

# BODY-MASS VARIATION IN BREEDING NORTHERN WHEATEARS: A FIELD EXPERIMENT WITH SUPPLEMENTARY FOOD<sup>1</sup>

JUAN MORENO<sup>2</sup>

Dept. of Zoology, Uppsala University, Box 561, S-751 22 Uppsala, Sweden

**Abstract.** Changes in body mass of breeding Northern Wheatears, *Oenanthe oenanthe*, on the island of Öland, south Sweden, were monitored during 1985-1987 in the context of a food provisioning experiment. Individuals were weighed periodically by attracting them to feeders which were placed on electronic digital balances. Rations of 7 g of mealworms per visiting individual were offered daily on certain territories (in 1987, some individuals were offered rations of 4.5 and 9 g). Unprovisioned birds were captured and weighed during the study. Males maintained constant body masses throughout the season. Females increased in mass up to laying, maintained relatively large masses during incubation, and dropped in mass by 14% during the first week after the young hatched. Mass then attained constant levels until the time of offspring independence. There was a positive correlation between brood size and the masses of unprovisioned females during the late nestling phase. Extra food had a positive effect on the general mass level of females but not of males. However, provisioning had no significant effect on the masses of females feeding thermoregulating nestlings, indicating that reproductive stress is not important in determining posthatching mass losses. All females lost mass after hatching, and the heaviest lost proportionally more. Extra food was delivered almost exclusively to the chicks a few days after hatching. Females apparently maintain reserves during incubation and transfer them to the young after hatching by a voluntary shift in the allocation of collected food. Males do not store reserves and have therefore no scope for significant mass changes.

**Key words:** *Body mass; food provisioning; electronic balances; incubation; mass losses; energy reserves; nestling feeding.*

## INTRODUCTION

Changes in body mass of breeding birds have frequently been cited as evidence of reproductive stress, body mass being traditionally used as an index of general condition in life history studies of birds (Hussell 1972, De Steven 1980, Nur 1984). However, caution has been recommended in the interpretation of mass fluctuations, because among other things changes in reproductive organs and tissues may be responsible for the mass changes (Ricklefs 1974, Ricklefs and Hussell 1984). The view that body mass decreases must be due to a failure to maintain energy balance during certain reproductive phases has also been challenged by authors who consider these changes as adaptations to changing needs and selective pressures during reproduction. Thus Freed (1981) and Norberg (1981) suggested that the frequently observed mass decreases of the

adults after hatching of the young in many altricial species are adaptive, because they reduce the energy costs of flight at a time when this activity becomes increasingly important. Furthermore, Sherry et al. (1980) and Mrosovsky and Sherry (1980) have shown that mass decreases during incubation in some bird species are the product of spontaneous shifts in energy balance allowing an increase in nest attentiveness during this critical phase.

Information on mass changes of individual birds through the breeding cycle is scarce. In only a few cases have techniques been used allowing repeated weighings of undisturbed birds in the field (but see Carpenter et al. 1983, Crick and Fry 1986). Placing a balance under the nest (Sibly and McCleery 1980, Westerterp et al. 1982, Jones 1987) is frequently impossible for practical reasons. In the present case I attracted certain individuals to specific sites where they could be repeatedly weighed without disturbance by offering food. My aim was to explore the degree of flexibility of the normal pattern of mass changes in a breeding population of Northern Wheatears

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<sup>2</sup> Present address: Museo Nacional de Ciencias Naturales, J. Gutierrez Abascal 2, 28006 Madrid, Spain.

(*Oenanthe oenanthe*) by offering different quantities of food to certain breeding pairs and comparing their body masses with those of unsupplemented individuals (resulting from captures). Extra food should reveal the importance of energy stress as a determinant of mass losses.

#### STUDY AREA AND METHODS

The study was conducted during the breeding seasons of 1985–1987 on a 60-ha plot of limestone grassland on the island of Öland in the Baltic Sea (56°34'N 16°36'E). The area is barren, covered by a very thin layer of vegetation and by irregularly distributed juniper (*Juniperus communis*) bushes. It forms part of the Stora Alvaret, the climate, topography, and vegetation of which have been described by Rosén (1982). Approximately 30 pairs of wheatears breed in the study plot, the number fluctuating slightly from year to year (Moreno, unpubl.). Most nests were found when under construction or after initiation of egg laying.

