

Does loss of mass during breeding correlate with reproductive success? A study on Blue Tits *Parus caeruleus*

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Substantial loss of mass of female Blue Tits *Parus caeruleus* during breeding is commonly explained by three not mutually exclusive explanations: shrinking of gonadal tissues, cost of reproduction and adaptation to save energy during flight. This study showed that loss of body mass was inversely correlated with reproductive success of individual females. Female tarsus length and timing of breeding correlated with loss of body mass, whereas ectoparasite loading had no significant effect on body mass. Loss of body mass during the rearing of young could be a useful measure of cost of reproduction by accounting for individual variation in female quality.

Loss of mass during reproduction characterizes many animals including birds. Several hypotheses have been proposed to interpret this loss of mass in breeding birds (especially in females). Mass decrease during incubation could simply be a result of the shrinking of gonadal tissue (Perrins 1979, Ricklefs & Hussell 1984). Additionally, loss of mass whilst raising the young has been interpreted as evidence for an energetic cost of reproduction, i.e. that energy expenditure is increased while energy intake is not increased to the same degree. This interpretation has found support from the observation that, in some bird species, loss of mass increased with brood size (Ricklefs 1974), and brood size manipulation experiments showed an increase of loss of mass with increased brood sizes (Askenmo 1977, Ricklefs & Hussell 1984, Gebhardt-Henrich & van Noordwijk 1991).

The hypothesis that loss of body mass is caused by the stress of reproduction has been challenged by the idea that birds lose mass in order to lower the cost of flight when rearing the young (Freed 1981, Norberg 1981, G. Jones, 1987, Gaston & Jones 1989, Gaston & Perin 1993, I.L. Jones 1994). However, the two hypotheses are not mutually exclusive, and loss of mass may reflect a trade-off between an increased risk of starvation because of low fat levels and reduced energy costs during flight when feeding nestlings (Norberg 1981, Nur 1984).

Not much is known about how individual differences in loss of mass by females correlate with reproductive success. The hypotheses regarding the meaning of mass loss during breeding predict distinguishable relationships between loss of mass during breeding and reproductive success (Table 1). The following three hypotheses apply primarily to bird species where the females feed themselves during incubation (Table 1). (1) If changes of mass reflected only changes in gonadal tissue, no relationship between loss of mass and reproductive success would be expected. (2) If loss of mass were a direct measure of investment in reproduction, fe-

males investing more in current reproduction would be expected to lose more mass and to have a higher reproductive success. Females that are heavy during incubation can afford to lose more mass during the rearing of young than initially light females. (3) Body mass at the beginning of the breeding period could be used as an insurance by those females that will lose more mass during the rearing of young because of various causes (e.g. poor territory, inefficient mate, poor physical ability). These "lower quality" females lose more mass and are also expected to have a lower reproductive success.

Parasites can alter host energetics and thus affect their hosts in a way that is not easily detected in laboratory studies (Booth *et al.* 1993). Ectoparasites (namely Hen Fleas *Ceratophyllus gallinae*) can add to the cost of reproduction in Great Tits *Parus major* (Richner *et al.* 1993) and Blue Tits *Parus caeruleus* (Tripet & Richner 1997). We therefore tested whether the presence of Hen Fleas in the nest influenced changes of mass in Blue Tit females.

METHODS

Twenty-four nestboxes with 26-mm entrance holes were occupied by Blue Tits in the study area in a forest northwest of Berne, Switzerland. The canopy consisted mainly of Beech *Fagus sylvaticus* mixed with oak *Quercus* sp. and pines *Pinus* sp. The undergrowth was moderate to locally dense.

After the second egg was laid, the Blue Tit nest material was cleared of ectoparasites in a microwave oven. Half of the nests were then infested with 40 adult fleas (method described in Richner *et al.* 1993).

