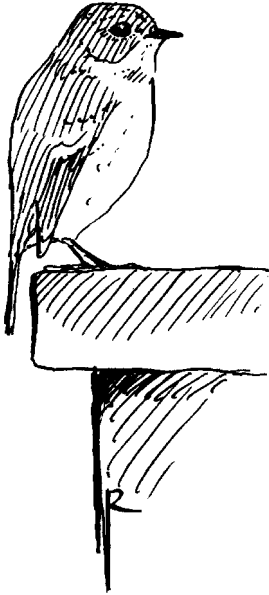


# MASS LOSS IN FEMALE PIED FLYCATCHERS *FICEDULA HYPOLEUCA* DURING LATE INCUBATION: SUPPLEMENTATION FAILS TO SUPPORT THE REPRODUCTIVE STRESS HYPOTHESIS

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In most species of altricial birds, females experience great changes in body mass during the reproductive period. Mass loss of females after hatching of the young has commonly been regarded as a result of increased reproductive stress. Alternatively, the loss of body mass during this period is an adaptive trait that increases feeding ability and reduces the risk of predation through reduced wing loading. The reproductive stress hypothesis was tested by providing extra food inside the nestbox to female Pied Flycatchers *Ficedula hypoleuca* during incubation and hatching. A pairwise design was used, with one supplemented and one control female in each pair ( $n = 32$ ), to account for variation in hatching date. Body mass was strongly reduced after hatching, in particular in females with high initial body mass. However, mass reduction was similar in supplemented and control females. Hence, the result was consistent with the adaptation for flight hypothesis but not with the reproductive stress hypothesis.

Key words: *Ficedula hypoleuca* - cost of reproduction - reproductive stress - mass loss - supplementary food

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## INTRODUCTION

Mass loss during the breeding cycle is commonly observed in birds (Silverin 1981; Ricklefs & Husell 1984; Jones 1987; Moreno 1989a; Pietiäinen & Kolunen 1993) and has traditionally been regarded as a result of the physiological stress of egg production, incubation and feeding of the young (Askenmo 1977; Bryant 1979; Drent & Daan 1980). However, Freed (1981) and Norberg (1981) independently criticized this view and argued that loss of body mass could be an adaptive response to ease feeding of the young by increasing flight ability and by saving energy during foraging.

We studied mass loss in female Pied Flycatchers *Ficedula hypoleuca*. Pied Flycatchers are small insectivorous passerines. They are single brooded and only the female incubates and

broods the young. The male feeds the female during incubation, and this feeding may be of essential nutritional value to the female, in particular in periods of bad weather (von Haartman 1958; Lifjeld & Slagsvold 1986; Lifjeld *et al.* 1987; Smith *et al.* 1989). Female body mass reaches a peak during the egg-laying period and remains high during incubation. It drops significantly at hatching time and reaches its lowest level by the end of the nestling period (a mass reduction of about 20% compared with the incubation period; von Haartman 1954; Winkel & Winkel 1976; Silverin 1981; Hillström 1995; Potti & Merino 1995). In contrast, male body mass is almost constant throughout the breeding cycle in this species and in many other passerines (Moreno 1989a). In female Pied Flycatchers, repeatability of mass loss during breeding is low, showing that environmen-

tal factors could play a significant role (Potti & Merino 1997).

