or mean laying date, we have tried to determine the characteristics of females which did or did not start a second clutch in each year.

In Table 1 we have summarized, for first broods, the mean laying date, mean clutch size and mean number of fledglings in relation to whether or not a female started a second clutch. A two-way analysis of variance with year as one factor, and starting or not starting a second clutch as the second factor, shows significant year effects for all three variables. Females that started a second brood laid significantly earlier and raised significantly more young than those that did not start a second brood. Clutch size was not significantly different between the two groups.

Table 1. *Mean laying date (1 = 1 April), clutch size and fledging number of Great Tit first broods with and without a second brood (two-way ANOVA test), the laying date of Blue Tits without a second brood, and the proportion of adult and juvenile females that proceeded to a second clutch (Wilcoxon matched-pairs signed ranks test)*

	Great Tit laying date						Blue Tit laying date			Great tit clutch size				Great tit fledging number					
	With			Without			Without			With		Without		With		Without			
Year	*n*	mean	s.e.	*n*	mean	s.e.	*n*	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	% Adult	% Juvenile
1976	12	19·50	1·39	10	23·10	1·58	17	23·76	1·21	7·90	0·45	9·00	0·47	7·58	0·69	8·40	0·75	74·00	33·33
1977	9	9·88	1·60	8	19·37	1·70	25	15·08	1·00	8·67	0·50	7·67	0·61	6·00	0·79	3·67	0·97	50·00	60·00
1978	4	19·00	2·40	19	23·74	1·15	27	23·14	0·96	8·50	0·75	8·11	0·34	6·00	1·19	6·32	0·54	20·00	09·09
1979	6	19·00	2·05	14	21·29	1·29	33	21·21	0·87	9·67	0·61	8·57	0·40	8·17	0·97	6·64	0·63	33·33	33·33
1980	2	9·50	3·55	26	18·83	0·98	33	19·75	0·87	9·00	1·06	8·35	0·29	7·00	1·68	6·85	0·47	8·33	6·25
1981	7	7·71	1·82	13	12·92	1·39	26	13·34	0·98	7·29	0·57	9·15	0·42	4·86	0·90	5·38	0·66	41·67	12·50
1982	2	22·50	3·39	18	22·44	1·18	13	17·84	1·39	7·50	1·06	8·50	0·35	7·50	1·68	6·61	0·56	15·38	0·00
1983	12	18·58	1·45	30	21·13	0·91	34	21·11	0·86	9·08	0·43	8·63	0·27	6·92	0·69	6·07	0·43	46·67	9·68
1984	8	23·87	1·77	29	25·34	0·93	31	24·22	0·90	7·63	0·53	7·07	0·28	4·50	0·84	3·24	0·44	26·09	9·09
1985	8	20·38	1·70	21	21·85	1·09	20	21·65	1·12	9·13	0·53	8·14	0·33	7·13	0·84	6·38	0·52	57·14	6·67
1986	13	29·15	1·33	23	28·52	1·04	21	29·33	1·09	8·54	0·42	8·87	0·31	7·62	0·66	6·83	0·50	50·00	19·50
Total	83	19·12	0·55	211	22·18	0·34	280	20·91	0·30	8·47	0·16	8·32	1·60	6·70	0·25	6·00	0·30		
F_{years}	= 24·26, d.f. = 10, 272, $P < 0·001$									2·25		$P = 0·01$		7·84		$P < 0·001$			$T = -3$,
$F_{with/without}$	= 23·74, d.f. = 2, 272, $P < 0·001$									0·11		n.s.		5·21		$P = 0·02$			$P < 0·01$
$F_{interaction}$	= 0·25, d.f. = 10, 272, n.s.									0·79		n.s.		0·75		n.s.			

