

Fig. 5. Finding the end of brooding phase. The difference between the two histograms of length of visits is striking. The number of longer visits is decreasing throughout the brooding period. In the later feeding period we could hardly find brooding visits.

3.2. Four phases of breeding

Further analysis of the females' roosting weights showed three different weight levels and a transitional period. These weight levels can be related to the different periods of breeding: laying, incubation and late feeding (Fig. 4).

During the egg-laying period the female lays one egg each day, before she leaves the nest in the morning. During this phase she spends more of her day out of the nest.

We consider the incubation period from the completion of clutch although the female can start incubation earlier. Both females, measured in this period, started incubation after clutch completion.

The feeding period may be divided into two parts: brooding and late feeding (Freed 1981). During the brooding phase the nestlings are mostly unfeathered and need to be warmed by their mother. This

means that the female cannot leave them alone for long intervals. As the nestlings and their feathers grow, they become capable of regulating their body temperature, and both the frequency and the length of the female's brooding visits decrease gradually. In order to find the end of the brooding phase, we studied the distribution of visit length day to day (Fig. 5). We define the brooding phase to be over if the proportion of visits longer than 120 seconds is under 5% of the total number of visits per day. Thus the female's visits are nearly always short and serve only feeding purposes during the late feeding period. (The length of brooding varied between five and twelve days.)

By comparing the variances of weights in the four periods, we found that the brooding phase causes significant difference between the variances (Levene's tests, $df = 3, 37$, $p < 0.001$ for both weight profiles of nest G16-95). Excluding the

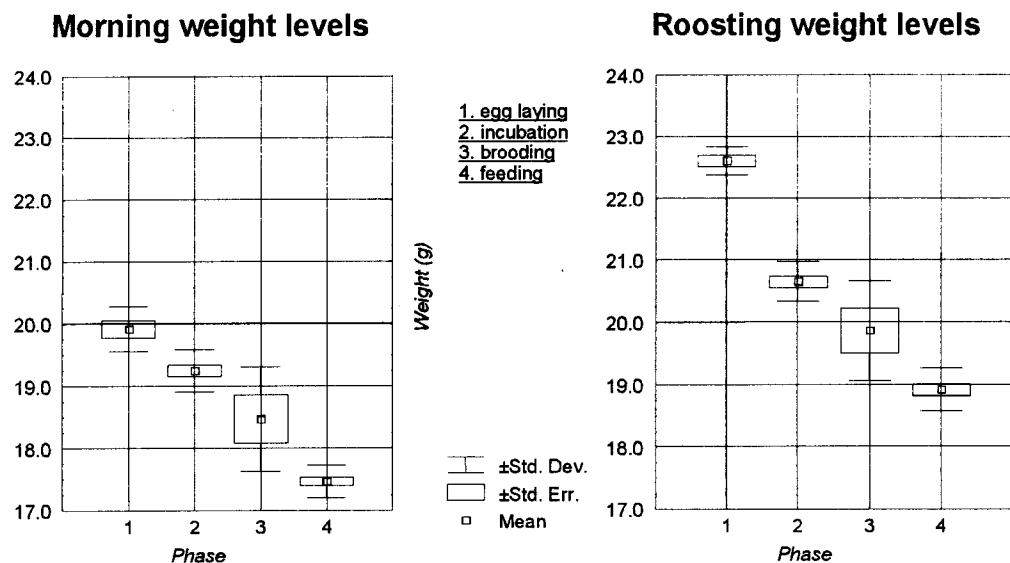


Fig. 6. Means, standard errors and standard deviations of the different weight levels (nest G16-95). For both weight profiles the standard deviation of the female's weight during the brooding phase is very high. This is due to the sharp decrease in body weight.

brooding phase from the analysis resulted homogeneity in the variances of the remaining three periods (Levene's tests, $df = 2, 33$, $p > 0.15$). The analysis of the other two nests where appropriate data were available showed similar results.

By comparing the mean weights in the different periods, we found a significant difference between the incubation and the late feeding periods of each female (Fig. 6, Scheffe-tests, $p < 0.001$ for both weight profiles, $N = 4$ females).

3.2.1. Egg-laying

During the egg-laying period we found a significant decrease in the roosting weights but not in the morning weights in one of the two nests (slope = -0.07 g/day, $R^2 = 0.5570$, $F(1,6) = 7.5442$, $p < 0.0334$ for the roosting weights, nest G16-95).

We found a significant difference in the roosting weight profile between the egg-laying and the incubation phase

(Scheffe-test, $p < 0.001$, $N = 2$ females). The female collects the material required for the formation of the egg during the day and lays the egg at dawn. This explains the $7.99 \pm 0.20\%$ (mean \pm SD, $N = 2$ females) decrease in the roosting weight after clutch completion. In contrast this decrease is smaller (nest G16-95: 3.35% , $p < 0.01$) or not significant (nest G225-95: 1.62% , $p > 0.35$) in the morning weight profiles.

3.2.2. Incubation

Over the incubation phase there was no significant trend in the weight profiles in any of the observed cases (linear regression, $N = 4$ females).

3.2.3. Brooding

Both the morning and roosting weight profiles of the brooding phase show a significant decreasing trend so we did not con-

sider it as a constant weight level. The slopes of the fitted lines ranged from -0.06 to -0.50 g a day and they differed significantly from each-other (test of parallelism, $df = 3, 17$, *Morning weights*: $F = 7.48$, $p < 0.01$, *Roosting weights*: $F = 3.32$, $p < 0.05$). All measured females lost weight throughout the five to eight days in this phase. The females lost $10.0 \pm 1.5\%$ (Mean \pm SD, $N = 4$) of their incubation weight on average, that is about 2 g.

3.2.4. Late feeding

There was no significant trend in the weight profiles (linear regression) in the majority of cases. None of the females gained weight and only 2 of the observed 12 females lost weight in the late feeding phase. One of the females lost 0.76 g over 11 days and the other one lost 1.23 g over 13 days.