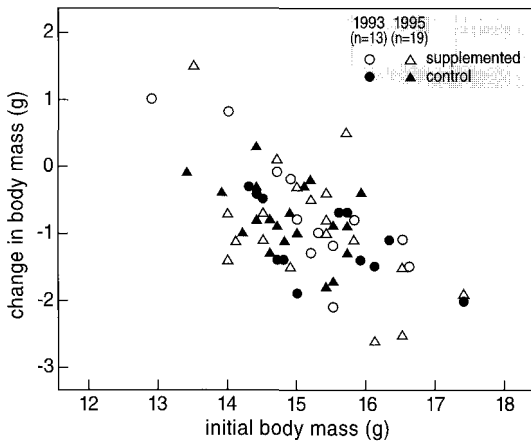
We tested the stress hypothesis by asking whether females provided with extra food around hatching time showed a smaller reduction in body mass than a control group of conspecific females. At this stage of breeding, it may be costly for a female to hatch and brood chicks and at the same time collect food to the brood. Alternatively, body mass may drop to the same extent in all females to improve foraging ability (Freed 1981; Norberg 1981; Moreno 1989a) and reduce predation risks by European Sparrowhawks *Accipiter nisus*, a serious predator on female Pied Flycatchers (Slagsvold & Dale 1996). If reduction in female body mass at hatching reflects reproductive stress we predict that the reduction in mass of supplemented females would be less later in the breeding season, when conditions for feeding may be worse, than earlier in the breeding season (Källander 1975; Järvinen 1983).

## METHODS

In the present study we focus on female mass around hatching time, for the following reasons. (1) In Pied Flycatchers, except for the egg-laying period, the daily change in female body mass during the breeding cycle peaks when hatching starts (Von Haartman 1954; Winkel & Winkel 1976; Silverin 1981; Hillström 1995). The sudden drop in body mass is associated with hatching, because no corresponding mass reduction is found at the regular time of hatching if the eggs do not hatch and the female continues to incubate (Winkel & Winkel 1976). (2) It has been suggested that female Pied Flycatchers mobilize accumulated nutrients during this period as a response to a need for higher feeding activity (Silverin 1981). (3) For an experiment to be valid, the extra food provided should constitute a substantial part of the total energy budget of the female. This would be more easily achieved around hatching time than later in the nestling period when brood demands are greater.

The study was conducted during the breeding season in May and June 1993 and 1995. The study site was a mixed coniferous and deciduous woodland in Sørkedalen, near Oslo (60°N, 11°E), southeast Norway, with 267 wooden nestboxes erected about 1.5 m above the ground. A pairwise experimental design was used, picking out pairs of females with similar clutch size and date of final egg laid, and hence similar expected time of hatching. Which female in a pair was to be supplied with extra food was chosen randomly. Females were caught inside the nestboxes and body mass was recorded to the nearest 0.1 g using a 50 g Pesola spring balance. Measures were taken at all times of the day but always at the same time of day for the two females of a pair. Only monogamous ( $n = 48$ ) females or primary females ( $n = 16$ ) of polygynous males were used (eight primary females in both the supplemented and control group). Clutch size (4-8 eggs) was never manipulated, and it never differed by more than one egg between the two females in a comparison (paired  $t$ -test,  $t = 0.44$ ,  $df = 31$ ,  $P = 0.66$ ).

Females were first weighed during incubation. On the same visit (24 'pairs' of females), or on the following day (8 'pairs' of females) a small plastic cup for food was placed in all nestboxes just below the nest hole. Supplemented females were provided ca. 15 g mealworms *Tenebrio molitor*, which would constitute more than 50% of their daily energy needs (cf. Moreno 1989b; Hillström 1995; Merkle & Barclay 1996). Control females were provided a similar amount of small wooden sticks of larval size. Food (or sticks) was provided to the two females of a pair on the same day and almost at the same hour. Nestboxes were visited every second day to replenish mealworms, with a similar number of visits to control nests to equalize the stress of being visited. On the revisits most of the mealworms had disappeared but we do not know how many were taken by the female and male respectively. Food cups were removed when all chicks had hatched. For the present experiment to be valid, supplemented females must have eaten a substantial part of the extra food provided. This assumption seems likely because in two ear-



**Fig. 1.** Change in body mass of female Pied Flycatchers from the incubation period to hatching in relation to initial body mass ( $r = -0.60$ ,  $n = 64$ ,  $P < 0.001$ ). Circles: data from 1993 ( $n = 13$ ), triangles: data from 1995 ( $n = 19$ ). Open symbols: supplemented females, filled symbols: control females.

lier experiments, also providing mealworms inside nestboxes occupied by incubating female Pied Flycatchers, males reduced their feeding rate of supplemented females compared to controls (Lifjeld & Slagsvold 1989; Smith *et al.* 1989). Moreover, in 1996, videofilming of food cups with mealworms erected just outside nestboxes occupied by Pied Flycatchers showed that females (and males and other species) regularly fed from them. Observations were made just before the females started egg laying (T. Slagsvold, unpublished data).