Table 2. *Mean initial weight, proportional weight change and final weight of female Great Tits raising first brood young in relation to whether or not they initiated a second brood (two-way ANOVA test)*

		Initial weight						% Weight change				Final weight			
		With			Without			With		Without		With		Without	
Habitat	Year	*n*	mean	s.e.	*n*	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.
Hutsepot	1977	8	18·31	0·29	4	18·99	0·41	−3·09	1·05	−5·82	1·49	17·73	0·27	17·89	0·38
Hutsepot	1978	3	18·25	0·48	13	18·27	0·23	−1·20	1·71	−4·62	0·83	18·00	0·44	17·42	0·21
Hutsepot	1979	6	17·39	0·34	8	17·57	0·29	−5·57	1·22	−3·68	1·05	17·31	0·31	16·94	0·27
Mar. Mid.	1977	5	18·65	0·37	4	18·50	0·41	−2·70	1·33	−4·83	1·49	18·13	0·34	17·60	0·38
Mar. Mid.	1978	0			4	18·56	0·41			−6·21	1·49			17·41	0·38
COO	1977	1	17·70		7	17·96	0·31	−2·26		−5·58	1·13	17·30		16·94	0·29
Total		23	18·15	0·17	40	18·20	0·14	−2·07	0·60	−5·11	0·40	17·17	0·15	17·26	0·13
$F_{\text{years + habitat}}$	$=3{\cdot}17$, d.f. $=5, 51$, $P<0{\cdot}02$							1·55		n.s.		2·29		n.s.	
$F_{\text{with/without}}$	$=0{\cdot}18$, d.f. $=1, 51$, n.s.							13·25		$P<0{\cdot}001$		4·45		$P<0{\cdot}05$	
$F_{\text{interaction}}$	$=0{\cdot}36$, d.f. $=5, 51$, n.s.							0·07		n.s.		0·38		n.s.	

Weight and the initiation of second broods

The difference in evening weights when first brood nestlings were 5 days and 13 days old was determined for 63 Great Tit females. In 56 of these weight decreased. Average female weight decreased by 3·87% in 8 days while raising their first brood (Paired t-test: $t = 2{\cdot}58$, d.f. = 62, $P < 0{\cdot}02$). A two-way analysis of variance with year/study plot as one factor and whether or not a second clutch was started as the second shows that the initial weight differed significantly between years and habitats (Table 2). No significant differences were found for percentage weight change or for final weights. We found no difference in initial weight between females that started or did not start a second clutch, but found that females that started a second brood lost a significantly lower proportion of their initial weight ($P < 0{\cdot}001$) resulting in a significantly higher final weight in that group ($P < 0{\cdot}05$) (Table 2).

To combine the effects of laying date (Table 1) and weight (Table 2) on second brood initiation we performed a stepwise multiple regression analysis (Hebrant 1975) using the entire data set (Table 3). Weight loss (partial regression coefficient $11{\cdot}20 \pm$ s.e $2{\cdot}55$, $P < 0{\cdot}02$) and laying date (partial regression coefficient $2{\cdot}87 \pm$ s.e. $0{\cdot}92$, $P = 0{\cdot}05$) each contributed significantly to explain variations in percentage

Table 3. *Data used in a multiple regression analysis between the proportion of second broods, laying date (1 = April), initial weight, final weight and the percentage weight loss of Great Tit females raising first brood young*

		Laying date			Initial weight			% weight change		Final weight		% second
Habitat	Year	*n*	mean	s.e.	*n*	mean	s.e.	mean	s.e.	mean	s.e.	broods
Hutsepot	1977	22	12·73	0·72	12	18·53	0·20	−4·00	0·65	17·78	0·14	50·00
Hutsepot	1978	26	23·19	0·20	16	18·27	0·23	−3·98	0·63	17·53	0·17	30·43
Hutsepot	1979	26	20·92	0·11	14	17·50	0·20	−2·35	0·60	17·08	0·15	33·33
Mar. Mid.	1977	12	14·42	0·51	9	18·58	0·24	−3·64	1·01	17·89	0·18	45·45
Mar. Mid.	1978	20	19·50	0·29	4	18·56	0·50	−6·21	0·13	17·41	0·23	00·00
COO	1977	32	18·19	0·35	8	17·93	0·27	−5·14	0·63	16·09	0·09	12·50

Table 4. *The proportional weight change of Great Tit females (all years and habitats) and Blue Tit females (Hutsepot 1977) according to age and in relation to whether or not they initiated a second brood (two-way ANOVA test and Mann–Whitney U-test)*