3.3. Daily mass changes

During daytime the males gained $7.46 \pm 1.61\%$ (mean \pm SD, $N = 103$ days) while the females gained $6.53 \pm 1.97\%$ ($N = 178$ days) of their morning weights. These averages do not include data of the egg-laying periods for the females, when the daily weight gain was $13.73 \pm 0.13\%$ ($N = 15$ days).

Overnight the males lost $7.49 \pm 1.49\%$ ($N = 103$ nights) while the females lost $6.66 \pm 1.76\%$ ($N = 181$ nights) in comparison to their following morning weights. (In comparison to their evening or roosting weights, males: $7.06 \pm 1.32\%$ ($N = 89$ nights), females: $6.12 \pm 2.15\%$ ($N = 174$ nights)) These means do not include data of the egg-laying periods when the females' overnight weight loss was $12.09 \pm 0.17\%$ ($N = 15$ nights) due to the laid egg.

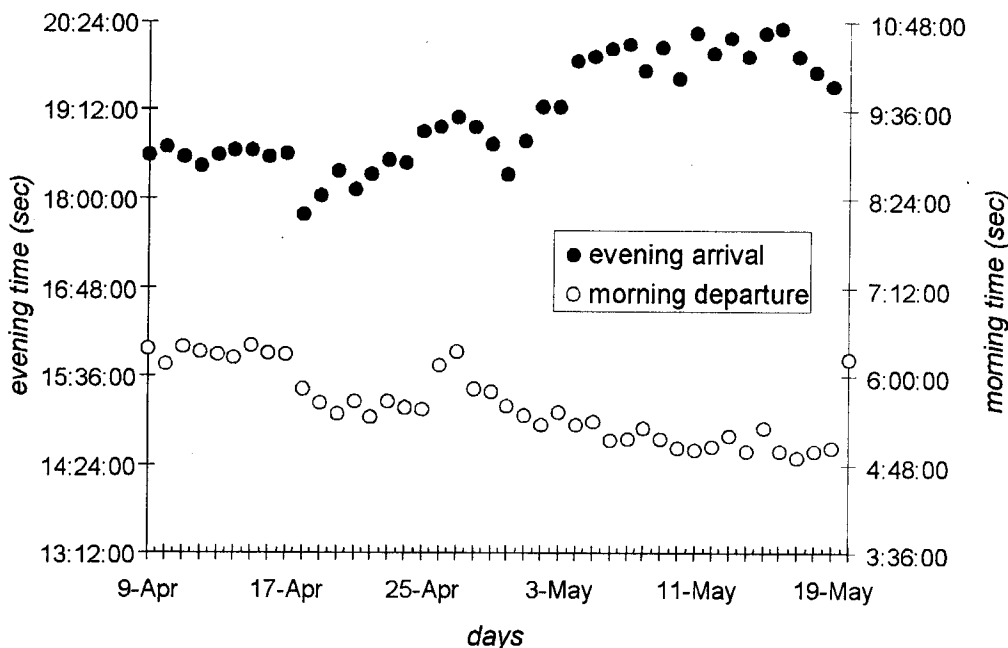


Fig. 7. Female's daily timetable (nest G16-95). As the breeding season proceeds the days become longer and the nights get shorter for the female.

We found no difference between the average daily gains and overnight losses of either the females (t-tests, $df = 357$, $p > 0.62$) or the males (t-tests, $df = 204$, $p > 0.92$). However, we found that the males lost and gained more weight than the females (t-tests, $p < 0.0001$).

As the energetic demands of incubation, brooding and late feeding may differ, we compared the average weight gained or lost per hour in the four periods. Both the lengths of the working days and the duration of roosting vary throughout the breeding season (Fig. 7). We calculated the difference between the time of the first departure in the morning and of the last arrival for each female for each day. We calculated the body-weight increase per hour as the ratio of the proportional gain in body-weight from morning until night and the duration of the working day. We determined the proportional continuous weight-loss per hour similarly. To our surprise, we could not show any differences in the rate of body-weight change between the periods (Tab. 4, 5).

We also calculated the weight lost during the first foraging trip. This usually gives a minimum estimate for the weight of the faeces as the female defecates after her first departure in the majority of cases but she also eats during these foraging trips (Tab. 6). The apparent difference in the average faecal loss between the periods is partly due to the difference of the average length of the first foraging trip. These foraging trips were significantly the shortest on average and had the smallest standard deviation during the brooding period, while it was by far the longest during egg-laying.

4. Discussion

4.1. Male weight levels

In our sample the males maintained their weight throughout the observation periods. Males are on average heavier than females outside the breeding season (Kluyver 1952, own unpublished data). The male was heavier than the female in five pairs while the female was heavier in seven pairs during the observation periods. The weight profiles belonging to a pair never crossed during the observation period. As before hatching the males do not visit the nest early in the morning we have no opportunity to determine their exact morning weight in the beginning of the breeding season by weighing at the nest. It would be interesting to study whether the males lose weight in those early days when they feed the females before and during laying. In the case of non-incubating, non-brooding males the energetic demands are probably more evenly distributed than on the females.

4.2. Female weight levels

4.2.1. Egg-laying

The females start to increase their body weight some days before the first egg is laid (Woodburn & Perrins 1997). The only female whose weight was measured in the pre-laying period also showed a large increase in weight during the four days before laying (Fig. 2). This increase in weight is mainly due to the increase of body water content (Woodburn & Perrins 1997). The function and fate of this water are unclear. Both Mertens (1987) and

Woodburn & Perrins (1997) report water loss at the beginning of incubation and after hatching.

Egg production is energetically costly for small birds. During a breeding season Great Tits have to produce an egg, weighing nearly 10% of their own weight, on each day. To collect the required materials, the pair must co-operate, and the supplementary or courtship feeding by the male (Royama 1966, Krebs 1970) may have an important role in achieving the target: a clutch of 6 to 13 eggs.

The requirements of the laying period are high and thus the environment can affect its characteristics to a great extent. Food availability is the main signal for the timing of egg laying (Nilsson & Svensson 1993, Nilsson 1994, Nager *et al.* 1997), which may be influenced by temperature. When laying has already started, poor feeding conditions, due to bad weather or high population density, can cause laying interruptions in Great Tits (Dhondt *et al.* 1981). There was no such interruption in our two nests.