In 1993, 26 females were weighed 3-7 days before all chicks in the brood had hatched (mean value of 4 days for each group of females), and again on the day when all chicks had hatched. Hatching date was similar for supplemented and control females (range 8 - 25 June; paired  $t$ -test,  $t = 0.37$ ,  $df = 12$ ,  $P = 0.72$ ). In 1995, 38 females were weighed 4-10 days before all chicks in the brood had hatched (mean value of 5 days for each group of females), when all chicks had hatched, and two days thereafter. The final measure was taken to see if possible differences in body mass between females persisted also on the first few days

after hatching. Hatching date was similar for supplemented and control females (range 14 - 28 June; paired  $t$ -test,  $t = 1.16$ ,  $df = 18$ ,  $P = 0.26$ ).

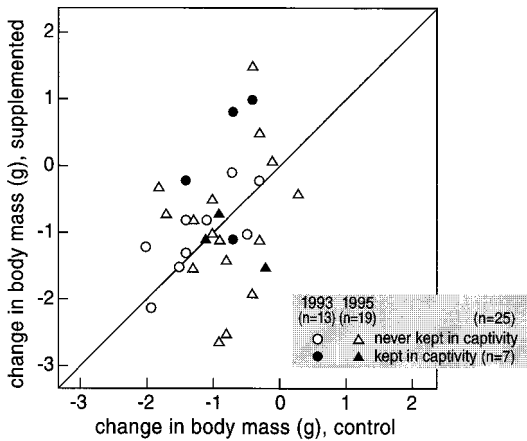
Some females had been kept in captivity for at least a week before they were released and started to breed in our study area (Dale & Slagsvold 1996). This amounted to 8 females in 1993 (4 supplemented, 4 controls) and 6 in 1995 (3 supplemented, 3 controls). In the period of captivity, the only food source available was mealworms. Below we have made a separate analysis of the data for these females because they were initially familiar with the kind of extra food provided. If females hesitated to utilize the extra food, a difference in body mass between females familiar and unfamiliar with the food would be expected.

Statistical tests are two-tailed.

## RESULTS

In 1993 (but not in 1995), on the first visit after food (or sticks) had been provided, we recorded whether the female was inside the nestbox when the observer arrived. This was the case for 9 of the 13 supplemented females, but only for 1 of the 13 control females ( $\chi^2 = 7.96$ ,  $df = 1$ ,  $P = 0.005$ ). Hence, females responded to the experimental treatment, apparently spending more time incubating when extra food was provided. The low number of control females present on these occasions (8%) was probably not reflecting true attentiveness. Many females left the nestbox just before we arrived probably because they had recently been handled by us and because our visits were usually in the middle of the day when ambient temperatures were high and it was not very costly for females to be absent from incubating.

Most females had lower body mass after hatching than during incubation (paired  $t$ -test,  $t = 8.86$ ,  $df = 63$ ,  $P < 0.001$ ), with a mean ( $\pm$  SD) reduction of  $0.85 \pm 0.77$  g ( $n = 64$ ; Fig. 1), which meant a reduction of  $5.5 \pm 5.0\%$  ( $n = 64$ ). The reduction was similar in 1993 (mean  $\pm$  SD  $0.87 \pm 0.76$  g,  $n = 26$ ) and in 1995 ( $0.84 \pm 0.78$  g,  $n = 38$ ;  $t = 0.13$ ,  $df = 62$ ,  $P = 0.90$ ). Great variation