Birds were captured throughout the season with mist nets and spring traps baited with a single mealworm. Mist nets were usually checked every 30–60 min. Birds were weighed with a Pesola spring balance accurate to 0.1 g. Flattened wing length and tarsus length were measured. Unfortunately very few incubating females were captured due to their reduced activity and sensitivity to disturbance at this stage. The following breeding phases will be considered here: Prelaying (P), laying (L), incubation (beginning the day on which the last egg was laid) (I), brooding (from hatching of the first egg to the seventh day after hatching) (B), late nestling (from the seventh day until fledging) (N), and postfledging (F). The nestling period of 2 weeks (Moreno 1987) consists of B + N, and the period of offspring dependence of B + N + F (offspring dependence after fledging lasts 2 weeks, Moreno 1984).

Perches (1 m) with plastic cups at the top were placed in different territories at the beginning of the season. Different amounts of mealworms (larvae of *Tenebrio molitor*) were offered in these cups, depending on if one or both mates visited the feeders (Table 1). In 1987, I varied the amount of food offered to different pairs to look at its effects on body mass (Table 1). The territories on which perches were placed were selected randomly, and perches were removed a few days after placement if, as happened in half of the cases, no wheatear started to visit them. A few

days after the first confirmed visit to such a feeder by one of the territory owners, I moved the cups to shorter, 40-cm tall perches. In order to weigh the individuals visiting the cups, the perches were fixed on top of A & D (model EW-300B) electronic digital balances, accurate to 0.1 g. Weighing perches were always placed in the cover of some dense juniper, in order to shelter the perch balance from the effects of wind. The birds visiting the cups usually remained for long enough on the perch for the digital display to stabilize. In some cases, no weights could be obtained due to birds moving on the perch or strong winds. Readings were made from 10–20 m with a telescope of 25× magnification. Figure 1 presents some examples of the data sets obtained with the perch balance. In 1985 feeding and perch weighing were discontinued after hatching. To standardize mass data with respect to body size, I have divided mass by tarsus length in all further analyses (e.g., Jones 1987), as wing length depends on the nutritional condition during the last molt (Pehrsson 1987) and on the degree of wear of the primaries. Not all provisioned birds were captured and measured, which explains the discrepancy in sample sizes of masses and size-corrected masses. Most weighings (60%,  $n = 600$ ) were concentrated to the middle third of the daylight period (10:00–16:00), making it difficult to detect any effects of time of day.

Assuming that the assimilation efficiency of mealworms is 0.65 (Kacelnik 1984), the rations of 4.5, 7.0 and 9.0 g of mealworms would correspond to daily energy intakes per individual of 25, 39, and 50 kJ (energy content of mealworms = 8.54 kJ/g from McCaule and Widdowson 1960). Wheatears feeding nestlings expend on average 87 kJ daily and have to collect 243 kJ to supply half of an average-sized brood (Moreno 1989). The food supplements thus constitute a substantial contribution to the energy requirements of breeding wheatears. It was impossible to measure the proportions taken by male and female respectively when both members of the pair learned to use the feeders. Therefore I have assumed that the mates took equal amounts of food as no significant interference was observed at the perches.

Weather data were available from the nearest meteorological station (Ottenby) which was 40 km from the study area. The following variables were derived from the meteorological information and used in statistical analysis: the mean,