Female body masses were recorded in late morning on days 3 and 10 after the start of incubation by weighing the entire nestbox with and without the incubating bird with a Mettler electronic balance (SM 3000, precision 0.1 g over the total range 0–3000 g). On day 13 after the young hatched, combined female and male feeding frequencies

Table 1. Hypotheses regarding the relationship between changes in body mass of female birds and reproductive success

Hypothesis	Expected correlation between reproductive success and	
	Body mass during incubation	Loss of body mass during rearing
Change in gonadal size	No correlation	No correlation
Investment hypothesis	Positive	Positive
Quality hypothesis	Negative	Negative

were recorded during a 45-min morning period. The following day, both parents were captured, weighed, sexed according to the presence of a brood patch and aged as first-year breeders or older according to the colour of the primary coverts (see Svensson 1984). Tarsus-length was measured with vernier callipers. Afterwards, contents of boxes were inspected regularly until fledging.

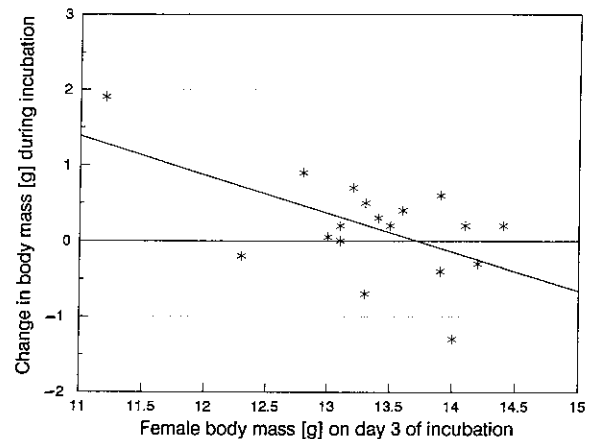
Statistical analyses were performed with SYSTAT (Wilkinson 1989) and SAS (SAS Institute Inc. 1985) statistical packages. Pearson correlation coefficients are given. Females were classified as either "heavy" (body mass on day 10 of incubation greater than the median body mass of all females [13.7 g]) or "light". Mass gain during incubation was calculated as female body mass on day 10 of incubation minus mass on day 3 of incubation. Loss of body mass in females was calculated as female body mass on day 10 after the start of incubation minus female body mass on day 14 after hatching. Heritabilities were estimated by regression of the mean of the nestlings on day 14 on the mean of the parents (Kempthorne & Tandon 1953).

No nestbox was deserted. In one case, the male was never observed feeding the brood or his mate, and data on that brood were excluded from the analyses.

Temperatures were obtained from the Schweizerische Meteorologische Anstalt station, Liebefeld (4 km SE of the study area).

RESULTS

Female body mass during incubation was about 2 g higher than on day 14 after hatching (Table 2). Mass gain during incubation was small and not significantly different from zero (mean [\pm s.d.] = 0.17 ± 0.64 g, $n = 21$, n.s.), but

**Figure 1.** Female Blue Tits that were relatively heavy on day 3 of incubation gained less mass (or even lost mass) during incubation compared with females that were relatively light at the beginning of incubation.

females lost mass between the beginning of incubation and day 14 after hatching (mean [\pm s.d.] = 2.34 ± 0.54 , $n = 21$, $P < 0.001$). Variance of female body mass decreased (not significantly) during the season (Table 2) as a result of a negative correlation between female body mass on day 3 of incubation and mass gain during incubation ($\text{mass}_{\text{day 10}} - \text{mass}_{\text{day 3}}$; $r_{19} = -0.56$, $P < 0.01$; Fig. 1) and the positive correlation between female body mass on day 10 of incubation and female loss of mass during the rearing of young (slope [\pm s.d.] = 0.48 ± 0.16 , $r_{19} = 0.57$, $P < 0.007$; Fig. 2). Thus, heavier females on day 3 of incubation "gained" less mass during incubation and females that were heavier on day 10 of incubation lost more mass than lighter females. Heavy females (see Methods and Table 2) lost significantly more mass during the rearing of young than lighter females ($F_{1,14} = 13.3$, $n = 15$, $P < 0.003$). Female mass gain between day 3 and day 10 of incubation decreased with laying date (slope [\pm s.d.] = -0.16 ± 0.04 g/day, $r^{19} = 0.65$, $P < 0.002$). Female mass on day 3 of incubation increased during the season ($r_{19} = 0.51$, $P < 0.02$).