**Fig. 2.** Change in body mass of female Pied Flycatchers from the incubation period to hatching. A pairwise experimental design was used. Points above the  $y = x$  line means that food supplemented females dropped less in body mass than the respective control females. Circles: data from 1993 ( $n = 13$ ), triangles: data from 1995 ( $n = 19$ ). Open symbols: females never kept in captivity ( $n = 25$ ), filled symbols: females kept in captivity prior to breeding ( $n = 7$ ).

existed in the initial body mass of the females and those with high body mass lost more mass than those with low body mass (Fig. 1). There was no correlation between change in body mass and the number of days elapsing between first and second

weighing (range 4-10 days;  $r = 0.08$ ,  $n = 64$ ,  $P = 0.77$ ). Hence, the later variable was not considered further in the subsequent analyses.

The reduction in body mass was significantly smaller for supplemented than for control females in 1993 but not in 1995 (Fig. 2, Table 1), nor for the data from the two years combined (paired  $t$ -test,  $t = 0.65$ ,  $df = 31$ ,  $P = 0.52$ ). We used ANOVA to test whether or not the interaction between year and treatment was significant. This was done by analysing change in body mass as dependent variable and using as independent variables: experimental treatment, the interaction between year and treatment, and a factor with a level for each experimental pair (this would take into account the pairwise design of the study). We found no significant effect of experimental treatment ( $P = 0.34$ ) or of the interaction term year \* treatment ( $P = 0.11$ ). However, there was a significant effect of the experimental pair factor ( $P = 0.044$ ), showing that it had indeed been meaningful to adopt a pairwise design of the study. As mentioned above, initial body mass was important. If this variable was taken into account, none of the three independent variables had a significant effect on change in body mass (experimental treatment:  $P = 0.19$ , year \* treatment:  $P = 0.35$ , experimental pair:  $P = 0.15$ ; initial body mass:  $P = 0.003$ ). Probably, the experimental pair factor failed to be significant in

**Table 1.** Body mass (g) measurements of two groups of female Pied Flycatchers (\* =  $P < 0.05$ , \*\* =  $P < 0.01$ ).

| Year | Variable                  | Supplemented females |      |     | Control females |      |     | Paired $t$ -test |
|------|---------------------------|----------------------|------|-----|-----------------|------|-----|------------------|
|      |                           | Mean                 | SD   | $n$ | Mean            | SD   | $n$ | $t$              |
| 1993 | Body mass, incubation (1) | 15.16                | 0.97 | 13  | 15.35           | 0.91 | 13  | 0.73             |
|      | Body mass, hatching (2)   | 14.51                | 0.57 | 13  | 14.28           | 0.74 | 13  | 1.22             |
|      | Change in body mass (1-2) | 0.65                 | 0.89 | 13  | 1.08            | 0.57 | 13  | 2.31 *           |
| 1995 | Body mass, incubation (1) | 15.19                | 1.00 | 19  | 14.86           | 0.67 | 19  | 1.53             |
|      | Body mass, hatching (2)   | 14.30                | 0.93 | 19  | 14.08           | 0.66 | 19  | 0.91             |
|      | Body mass, nestlings (3)  | 13.63                | 0.66 | 19  | 13.80           | 0.56 | 19  | 1.06             |
|      | Change in body mass (1-2) | 0.90                 | 0.98 | 19  | 0.78            | 0.55 | 19  | 0.47             |
|      | Change in body mass (2-3) | 0.67                 | 0.70 | 19  | 0.28            | 0.47 | 19  | 2.14 *           |
|      | Change in body mass (1-3) | 1.56                 | 0.59 | 19  | 1.07            | 0.57 | 19  | 3.06 **          |

the latter analysis because one of its important components was taken into account by another factor, viz. initial body mass. We also analysed if an interaction term between experimental treatment and initial body mass was significant, but it was not ( $P = 0.18$ ; experimental treatment:  $P = 0.16$ , initial body mass:  $P < 0.001$ ). We conclude that food supplementation had no significant effect on mass change from incubation to hatching but that this change was mainly related to initial body mass.