	Great Tit						Blue Tit		
	With			Without			Without		
	n	mean	s.e.	*n*	mean	s.e.	*n*	mean	s.e.
Juvenile	13	−2·05	0·81	22	−4·36	0·26	14	−8·46	0·39
Adult	10	−2·09	0·92	18	−5·56	0·69	3	−9·46	0·29
Total	23	−2·07	1·38	40	−4·90	0·60	17	−8·62	0·36
$F_{\text{Adult/Juvenile}}$	= 1·24, d.f. = 1, 19, n.s.						*U*-18, n.s.		
$F_{\text{With/Without}}$	= 13·88, d.f. = 1, 19, $P < 0{\cdot}001$								
$F_{\text{Interaction}}$	= 0·57, d.f. = 1, 19, n.s.								

second brood. Together they explained 90·5% of the variation ($P < 0·05$). The residual effect of initial weight and final weight were not statistically significant. Thus females that laid early *and* lost relatively less weight while raising their first brood were more likely to start a second brood, both factors having an independent effect.

In Great Tits the proportional weight change was negatively correlated with the initial weight (Spearman rank correlation coefficient $r_s = -0·365$, $n = 63$, $P < 0·01$) and positively with the final weight ($r_s = 0·269$, $n = 63$, $P < 0·05$). In Blue Tits a significant positive correlation was found only with final weight ($r_s = 0·441$, $n = 17$, $P < 0·005$). In both species the proportional weight loss increased significantly with laying date (Great Tit: $r_s = -0·446$, $n = 63$, $P < 0·01$; Blue Tit: $r_s = -0·431$, $n = 17$, $P < 0·05$).

The effect of female age

Our results confirm those of Kluyver (1951) that a higher proportion of adult than juvenile females undertake a second brood (Table 1). In Table 4 we present the data on weight loss per age class and according to whether the female started a second clutch or not. Great Tit females that started a second clutch lost significantly less weight than those which did not, but there was no effect of age on weight loss in either Great Tits or Blue Tits.

A comparison of Great and Blue Tits

In Hutsepot, 1977, Great Tit females lost on average 4·00% ± 0·76 of their initial weight compared with 8·62% ± 0·36 in Blue Tits, a difference that is statistically significant (Mann–Whitney U-test: $n_1 = 12$, $n_2 = 17$, $U = 31$, $P < 0·001$). Very few Blue Tits started a second clutch and no weight data were available for these. Comparing females which did not start a second clutch in the two species we still find a significant difference in weight loss (Table 4), with Great Tit females losing less

Table 5. *Mean number of young (first broods + repeat clutches) fledged by Great Tit and Blue Tit females at Hutsepot (two-way ANOVA test)*

	Great Tit			*Blue Tit*		
Year	*n*	mean	s.e.	*n*	mean	s.e.
1976	26	7·38	0·62	20	9·20	0·71
1977	22	5·50	0·68	26	8·81	0·62
1978	26	5·54	0·62	15	6·07	0·82
1979	26	5·88	0·62	20	8·95	0·71
1980	31	6·03	0·57	33	8·52	0·55
1981	27	4·33	0·61	23	5·65	0·66
1982	22	6·32	0·68	13	8·46	0·88
1983	51	5·82	0·44	37	7·35	0·52
1984	47	3·38	0·46	32	5·00	0·56
1985	36	5·97	0·53	19	8·95	0·73
1986	45	6·47	0·47	19	8·42	0·73

$F_{\text{Years}} = 8·92$, d.f. = 10, 595, $P < 0·0001$
$F_{\text{Species}} = 61·97$, d.f. = 1, 595, $P < 0·0001$
$F_{\text{Interaction}} = 0·83$, d.f. = 10, 595, n.s.

weight (4·90%) than Blue Tits (8·62%) (Mann–Whitney U-test: $n_1 = 17$, $n_2 = 40$, $z = 3{\cdot}48$, $P < 0{\cdot}001$).

Very few data are available for the laying dates of Blue Tits which undertook a second brood, since only three cases were observed in 11 years in Hutsepot. All three started their first clutch very early: 12 April and 16 April 1976, and 5 April 1981. Using the data in Table 1 it can be shown that Blue Tits which did not start a second clutch laid significantly later ($20{\cdot}91 \pm 0{\cdot}30$; 1 = 1 April) than Great Tits that started a second clutch ($19{\cdot}12 \pm 0{\cdot}55$), but significantly earlier than Great Tits which did not start a second brood ($22{\cdot}18 \pm 0{\cdot}34$; two-way ANOVA, $F_{\text{years}} = 39{\cdot}88$, d.f. = 10,552, $P < 0{\cdot}001$; $F_{\text{species or category}} = 11{\cdot}11$, d.f. = 2,552, $P < 0{\cdot}001$).