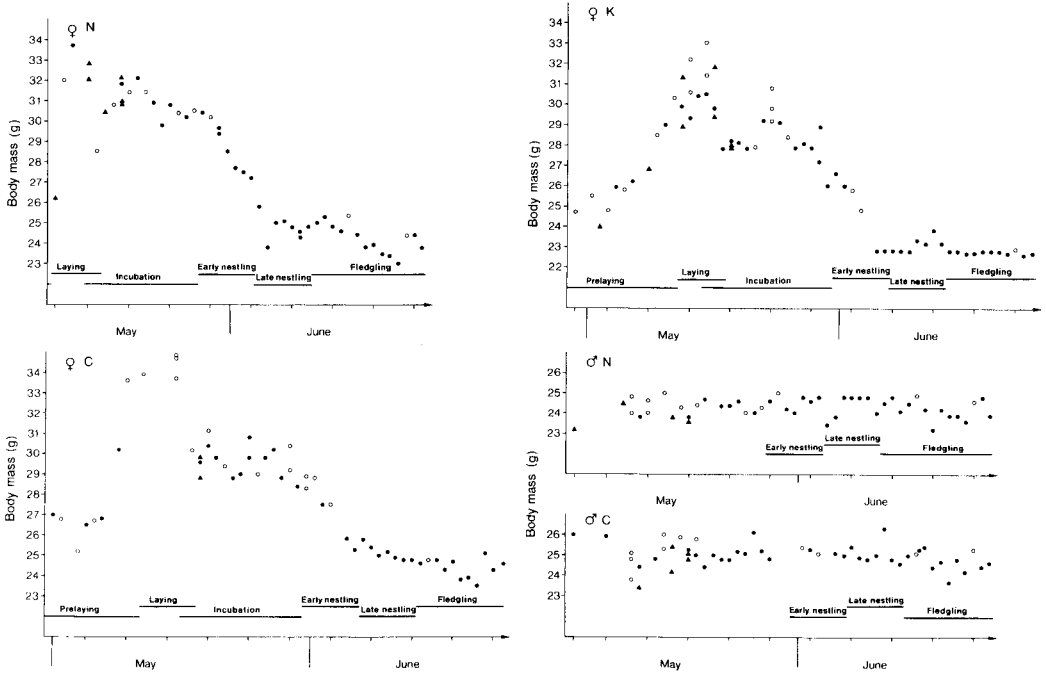


FIGURE 1. Seasonal variation in body mass of three females and two males during the 1986 breeding season. Birds were weighed periodically on a perch balance while consuming supplementary food. ▲ recorded between 05:00 and 10:00; ● between 10:00 and 15:00; ○ between 15:00 and 20:00.

TABLE 1. Description of food provisioning experiments made during the breeding seasons of 1985–1987 on a population of Northern Wheatears (*Oenanthe oenanthe*) breeding in Öland, south Sweden. Supplementary feeding was interrupted at hatching of the young in 1985. In the other years, interruption prior to fledging was due to disappearance of one or both mates.

Year	Nest	Supplement (g)	Use of feeders		Phases* covered
			Male	Female	
1985	D	7		+	I
	G	7		+	I
	N	7		+	I
	R	7		+	I
1986	C	14	+	+	P-F
	K	7		+	P-F
	N	14	+	+	P-F
1987	B	18	+	+	P-B
	C	18	+	+	P-F
	F	14	+	+	P-B
	G	9	+	+	P-B
	H	9	+	+	P-F
	Y	14	+	+	P-F

\* P = Pre-laying, I = Incubation, B = Brooding, F = Postfledging.

maximum, and minimum temperatures for the date of the observation, the precipitation (mm) of the previous day, the sum of the precipitation of the two previous days, the mean wind speed (m/sec) measured the previous day, and the wind speed measured at the time of the observation. The temperature, at the specific time when the bird was weighed, was measured in the study plot. Mean values for each individual and breeding phase will be considered as independent observations in all ANOVAs, in order to avoid pseudoreplication. Data which did not fulfill the prerequisites for parametric statistics have been transformed.

RESULTS

MASS CHANGES WITH SEASON IN RELATION TO SEX

Table 2 presents the mean body masses of captured wheatears during different phases of the reproductive cycle. Masses have not been cor-

TABLE 2. Body masses (g) of captured males and females during different phases of the breeding cycle. Mean values for the same individual and phase have been averaged.