The presence or absence of fleas had no significant effect on mass changes or other variables in the analyses, so analyses were performed with the pooled data set regarding fleas.

The heritability estimate of body mass based on parent-offspring regression was not significantly different from zero, but the heritability estimate of tarsus-length was high and significant ($h^2 = 0.77$, $P < 0.01$, $n = 18$).

Table 2. Body mass (g) of female Blue Tits at different times during the breeding cycle (mean \pm s.d.; sample size in parentheses)

	Day 3 of incubation	Day 10 of incubation	Day 14 after hatching
Mass	13.30 ± 0.75 (21)	13.47 ± 0.64 (23) ^a	11.12 ± 0.49 (20)

^a Median = 13.7 g.

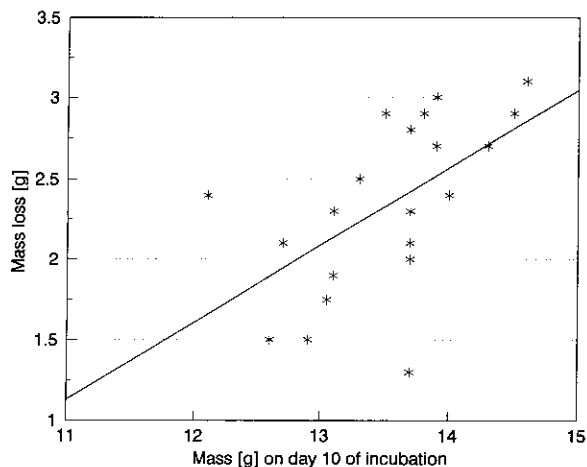


Figure 2. Female Blue Tits that were relatively heavy on day 10 of incubation lost more mass, on average, than females that were relatively light on day 10 until 14 days after the hatching of young.

Reproductive success of the pair

The number of fledglings was not correlated with any of the studied variables besides body mass of the male ($r_{18} = 0.50$, $P < 0.001$). Female and male body masses were not correlated ($r_{18} = 0.16$, n.s.). Females from pairs with higher feeding rates on day 13 lost more mass, as did females whose broods hatched later in the season (Table 3), but there was no relationship between feeding rate and the number of offspring that were fledged ($r_{19} = 0.21$, n.s.). Body masses of 14-day-old nestlings were negatively correlated with brood size and loss of mass of the female (Table 4). The extent of female loss of mass explained an appreciable proportion (38%) of the total variation in body masses of the fledglings (Table 4). Females with longer tarsi lost less mass than females with shorter tarsi (Table 3).

DISCUSSION

In our study, the loss of mass during the rearing of young was negatively correlated with the body mass of fledglings and thus the potential reproductive success. Body mass of fledglings is known to correlate with future survival (Garnett 1981, Gebhardt-Henrich & van Noordwijk 1991). This supports the hypothesis that individual differences in loss of mass may indicate female "quality", and the females that

Table 4. Stepwise regression of 14-day mass of Blue Tit nestlings on breeding parameters and parental traits. The variable female mass on the three measured days and hatching date was not significant. Constant = 12.9, $n = 18$

Variable	Coefficient	Partial r^2	F	P
Weight loss	-0.72 ± 0.21	0.38	9.87	<0.006
Brood size	-0.19 ± 0.07	0.16	5.01	<0.04
Feeding rate	0.02 ± 0.01	0.11	4.32	n.s.

lost less mass on average were those with a potentially higher reproductive success (Table 1, hypothesis 3). However, no significant correlation was found between mass during incubation and reproductive success.