In seven 'pairs' of females, both members had been kept in captivity prior to breeding and so were familiar with mealworms as food. The data for these pairs are shown with separate symbols in Fig. 2. We analysed by ANOVA ( $n = 64$ ) change in body mass as dependent variable against initial body mass and female category (kept in captivity or not) as independent variables. There was no significant effect of female category ( $P = 0.77$ ).

The feeding situation may have been worse late than early in the breeding season. Hence, if reduction in female body mass at hatching reflects reproductive stress, the reduction may have been greater late than early in the breeding season in the control group but not in the supplemented group. However, change in female body mass was not correlated with hatching date in any group (supplemented:  $r = 0.12$ ,  $n = 32$ ,  $P = 0.53$ ; control:  $r = 0.19$ ,  $n = 32$ ,  $P = 0.29$ ).

In 1995, females were also weighed two days after hatching and so two days after the food cups had been removed. Body mass had dropped on average ( $\pm$  SD) by  $0.48 \pm 0.62$  g ( $n = 38$ ; paired  $t$ -test,  $t = 4.74$ ,  $df = 37$ ,  $P < 0.001$ ) from the level at hatching. The reduction was significantly greater for supplemented than for control females both when compared to body mass recorded on the day of hatching and when compared to that recorded during incubation (Table 1). However, note that mean body mass never differed significantly between the two groups of females in any particular period (Table 1). We used ANOVA ( $n = 38$ ) to analyse change of body mass as dependent variable in relation to experimental treatment and initial

body mass. A factor for individual experimental pair was excluded from the model because the factor was never significant (analyses not shown). For change in body mass between incubation and two days after hatching, both experimental treatment ( $P = 0.019$ ) and initial mass ( $P < 0.001$ ) had a significant effect. Supplemented females had dropped more in body mass than control females, and heavy females had dropped more in body mass than light females. Change in body mass between hatching and two days after hatching showed similar trends. Supplemented birds had a nearly significantly stronger reduction in body mass than control birds ( $P = 0.070$ ) and birds with high initial body mass had a significantly stronger reduction than those with low initial body mass ( $P < 0.001$ ). We also ran analyses with the interaction term experimental treatment \* initial body mass but this factor had no significant effect ( $P = 0.76$  and  $P = 0.53$  in the two cases, respectively).

We conclude that the reduction in female body mass from the incubation and the hatching period until two days after hatching, was primarily related to initial body mass. However, there was also a tendency for supplemented birds to lose more mass than control birds.

## DISCUSSION

In most female Pied Flycatchers examined in this study body mass dropped from the incubation to the hatching period; on average by 5-6%. The reduction was strongly correlated with initial body mass, heavier birds losing more mass than lighter birds. The reduction was slightly lower for supplemented than for control females in 1993 but not in 1995, nor for the total data combined. Hence, the results were consistent with the 'adaptation for flight' hypothesis but not with the reproductive stress hypothesis. The reduction in mass was independent of the time of breeding (hatching date). This is also inconsistent with the stress hypothesis if we assume that conditions for feeding were worse later than earlier in the breeding season (because of lower food availability, be-

cause late females were younger and less experienced birds, and/or because late birds held poorer territories). Hence, the present study confirms the findings of an earlier study of the same species (Hillström 1995) that showed no effect of food provisioning on mass loss in females. In the latter study, mealworms were supplied on a tray near the nestbox and not directly into the nestbox and so it is unknown how much food was eaten by females, by resident males, or by other birds. Moreover, females in the supplemented group were pooled in the statistical analyses and compared with a group of control females. In the present study, a pairwise experimental design was used, comparing females with similar hatching date, and measuring the two females in a pair on the same day and at the same time of the day, thereby also taking variable weather conditions into account.