Poor feeding conditions may also be reflected in either decreasing body weight or decreasing egg weight in the course of the laying period (Nager & Noordwijk 1992, Ramsay & Houston 1997). In one of the two nests the female's roosting weight decreased but her morning weight remained stable in the laying period. This suggests that egg weight decreased, although we did not measure the eggs separately. It is important to keep in mind that besides other nutrients the availability of calcium for the egg-shell could also be a limiting factor (Graveland *et al.* 1994). The calcium comes mainly from small snails (Graveland & van Gijzen 1994). The females usually go roosting with a snail in their gizzard

(Perrins 1996) because they digest it slowly overnight and thereby their digesting capacity is maximised during the day (Woodburn & Perrins 1997).

Similarly to others (Jones 1987c, Woodburn & Perrins 1997) we found that the female's body weight is greatest in this period.

4.2.2. Incubation

After the last egg is laid (sometimes earlier) the female starts to incubate the eggs. The start of incubation is also influenced by food availability (Nilsson & Svensson 1993, Nilsson 1994, Nager *et al.* 1997).

After clutch completion the reproductive organs regress and some water is lost, while the weight of the carcass, carcass fat and flight muscle increase (Mertens 1987, Woodburn & Perrins 1997). Woodburn & Perrins (1997) found that this caused considerably higher weight loss after egg-laying than the average egg weight in Blue Tits (*Parus caeruleus*). However, the difference between the roosting weights of the two females observed in our sample was not much bigger (0.07 g and 0.26 g) than the average egg weight. The maintenance of fat reserves may help the females to continue incubation at lower temperatures when their energy expenditure grows considerably (Mertens 1987) and when they need to stay longer on the eggs. Besides relying on their fat storage, females may count on the males' supplementary feeding.

None of the females in our sample (N = 4) lost weight during incubation. In two of three years Mertens (1987) found that Great Tit females lost more than 1 g during incubation; similarly Woodburn & Perrins (1997) also found decreases in the weight

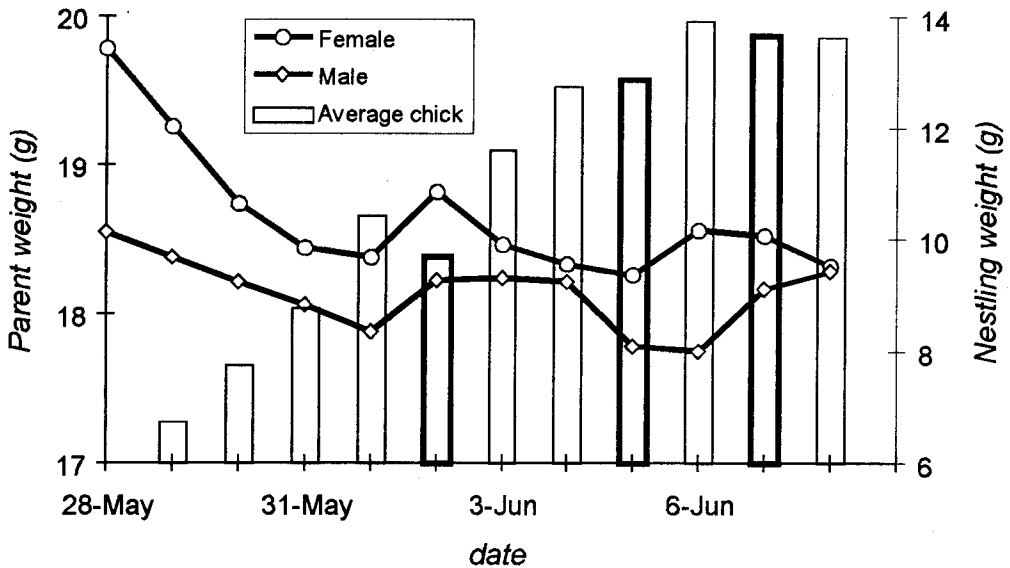


Fig. 8. A "disaster-struck" nest (nest G375-93), where 3 chicks have died one after the other (the last on 1 June) and 6 fledged. There were several rainy days when the nestlings lost weight (darker bars). On those days the parents maintained or gained weight. This example suggests the shortage of fat reserves.

of four Blue Tits. Ricklefs & Hessel (1984) reported weight decrease in female but not in male Starlings (*Sturnus vulgaris*) though both sexes take part in incubation. While short-term weight changes of incubating Swallows (*Hirundo rustica*) were related to the prevailing weather, Jones (1987c) did not find long-term weight-loss during incubation ($N = 5$ females). These different results suggest that the body weight of incubating females is sensitive to the prevailing conditions yet females are always heavier during incubation than during nestling rearing. Females typically do not lose all their reserves by the end of incubation.

4.2.3. Brooding

All the females lost weight over five to eight days after hatching ($N = 5$). Freed (1981) described the same phenomenon in

House Wrens (*Troglodytes aedon*), Jones (1987a) in Swallows, Ricklefs & Hessel (1984) in Starlings, Moreno *et al.* (1991) in Collared Flycatchers (*Ficedula albicollis*) and Woodburn & Perrins (1997) in Blue Tits. Merila & Wiggins (1997) showed that the rate of re-growth of feathers removed earlier correlated negatively with the amount of weight loss, which could indicate stress in this period. There is accumulating evidence that female weight loss immediately after incubation may be a general phenomenon among Passerines, though data are still scarce. The magnitude of this weight loss may depend on the incubation weight of the females and the number of nestlings (Jones 1987a, Johnston 1993, Merila & Wiggins 1997).