Mass changes during incubation

Because of the growth of gonads, female Blue Tits may increase their body mass by 50% during egg laying (Perrins 1979). However, female mass is expected to decrease sharply after egg laying and during incubation, because of both the shrinking of gonadal tissue (Perrins 1979) and the energy expenditure (Yom-Tov & Hilborn 1981, Haftorn & Reinertsen 1985). We did not observe this mass decrease during incubation; thus, we conclude that our observed mass changes were not (primarily) caused by changes in gonadal tissue (Table 1, hypothesis 1). The energetic costs of incubation vary with clutch size and temperature (Haftorn & Reinertsen 1985, Mertens 1987), and temperature could explain the lack of mass decrease during incubation since the mean daily temperatures in March to May of the study were $1.23 \pm 0.66^\circ\text{C}$ warmer than the mean temperatures of those months in the 10 preceding years.

Loss of mass during the nestling period

Johnston (1993) claimed that extra food provisioning for the nestlings decreased loss of mass of female Great Tits during the same period. Unfortunately, he failed to show that the extra food (and not the lower mass during incubation) of his food-supplemented group was the cause of the lower loss of mass. Without supplementary food, we found that during

Table 3. Stepwise regression of female Blue Tit loss of mass (g) on female tarsus-length, the pair's combined feeding rates and hatching date. Constant = 6.11, $n = 20$

Variable	Coefficient	Partial r^2	F	P
Tarsus-length (mm)	-0.36 ± 0.13	0.29	10.64	<0.005
Feeding rate (in 45 min)	0.02 ± 0.005	0.24	5.68	<0.03
Hatching date (days after 1 April)	0.06 ± 0.02	0.13	5.91	<0.03

incubation lighter female Blue Tits lost significantly less mass than heavier females (Fig. 2).

In this context, it is necessary to mention the original (19th century) definition of "regression", meaning that the extremes tend to regress towards the mean (F. Galton in Crow 1986, p. 118). Females that are very heavy because of a combination of circumstances are likely to be lighter during the second measurement regardless of the "true" mass change. This could also lead to a correlation between body mass at the end of incubation and loss of mass or strengthen the existing correlation. However, the significant difference in loss of mass between females that were heavier than the median body mass and those with body masses below the median could not arise by this statistical artifact.

We propose that individual differences in female "quality" determined loss of mass to a significant degree, and the females that lost less mass, on average, were those with higher reproductive success. Possible aspects of female quality were the timing of breeding or the size of the female because late-breeding females as well as females with shorter tarsi lost more mass. Another potential cause of differential loss of mass is the degree of male cooperation, as shown in Green-rumped Parrotlets *Forpus passerinus* (Curlee & Beissinger 1995). In our study, however, no such influence of male behaviour was found.

In contrast to the study on Great Tits by Richner *et al.* (1993), which used the same level of flea infestation, the presence of fleas had no significant influence on body mass of fledgling Blue Tits in our study; neither was the extent of loss of mass in females affected by the parasites.

Loss of mass during the rearing of young could be a useful measure of cost of reproduction, reflecting individual variation in female quality. In our study, females with higher reproductive success lost less mass than less successful females. Breeding success was low in this study area in 1993 (fledging success: 0.44 ± 0.22 fledglings/egg), and the absence of significant heritability of mass, but a high heritability of tarsus-length, is an indication of poor conditions during the nestling period (Gebhardt-Henrich & van Noordwijk 1991). It remains to be seen if the mass changes of female Blue Tits are consistent in different years and what are the life-history trade-offs between years.

We gratefully acknowledge financial support by the Swiss National Science Foundation (grant #31-34020.92 to H.R.). Temperature records were kindly made available to us by the Schweizerische Meteorologische Anstalt, Zürich. J. C. Coulson and anonymous referees improved the manuscript.

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