In these studies, females were provided with extra food. Alternatively, one might increase reproductive stress on females and then measure changes in body mass. When clutch size was experimentally increased in Pied Flycatchers, female body mass dropped more than in a control group in one study (Moreno & Carlson 1989) but not in another (Siikamäki 1995), nor in a study of the closely related Collared Flycatcher *Ficedula albicollis* (Moreno *et al.* 1991). In a study of Pied Flycatchers, where the length of the brooding period was manipulated, mass loss of females appeared unrelated to brooding effort (Sanz & Moreno 1995). We conclude that 'stress' manipulation experiments of female Pied Flycatchers do not provide any strong support to the reproductive stress hypothesis.

Another possibility is that reduction in body mass at hatching time was caused by regression of reproductive organs. Pied Flycatchers are single brooded but may renest if nesting fails before hatching (Silverin 1980; Lifjeld & Slagsvold 1988), and if it fails early in the breeding season (Bauchau & Seinen 1997). In the present study, mean reduction of female body mass over the hatching period was 0.85 g. The mass of the ovary and oviduct peaks during the egg-laying period

(mean value of 1.190 g), but drops soon after laying, with a mean change of only 0.012 g between late in the incubation period and early in the nestling period (mean values of 0.037 and 0.025 g, respectively; Silverin 1980; Table 1). These data show that atrophy of reproductive organs in female Pied Flycatchers alone can hardly account for the great reduction in body mass at hatching.

Supplemented females lost more body mass than control females from the stage of incubation to two days after hatching, despite the fact that initial body mass had been recorded before supplementation of food had started and final body mass had been recorded two days after supplementation had ended (i.e. two days after hatching). Sample size was reasonably large (38 females) and the significance relatively strong ( $P = 0.019$ ), even when taking initial body mass into account in an ANOVA. This finding is hard to explain because an opposite result might have been expected, namely that supplemented birds would maintain body mass more than control birds because they had been less energetically stressed, and/or because they had needed to forage less and so had less need of reducing body mass adaptively. One speculation is that supplemented females became adjusted to the extra food and when such food was no longer provided some time elapsed before this was fully realized and hence they lost body mass. An alternative explanation is that they reduced body mass adaptively to the new situation but that the reduction was stronger than strictly needed because of the sudden disappearance of food.

The pattern of mass reduction from incubation to hatching observed was best explained by the adaptability hypothesis. Females may lose body mass after hatching to reduce cost of flight and increase manoeuvrability (Freed 1981; Norberg 1981; Wright & Cuthill 1989; Tinbergen & Dietz 1994). In our study area, the European Sparrowhawk may kill as many as 10% of the female Pied Flycatchers during breeding. Risk of predation during incubation is low but may increase after hatching by a factor of seven from the level during incubation (Slagsvold & Dale 1996).

**Table 2.** Effect of food supplementation on body mass of females and nestlings. Species listed in the order of the period of breeding in which supplementation began.

| Species                     | Food         | Start of supplementation | Effect on body mass |        | Reference                 |
|-----------------------------|--------------|--------------------------|---------------------|--------|---------------------------|
|                             |              |                          | fem.                | nestl. |                           |
| <i>Oenanthe oenanthe</i>    | mealworms    | before egg-laying        | No                  | -      | Moreno 1989b              |
| <i>Sialia currucoides</i>   | mealworms    | 2nd d of incubation      | No                  | No     | Merkle & Barclay 1996     |
| <i>Ficedula hypoleuca</i>   | mealworms    | 6-7 d before hatching    | No                  | No     | Hillström 1995            |
| <i>Ficedula hypoleuca</i>   | mealworms    | 4-5 d before hatching    | No                  | -      | Present study             |
| <i>Sialia currucoides</i>   | mealworms    | after hatching           | Yes                 | Yes    | García <i>et al.</i> 1993 |
| <i>Phoenicurus ochruros</i> | caterpillars | after hatching           | Yes                 | -      | Cucco & Malacarne 1997    |

Hence, after hatching it would be important to improve flight ability by reducing body mass.