There is a long-standing discussion in the literature over whether this weight-loss represents some costs of reproduction

or is a pre-adaptation to diminish the forthcoming increase in flight-costs (Drent & Daan 1980, Norberg 1981, Freed 1981, Ricklefs & Husel 1984, Merila & Wiggins 1997). Gosler (1991) showed that females declined in protein reserves while feeding a brood. The proper timing of this weight-loss must be crucial for the female, as if she loses her reserves too early she may not survive unfavourable periods. If she is too late she unnecessarily keeps predation risk higher (Gosler *et al.* 1995) or retards nestling growth by inefficient energy utilisation. As the females lose most of their weight just after or during hatching, and not right before the peak feeding period (unpublished data), we think that flight-cost reduction does not have a major role in timing their weight loss. Houston (1993) showed in simple time budget models that the efficiency of mass loss, i.e. the value of the energy released by mass loss in terms of the increase in energy delivered to the young is lower than 1 if the bird loses weight during the peak feeding period. However, during brooding any saving of energy by the female can be given more directly, i.e. more effectively to the nestlings by brooding than in the late feeding period by decreased food demand.

The females still need some energy reserves because of the high and unpredictable energetic demands during brooding. In the first days of brooding, a female still spends much time in the nest, which imposes a heavy time constraint on her (Tóth & Pásztor 1997). She cannot leave the nestlings alone for too long while she also has to provide food for both them and for herself. This means that by minimising self-feeding she can gain valuable time that can be used for the other two activi-

ties. Both parents feed the young in this period and it is likely that the male gives less food to the female than earlier. Thus, it is possible that brooding is energetically even more demanding for the female than incubation and she is in need of her reserves. The energetic demands imposed by brooding on the parents may vary with the environmental conditions. We found that the length of the brooding period varied among nests. It ranged from 5 to 12 days in our sample.

As the first days after hatching may be critical for both the nestlings and their parents, the optimal number of nestlings may depend on the amount of reserves possessed by the female at hatching. We think that in order to understand the role of brooding in the optimisation of clutch size we need more studies, which concentrate on this period.

4.2.4. Late feeding

The feeding frequency reaches its maximum in the late feeding period. By that time the parents possess reduced reserves. When unpredictable bad weather causes limited food availability the parents have to decide whether to feed themselves or the chicks (Fig. 8). Restriction to self-feeding may be the only option in many cases, causing weight loss in the nestlings and reduced juvenile survival. The decision of the parents, and in turn their body weight, may depend on the number of nestlings, i.e. on the value of the brood (Smith *et al.* 1988).

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Összefoglalás

Költő széncinegék testtömeg-változásai

Automatikus elektronikus mérlegek segítségével 12 széncinege testtömeg változását követjük nyomon 6-47 napon át a költési szezonban 1993 és 1997 között. A "The Visitor" szoftver csomagot használtuk adatgyűjtésre és adatrendezésre. Tanulmányunkban a tojó és hím madarak reggeli és esti testtömeg változásának napról napra történő változását elemeztük.

1. A vizsgált 12 hím széncinege közül egyiknél sem következett be testtömeg változás.

2. Két tojónál sikerült a testtömeg változást a tojásrakás kezdetétől a kirepülésig követni. Esetükben három testtömeg szintet tudtunk elkülöníteni: átlagos éjszakázási tömeg a tojásrakás, kotlás és etetés alatt. A tojásrakás alatt egyik tojó sem veszített a tömegéből, bár az egyik egyed tojásainak súlya csökkent. A tojók reggeli testtömege hasonló volt a tojásrakás és kotlás alatt.

3. A tojók egyikének sem csökkent a tömege a kotlás alatt ($N = 4$). A testtömegük azután kezdett el csökkenni (átlagosan 10 %-al, $N = 4$), hogy a fiókák kikeltek. A késői etetés alatt tíz tojónak a tömege nem változott, kettőnek pedig csökkent.

4. Nem találtunk szignifikáns különbséget a napközbeni óránkénti tömegnövekedés, illetve az éjszakai óránkénti tömegcsökkenésben a négy költési szakasz között ($N = 5$).

Eredményeink és publikált adatok alapján úgy gondoljuk, hogy az énekesmadarakra általánosan jellemző a kotlás előtti jelentős tömegnövekedés és kisebb tömegvesztés a kotlás után. A jelentős testtömegnövekedés a tojásrakás előtt, és a tömeg megtartása a kikelés utánig részben magyarázható a tojásrakás és kotlás nagy energia igényével. A tartalékok előse-

gítik az esetleges kedvezőtlen időszakok átvészelését. Az etetés előtti tömegcsökkenés adaptív, mivel a nagy tömegű egyedek számára a repülés nagyobb befektetést igényelne, de a tömegcsökkenés időzítése és mértéke az adott fészekalj igényeitől függ. Az optimális fészekalj méret tehát attól is függhet, hogy a tojó mennyi tartalékot képes mobilizálni a kotlás után.

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Weight change patterns in breeding Great Tits (*Parus major*)

B. Halpern, Z. Tóth, and L. Pásztor

Halpern, B., Tóth, Z. and Pásztor, L. 1997. Weight change patterns in breeding Great Tits (*Parus major*). – Ornis Hung. 7: 1-17.

Between 1993 and 1997 we weighed 12 Great Tit nests automatically using electronic balances for periods of 6-47 days during the breeding seasons. We used "The Visitor" software package for collecting and processing the data. In this paper we publish the results of the analyses of the day to day changes of morning and evening body weights of females and males.

1. None of the 12 males lost or gained weight during the observation periods.
2. Those two females whose weight was measured from the beginning of egg-laying until fledging had three different weight levels: average roosting weight during egg laying, during incubation and during late feeding differed. None of these females lost weight during egg laying, but one female's egg weight decreased. The females' morning weight levels were similar at egg laying and incubation.
3. Each female maintained her weight through incubation ($N = 4$). Females lost weight (10% on average, $N = 4$) after hatching, in the brooding period. Ten females maintained their body weight, while two others lost weight in the late feeding period.
4. We did not find any significant difference either in the average weight gained per hour during a day or in the average weight lost per hour during a night between the four periods of breeding ($N = 5$ females).

Based on other published data and on our own results we think that a substantial gain in weight before egg laying and some weight loss of females after hatching is a general phenomenon among Passerines. The substantial increase in body weight just before laying and its maintenance until the brooding period can partly be explained by the high energetic demands of laying and incubation. Reserves can serve as buffers against unfavourable conditions during these periods. Flight cost of high body weight makes weight loss before the peak feeding period adaptive but the exact timing and amount of this weight loss may depend on the actual energetic demands of brooding. Thus, optimal clutch size may depend on the amount of reserves a female can mobilise right after incubation.