Blue Tit females raised significantly more young per brood than did Great Tit females (Table 5); in fact on average they raised as many young in a single brood ($8{\cdot}88 \pm$ s.e. 3·09) as Great Tits did in two broods ($8{\cdot}78 \pm 2{\cdot}91$).

Discussion

In this paper we tested a number of predictions following from the assumption that female weight loss, while raising first brood young, would influence their ability to start a second clutch. We found that females of both species lost weight while raising nestlings and in particular that Great Tit females which start a second brood lose less weight than females which do not (prediction 1), that the differences in the average weight loss between years and areas correlate with differences in the proportion of second broods undertaken (prediction 2), and that the relative weight loss in Blue Tits, which only rarely undertake second broods, is higher than in Great Tits, in which second broods are more common (prediction 3). However, we did find that additional factors are related to the probability of undertaking a second brood.

We could not confirm Kluyver's (1963) observation that the proportion of second broods increases with an increasing number of eggs laid and a decreasing number of young fledged. Rather we found no significant effect of clutch size and a significant positive relationship between number of young fledged and the probability of initiating a second brood. The more successful females thus initiated more second broods.

Females which undertake second broods lay earlier than those which do not, the effect being independent of, and additional to, the effect of weight loss. In our sample a delay of 10 days in laying date reduced the probability of starting a second brood by 0·31. Nevertheless, females which laid later lost more weight while raising their first brood young, showing that the later start of the first clutch resulted in a lower chance of starting a second one through two mechanisms: one operating directly via weight loss, the other operating through date independently of weight loss.

Although we found that over 11 years in Hutsepot a higher proportion of the adult females started a second brood, we did not find that juvenile females lost more weight while raising their first broods. We did find that in both age groups birds which did not undertake a second clutch lost more weight than those which did.

A comparison of Great and Blue Tits suggests that the two species use different reproductive strategies: Great Tits invest less in a first brood (smaller clutch, fewer fledged young) and lose relatively less weight while raising their first brood, but, if conditions are adequate, go on to raise a second brood. Blue Tits invest more in a first brood (larger clutch, more fledged young) and lose relatively more weight while raising their first brood. They only exceptionally proceed to a second clutch. However, on average the total number of young raised per pair and per season is very similar, although the yearly variation in the reproductive rate is much greater in

Great Tits than in Blue Tits. In both species the proportional weight loss was significantly influenced by their laying date, because less weight was lost when females started laying earlier.

The negative correlation between the initial weight and the proportional weight change is rather unexpected. Because of the positive correlation between initial weight and final weight and between final weight and the proportional weight change, a positive correlation between initial weight and proportional weight change should be more plausible. Nevertheless this confirms our previous result that initial weight does not contribute to the probability of initiating a second brood.

Food availability might influence, to a large extent, female weight change. Differences in weight change between females starting to lay on the same date could be caused by micro-habitat differences between territories. Food availability decreases rapidly in the course of the season as illustrated by the decrease in fledging weight of first brood young with later fledging date (Perrins 1965, Dhondt 1971). Females starting their first clutch later will face the decision of whether or not to initiate a second brood at a time when food conditions are worsening and after a more severe weight loss. Between year variations in the amount of food are important. Van Balen (1973) positively correlated the maximal amount of food available with the proportion of second broods in the Netherlands. On the other hand, Kluyver *et al.* (1977) concluded that whereas the interval between first and second brood was correlated with the amount of food when first brood young were in the nest, 'the feeding conditions in oak woods prevent the tits from starting a second clutch' (p. 167). Experimental food addition carried out by Den Boer (1979) largely confirmed the conclusion that extra food did not increase the probability of starting a second brood, but reduced the interval between first and seconds broods. Kluyver *et al.* (1977) concluded that because the second clutch is usually started about one day after the fledging of the first brood, and because it takes females about four days to produce their first egg, the 'decision' to produce a second brood has already been made during the nestling stage of the first brood or even earlier. We propose that this decision is influenced by the weight loss while raising the first brood.

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