	Breeding phase			
	Prelaying $\bar{x} \pm SD$ (n)	Incubation $\bar{x} \pm SD$ (n)	Brooding $\bar{x} \pm SD$ (n)	Late nestling $\bar{x} \pm SD$ (n)
Males	23.2 ± 1.1 (18)	25.5 ± 1.4 (2)	22.5 ± 2.1 (2)	24.6 ± 1.6 (10)
Females	23.8 ± 1.6 (14)	24.9 ± 0.6 (3)	26.4 ± 1.7 (9)	23.5 ± 1.4 (22)

rected for time of day, as a preliminary analysis showed no significant correlations between mass and time of day for either sex (Spearman's rank correlations). Breeding phase but not sex had significant effects on body mass (Two-way ANOVA,  $F = 7.3, P < 0.001, n = 111$ ). The absence of differences between sexes is due to the fact that only the samples for P and N are representative (Table 2). These are the phases when males and females have similar body masses (see below). I and B are characterized by significantly larger masses than P and N (Student-Newman-Keuls test, Table 2).

Considering now the detailed data for provisioned individuals, I have analyzed the intraphasic trends in mass with the advancement of the phase for every individual (only samples of five or larger have been included) (Table 3). Females maintain constant levels during incubation (five of six birds), decrease markedly during brooding (all four) and attain a new constant level during the late nestling and postfledging phases (four of five birds) (Table 2, Fig. 1). With some exceptions, males do not exhibit any trends at all (Table 2, Fig. 1). Males in contrast to females do not seem to accumulate body reserves.

TABLE 3. Pearson's correlation coefficients of body mass with advancement of different breeding phases (days before laying, eggs laid, day of incubation, and nestling or offspring age) for different provisional female (F) and male (M) Northern Wheatears. Advancement of season is indicated by a negative scale for the prelaying phase. Only samples with five or more observations have been analyzed. \*\*\* =  $P < 0.001$ ; \*\* =  $P < 0.01$ ; \* =  $P < 0.05$ ; ns =  $P > 0.05$ .

		Breeding phase*							
		P	L	I	B	N	F	B + N	B + N + F
F	C-86	-0.73 *	ns	ns	-0.89 *	ns	ns	-0.91 ***	-0.87 ***
F	K-86	-0.91 ***	ns	ns	-0.98 ***	ns	ns	-0.75 ***	-0.70 ***
F	N-86	—	ns	-0.58 *	-0.98 ***	ns	-0.67 **	-0.95 ***	-0.86 ***
F	B-87	—	—	ns	—	—	—	—	—
F	C-87	—	—	—	—	-0.93 *	ns	-0.97 ***	-0.51 *
F	G-87	—	—	ns	-0.95 ***	—	—	-0.95 ***	-0.95 ***
F	H-87	—	—	—	—	—	ns	-0.95 ***	-0.72 ***
F	Y-87	—	—	ns	—	ns	—	-0.77 *	-0.67 *
M	C-86	—	ns	ns	-0.96 **	ns	ns	ns	-0.50 *
M	N-86	—	ns	ns	ns	ns	ns	ns	ns
M	B-87	—	—	0.90 *	—	—	—	—	ns
M	C-87	—	—	—	—	—	—	ns	ns
M	G-87	—	—	ns	ns	—	—	ns	ns
M	H-87	—	—	—	—	ns	ns	ns	ns
M	Y-87	—	—	ns	—	ns	—	ns	ns

\* P = Prelaying, L = Laying, I = Incubation, B = Brooding, N = Late nestling, F = Postfledging.

TABLE 4. Results of multifactorial analyses of variance for the effects of year, treatment (provisioned vs. unprovisioned) and breeding phase on mass (g) and size-corrected body mass (mass/tarsus length) of males and females. *F*-values for the different factors are presented together with the probabilities (in parentheses).