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1. Introduction

There is a long-standing interest in understanding the breeding behavior of small Passerines and especially of Great Tits (Gibb 1950, Kluyver 1952, Noordwijk *et al.* 1995, Perrins 1996). Does egg laying, incubation or nestling feeding impose

some costs on the parents (*sensu* Williams 1966) or is parental effort always below the level that may influence parental survival (Gibb 1950, Lack 1947, Tuomi 1990)?

It is standard practice amongst field ornithologists that when birds are caught their body weight is also measured. Changes in body weight of the parents dur-



Tab. 1. An overview of the observed nests. The last 2 digits in the nest IDs give the year of observation. "Length" gives the number of days when a nest was actually measured. Thus, in the three cases denoted by *, the time spans of the observations were longer than the number of observation days.

Nest ID	Nest data			Observation	
	No. Eggs	Hatched young	Fledged young	Length (days)	Beginning from
G50-93	8	8	8	12 *	brooding
G165-93	8	6	6	11	late feeding
G375-93	9	9	6	13	late feeding
G18-94	7	7	8	11	late feeding
G40-94	7	6	6	17	brooding
G16-95	10	10	6	43	egg-laying
G40-95	7	7	6	11	late feeding
G47-95	9	9	8	8	late feeding
G225-95	8	6	5	41 **	egg-laying
G231-95	8	7	7	6	late feeding
G231-96	7	4	4	26 *	incubation
G65-97-1	6	5	5	28	incubation

* observation interrupted for 2 days

** observation interrupted for 6 days

ing the breeding season is often considered as a good indicator of physiological condition and parental costs (Drent & Daan 1980, Nur 1984, Jones 1987a, Kacelnik & Cuthill 1990, Johnston 1992, Martins & Wright 1993, Merila & Wiggins 1997). Decreased body weight in enlarged broods is considered as a result of optimal allocation of energy between self-maintenance and reproductive effort and a sign of potential reduction in future survival (Stearns 1992). There is plenty of evidence that nestling body weight at fledging influences future survival of the nestlings (Perrins 1965, Garnett 1982, Lindén *et al.* 1992). Brood size manipulation experiments show that reduced body weight of the parents rearing enlarged broods corresponds with reduced parental survival (Stearns 1992).

Another approach to interpret weight changes during breeding is to consider weight changes on a longer time scale and to examine the changing ecological costs and benefits of fat storage (Witter & Cuthill 1993). Females gain weight just before egg laying (Witter & Cuthill 1993, Woodburn & Perrins 1997). The birds often lose weight during incubation or after the chicks hatch (Freed 1981, Ricklefs & Husell 1984, Jones 1987a, Woodburn & Perrins 1997). A possible explanation for this pattern is that a bird needs her fat reserve during incubation as a buffer against long, unfavorable periods when she has to stay in the nest without self-feeding. The brooding birds lose these reserves before the peak feeding period when excess weight would increase their flight costs (Sanz & Moreno 1995).

Tab. 2. Comparison of the morning (MW) and roosting weights (RW) measured on the last day of incubation (Day -1) and the day before fledging (Day 18) for 4 females. The results of paired t-tests are shown (t and p values).

	Mean \pm SD (g)	Day 18 MW 17.40 \pm 0.46	Day 18 RW 18.47 \pm 0.73
Day -1 MW	19.31 \pm 0.38	4.87	0.0166
Day -1 RW	20.00 \pm 0.78	4.88	0.0164
			1.64
			2.37
			0.1997
			0.0985

Tab. 3. Daily body-weight changes expressed as percents of the morning weights (Mean \pm SD, No. of observations).

	Females	Males
Daily gain	6.53 \pm 1.97% N = 178	7.46 \pm 1.61% N = 103
Overnight loss	6.66 \pm 1.76% N = 181	7.49 \pm 1.49% N = 103

These two approaches to the interpretation of body weight changes throughout breeding can be combined. Body weight profiles (Fig. 1), or the amount of energy reserves during the course of breeding can also be considered as plastic traits that are optimized individually (Jones 1987a, Sanz & Moreno 1995). To solve this optimization problem each component of both the costs and benefits of gaining or losing weight at a certain time ought to be considered. By observing the entire weight profile we may also learn about the various components of costs and benefits of body weight change associated with different periods of breeding. For instance, if the birds regularly lose weight during the peak feeding period, weight loss can be

considered as the cost of heavy feeding activity, and not as an adaptation that reduces flight cost. If they lose weight just before the peak feeding period, the hypothesis that weight is lost to reduce flight costs cannot be excluded.

Timing of weight changes can be determined only by regular weighing of the birds. There is a major methodological problem of weighing the birds regularly during breeding, as catching them may influence their condition. Automatic weighing of nests solves this problem (Jones 1987b, Martins & Wright 1993, Szép *et al.* 1995). We used our own software package, called "The Wisitor", for the automatic weighing of 12 nests of Great Tits and also for data processing (Tóth 1994). This made it possible to carry out the observation and to analyze the complete weight profiles and weight changes over a day and a night.

We found that all the measured females lost about 10% of their weight on average just after hatching and only a minority lost weight during the late feeding period,