In Pied Flycatchers, Northern Wheatears *Oenanthe oenanthe*, and Mountain Bluebirds *Sialia currucoides*, no significant effect of food supplementation on change of female body mass was found (Table 2). However, in another study of Mountain Bluebirds supplemented birds had higher body mass in the nestling period than control birds, as was also found in a study of Black Redstarts *Phoenicurus ochruros* (Table 2).

The differences in female responses may have been caused by differences in food provisioning schedules (Merkle & Barclay 1996; Cucco & Malacarne 1997). In both studies showing a positive effect, food was supplied after hatching, whereas in every study showing no effect, food was provided before or during incubation (Table 2). With the former provisioning schedule, food may have appeared less predictable, and consequently females may have added body mass when an opportunity arised (Merkle & Barclay 1996; Cucco & Malacarne 1997). Another possibility is that natural foods may have been more abundant in some studies than in others, since food supplementation did not always have an effect on nestling body masses (Table 2). In each of the four studies showing no effect on female body mass, mealworms were provided, whereas in one of the two studies showing a positive effect, caterpillars were provided (Table 2). We conclude that future studies should take both provisioning schedule

and kind of food into account when testing hypotheses on variation in female body mass during breeding.

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## SAMENVATTING

Bij veel vogelsoorten met nestblijvende jongen wordt het lichaamsgewicht van de ouders in de loop van de broedtijd lager. Dit kenmerkende gewichtsverlies van vrouwtjes, met name bij het uitkomen van de eieren, werd lange tijd opgevat als een aanwijzing, dat de ouderlijke zorg een aanzienlijke aanslag op het welbevinden en de energie-reserves van de oudervogels betekent (de zogenaamde 'reproductive stress'-hypothese). Maar het zou natuurlijk ook kunnen dat gewichtsverlies een aanpassing is om ervoor te zorgen dat de oude vogels veiliger en efficiënter kunnen foerageren en voedsel voor de jongen kunnen aanbrenge, omdat ze met een lager lichaamsgewicht wendbaarder zijn en lagere vliegkosten hebben. De 'reproductive stress'-hypothese werd getoetst door vrouwelijke Bonte Vliegenvangers *Ficedula hypoleuca* de laatste dagen voor en tijdens het uitkomen van de eieren extra voer te geven door meelwormen in kleine koffiebekers naast het vlieggat in de nestkast te plaatsen. Deze experimenten werden 32 keer paarsgewijs uitgevoerd, waarbij iedere

keer aan één vrouwtje een bekertje met meelwormen werd gegeven, en aan een vergelijkbaar vrouwtje een bekertje met houten stokjes (nepwormen). Het lichaamsgewicht van de experimentele vogels daalde altijd met 5-6% bij het uitkomen van de eieren, en het gewichtsverlies was het grootst bij vrouwtjes die aanvankelijk het zwaarst waren. Hoewel de bijgevoerde vrouwtjes de aangeboden meelwormen altijd opaten, waren er geen verschillen tussen de gewichtsverliezen van vrouwtjes die meelwormen kregen aangeboden, en van vrouwtjes die nepwormen kregen. Dit resultaat wijst erop, dat de gewichtsverliezen tijdens het broeden niet zo zeer energetische tekorten weerspiegelen, maar eerder een adaptieve betekenis hebben in de zin dat lichte vogels goedkoper vliegen (en per eenheid ouderlijk energieverbruik meer voer voor de kuikens kunnen aanslepen) en door hun grotere wendbaarheid waarschijnlijk beter kunnen ontsnappen aan de Sperwers die in dit Noorse broedgebied immer op de loer 'liggen'. (TP)

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