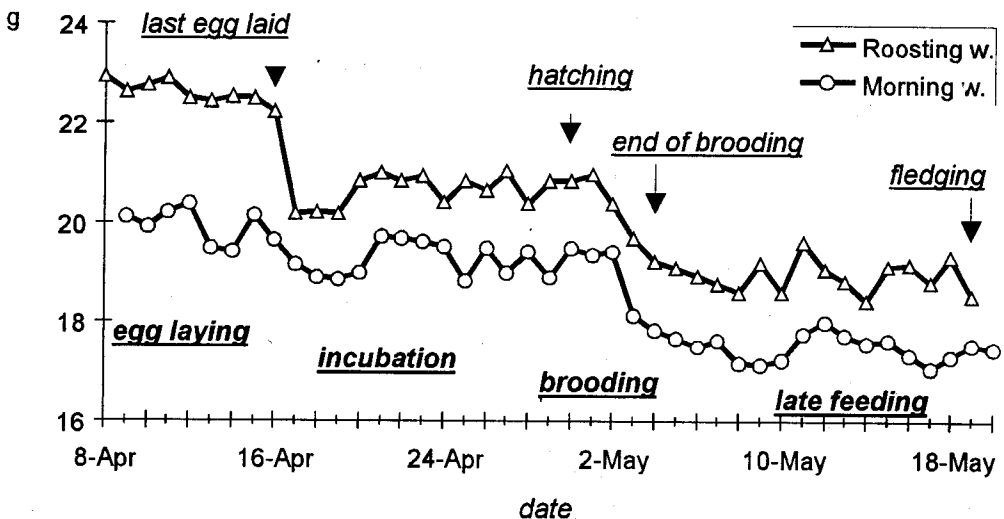


Fig. 1. A female's weight profiles (morning and roosting) during breeding (nest G16-95).

Tab. 4. Females' average weight gain per hour during daytime, in the four periods of nesting.

Nest	egg-laying	incubation	brooding	late feeding
G40-94	-	-	0.53 ± 0.09%	0.51 ± 0.07%
G16-95	1.08 ± 0.13%	0.61 ± 0.17%	0.54 ± 0.06%	0.56 ± 0.12%
G225-95	1.03 ± 0.16%	0.48 ± 0.14%	-	0.42 ± 0.10%
G231-96	-	0.33 ± 0.21%	0.34 ± 0.07%	0.43 ± 0.10%
G65-97-1	-	0.49 ± 0.15%	0.46 ± 0.18%	0.43 ± 0.17%
Average	1.05 ± 0.04%	0.48 ± 0.12%	0.47 ± 0.09%	0.47 ± 0.06%
Average time spent with daily activities (Hour: min: sec)	12:46:25	13:08:20	14:22:23	14:56:53

when brooding was over. The males' weight was stable without exception. In this paper we document all the weight changes we found and argue that flight cost reduction does not give a sufficient explanation for the observed weight change patterns.

2. Materials and methods

2.1. Subjects and study area

The Great Tit is a small, hole-nesting, resident Passerine that breeds commonly in all kinds of woods, in parks and gardens, and occupies artificial nestboxes readily. The female lays one egg daily, incubates alone and the male regularly feeds her during the two weeks of the incubation period. Both parents feed the young. The nestlings fledge about 18-20 days after hatching.

Fieldwork was carried out in the park of the Biological Research Station of Eötvös University in Göd. The area is a mixed habitat, with some parts having plantations of characteristic of a botanical garden. There are fragments of coniferous woods and riverine woodland of the river Danube, dense bushes and open fields. There were around 65 artificial nestboxes in the area, all fixed on tree trunks and some of them prepared for easy installation of an electronic balance. Data presented here were collected between 1993 and 1997.

2.2. Data collection

This study is based on data collected by a computerised weighing system. "Nest-Bug", the data collection module of "The Visitor" software package is used to monitor continuously the weight of nests mea-

Tab. 5. Females' average continuous weight-loss per hour overnight in the four periods of nesting.

Nest	egg-laying*	incubation	brooding	late feeding
G40-94	-	-	0.14 ± 0.03%	0.14 ± 0.05%
G16-95	0.14 ± 0.01%	0.13 ± 0.02%	0.14 ± 0.01%	0.14 ± 0.03%
G225-95	0.12 ± 0.02%	0.17 ± 0.04%	-	0.14 ± 0.06%
G231-96	-	0.11 ± 0.05%	0.12 ± 0.01%	0.09 ± 0.03%
G65-97-1	-	0.15 ± 0.03%	0.13 ± 0.09%	0.08 ± 0.00%
Average	0.13 ± 0.01%	0.14 ± 0.03%	0.13 ± 0.01%	0.10 ± 0.03%
Average time spent in the nest overnight	11:13:25	10:50:28	9:36:39	9:02:04

* The egg-laying period's data are reduced with the average weight of the egg, laid overnight.

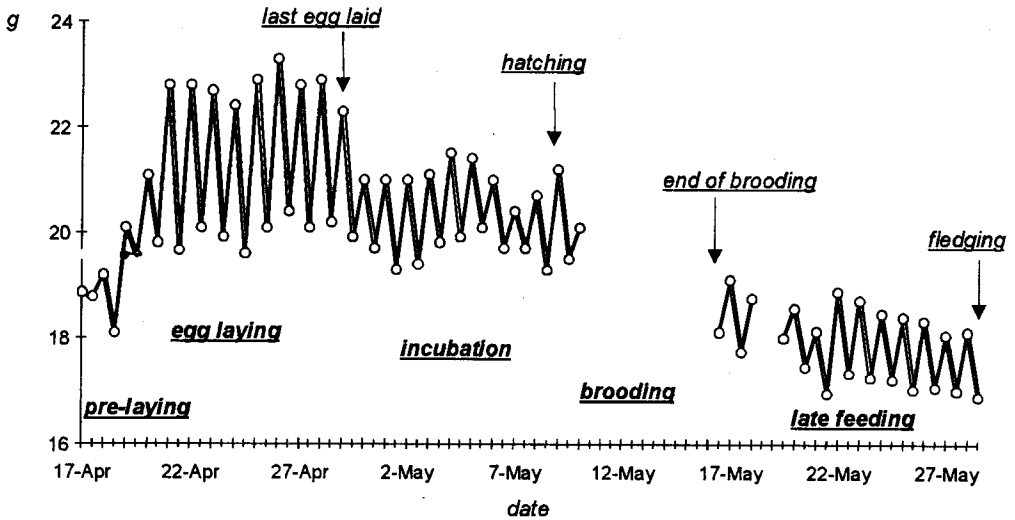


Fig. 2. A female's weight fluctuation during breeding (nest G225-95). The observed roosting and morning weights are connected to demonstrate the daily changes in weight during the whole season. On the first day of observation the female did not go roost in the nest. The observation was interrupted for 6 days.

sured by electronic balances connected to a central computer (Tóth *et al.* 1991, Tóth 1994, Szép *et al.* 1995). We used Mettler (PM4600, PM4800; Mettler-Toledo GmbH, CH-8606 Greifensee, Switzerland) and Sartorius (BA4100S; Sartorius AG, PO Box 32 43, D-3400 Goettingen) balances with an accuracy of 0.01 g and a capacity of 4000 g. One nest was partly measured with a Sartorius PT2100 that only has an accuracy of 0.1 g and a capacity of 2000 g.

Several nest boxes were pre-equipped with a shelf and a shielding outer box (called "windbox") to support the placing of a balance. The inner box containing the

nest was measured by the balance while the windbox protected the measurement from disturbance e.g. wind, rain, falling objects, and false visits by perching birds. This windbox makes it possible to obtain measurements with high accuracy (Tóth & Pásztor 1997).

Nests were regularly checked to determine laying date, clutch size, hatching date, number of eggs hatched, number of nestlings fledged. Also every evening in 1993 we measured manually the body-weight of each nestling in the measured nests with the "nestling weighing" function of NestBug.

Tab. 6. Females' average minimal faecal loss (g) in the four periods of nesting.

Nest	egg-laying	incubation	brooding	late feeding
G40-94	-	-	0.79 ± 0.09	0.74 ± 0.22
G16-95	0.36 ± 0.17	0.76 ± 0.12	1.03 ± 0.27	0.95 ± 0.16
G225-95	0.28 ± 0.12	0.53 ± 0.20	-	0.89 ± 0.23
G231-96	-	0.45 ± 0.41	0.58 ± 0.17	0.81 ± 0.23
G65-97-1	-	0.61 ± 0.36	0.51 ± 0.22	0.88 ± 0.34
Average	0.32 ± 0.05	0.59 ± 0.13	0.73 ± 0.24	0.85 ± 0.08
Average time spent away during the first trip (sec)	1992 ± 542	754 ± 217	369 ± 109	523 ± 177

We analysed data from 12 Great Tit nests. Nests were observed by the weighing system for a minimum of 6 and a maximum of 47 days. The measurements were started at different nest stages, but each nest was measured up until fledging. A set of analyses was performed only on the five nests with the longest periods of measurement, two of them monitored from egg-laying and two from incubation (Tab. 1).

2.3. Data processing

"NestBug", the data-collection module of "The Visitor" recognises arrival and departure events of the parents. It records the time of the event and relevant original weight data. "Estimate" is a data-processing module which estimates the two weight levels at each event: immediately before and after the event. "VisAna" is an analysis module which calculates weight changes and applicable variables at each event, builds up visit records, separates visits into those of each parent, based on their body weights, and supports manual correction of this identification on interactive graphs.

During the nestling feeding period we can determine the body weight of the visiting parent bird from the change in the nest weight at departure when the parent did not remove a faecal sac. Cases when a faecal sac was removed can be detected with high certainty, as a faecal sac is usually much heavier than a food load brought for the young (Woodburn & Perrins 1997 and our own unpublished measurements).

We collected the body-weights of the parents at the beginning and at the end of their "workday". We use the term "*morning weight*" (*MIW*) for the departure weight at the first visit each day and "*evening*

weight" (*EW*) for the departure weight at the last visit. When a female spent the night in the nest her "*roosting weight*" (*RW*) was estimated by her last arrival weight after which she stayed in for the night, and we also collected her "*departure weight*" (*DW*) at dawn. Departure weights are usually higher than the respective morning weights as the female loses weight through defecation during her first trip.

We analysed changes in the parents' morning and evening (roosting) body weight profiles and tried to find significant trends (Fig. 1). We calculated the changes in weight from day to day, as well as separately for daytime and overnight (Fig. 2). For the females we divided the overnight weight-loss into two parts. The first part was calculated from the difference between the *roosting weight* in the evening and the *departure weight* in the morning. This is the weight lost during the night through respiration and evaporation (*continuous overnight weight-loss*). The second part was calculated from the difference between the *departure weight* (leaving nest after the night) and the *morning weight* (leaving the nest after her first visit). This difference slightly underestimates the weight of the female's *faecal weight-loss* as she may also eat during this first trip.

Comparison of subsequent morning weights of males was problematic, as the time of their first visit to the nest varied to a great extent from day to day, while the body weights of the parents typically show a rapid increase during the first few hours of the day. To take this into account, we corrected all the morning weights of the males to the same time (5.00 am) by regressing their body weight on their arrival

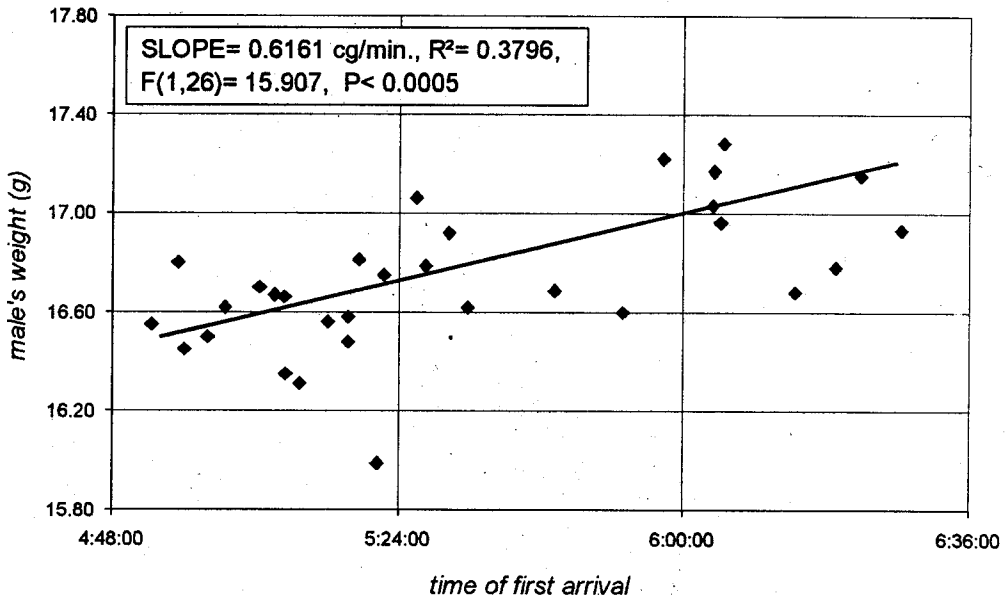


Fig. 3. Method of correction of the male's morning weight (nest G16-95). Each point on the graph represents the time of the first arrival and weight of the male on a certain day. The characteristics of the fitted line on the morning weight versus time of arrival diagram are shown.

time (Fig. 3). However, we could not include in the analysis those days when the male arrived after 7.00 am, as these arrival weights do not fit the "early morning line".

2.4. Statistics

Linear regression was used to demonstrate trends in the weight profiles in the different periods and also for the correction of the males' data. After testing for the homogeneity of variances, we performed single classification ANOVAs to investigate any significant differences between the different periods. The brooding period was eliminated from the ANOVA, because its variance caused significant inhomogeneity of variances. We compared the mean weights of the different periods (egg-laying, incubation, late feeding) with Scheffe's-test. We used t-tests to investigate differences in the overnight weight-

loss between two periods. Mann-Whitney U-tests were performed on the time components. All tests were carried out using the software package Statistica for Windows v5.1 (StatSoft Inc. 2300 East 14th str. Tulsa, OK 74104, USA).

3. Results

3.1. Weight profiles

We used linear regression for the initial tests. The fitted lines for the females' weight profiles of the whole measurement periods showed significant decreases in all the analysed cases. The slopes of the fitted lines ranged from -0.07 to -0.15 g a day and their slopes differed significantly from each-other (test of parallelism, $df = 4, 121$, Morning weights: $F = 3.51$, $p < 0.01$, Roosting weights: $F = 7.34$, $p < 0.001$).

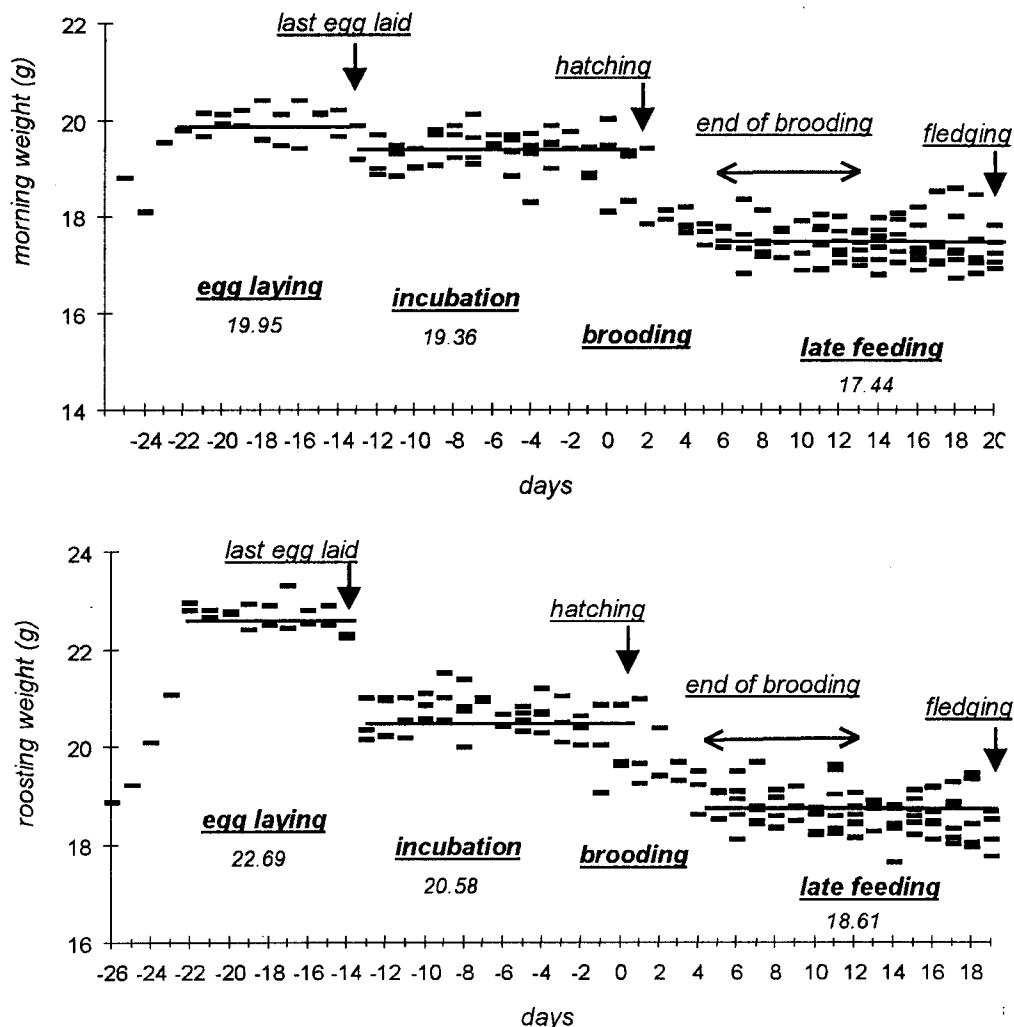


Fig. 4. Females' morning (above) and roosting weights (below). The data of the 6 nests are arranged according to the date of hatching. The average morning or roosting weights of all the females are shown under the periods' name. The length of brooding differed from nest to nest. The arrow under the "end of brooding" shows the period when broodings were finished.

The males' corrected weight profiles showed no significant trends in any of the observed individuals ($N = 12$ males). Therefore in this paper we shall concentrate on the females.

A standard method in bird studies is to catch the birds on certain days at various times and weigh them (e.g. Merila & Wiggins 1996). We checked whether

someone could still find a decrease in the females' weight between incubation and fledging by this method. We selected the morning and roosting weights of the last day of incubation (Day -1) and the last day before fledging (Day 18) from four nests. We used paired t-tests for comparison and we found significant difference only in half of the possible comparisons (Tab. 2).