	Model				Factors		
	<i>F</i>	<i>P</i>	<i>r</i> <sup>2</sup>	<i>n</i>	Year <i>F</i> ( <i>P</i> )	Treatment <i>F</i> ( <i>P</i> )	Phase <i>F</i> ( <i>P</i> )
<b>Males</b>							
Mass	1.7	0.114	0.20	70			
Corrected mass	1.7	0.120	0.28	45			
<b>Females</b>							
Mass	20.1	0.001	0.67	97	4.2 (0.018)	12.0 (0.001)	19.7 (0.001)
Corrected mass	16.8	0.001	0.65	90	5.7 (0.005)	8.9 (0.004)	16.6 (0.001)

#### SOURCES OF CONTINUOUS VARIATION

To understand the sources of continuous variation in body mass, I conducted stepwise multiple regression analyses of size-corrected masses derived from single weighings, with weather variables, date and time of day as independent variables. Nestling age and brood size were also included when analyzing posthatching phases. Sexes and treatments (provisioned, unprovisioned) were analyzed separately. All phases could be analyzed jointly for males, while the I and N phases (those with constant levels) were analyzed separately for females. Corrected mass of unprovisioned males was positively affected by temperature at the time of weighing ( $F = 8.01$ ,  $P < 0.01$ ,  $n = 27$ ). Masses of unprovisioned females during N were positively affected by brood size ( $F = 5.66$ ,  $P < 0.05$ ,  $n = 30$ ). The corrected mass of provisioned males was positively affected by mean wind speed ( $F = 5.55$ ,  $P < 0.05$ ,  $n = 95$ ). When nestling age and brood size were included in the analysis, the model including those two variables plus temperature, minimum temperature, and date explained 74% of the variation in corrected mass of provisioned males (model:  $F = 24.70$ ,  $P < 0.001$ ,  $n = 49$ ; brood size:  $F = 25.41$ ,  $P < 0.001$ ,  $b = 1.07$ ; nestling age:  $F = 9.28$ ,  $P < 0.01$ ,  $b = -0.08$ ; minimum temperature:  $F = 8.83$ ,  $P < 0.01$ ,  $b = -0.21$ ; temperature:  $F = 7.23$ ,  $P = 0.01$ ,  $b = 0.16$ ; date:  $F = 4.31$ ,  $P < 0.05$ ,  $b = 0.30$ ). The corrected mass of provisioned incubating females was negatively affected by date and positively by minimum temperature (model:  $F = 12.16$ ,  $P < 0.001$ ,  $n = 75$ ; date:  $F = 23.91$ ,  $P < 0.001$ ,  $b = -0.41$ ; minimum temperature:  $F = 11.97$ ,  $P < 0.001$ ,  $b = 0.29$ ). Finally for provisioned females during N, there

was again a negative effect of date independent of nestling age ( $F = 9.31$ ,  $P < 0.01$ ,  $n = 28$ ).

#### THE EFFECTS OF SUPPLEMENTARY FOOD

The different food rations offered during 1987 (Table 1) had no significant effect on male or female masses ( $F = 0.40$ ,  $P > 0.50$ ,  $n = 30$  and  $F = 0.48$ ,  $P > 0.50$ ,  $n = 31$  respectively), so birds receiving supplementary rations will be pooled in further analyses. The effect of supplementary food was tested by subjecting mass and size-corrected body mass of males and females to multifactorial analyses of variance with year, treatment, and breeding phase as classifying variables. No factor affected significantly the body mass of males, while all three factors were significant for females (Table 4). Females were lighter in 1985 than in the other years, although comparisons between means showed no significant differences (Table 5). Provisioned females were significantly heavier than unprovisioned females (Table 5). Females were heaviest during L, intermediate during I and B, and lightest during P, N, and F (Table 5).

The mass of females during N was not affected by either year or treatment (two-way ANOVA:  $F = 2.10$ ,  $P > 0.10$ ,  $n = 27$ ) (Table 6). However, year had a nearly significant effect in a one-way ANOVA ( $F = 3.29$ ,  $P = 0.055$ ). Females were heaviest in 1986 and lightest in 1987 (Table 6). The 1986 season was the most benign with respect to climate, while 1987 was exceptionally cold and wet (Table 7). Provisioned females lost on average 3.8 g (range = 1.4–5.2 g,  $n = 10$ ) during B, or 13.6% (range = 5.7–16.7%) of their prehatching mass. Both absolute and proportional mass losses were positively affected by size-

TABLE 5. Body masses (g) and size-corrected masses (mass/tarsus length [mm]) of males and females according to breeding season, phase and treatment (provisioned vs. unprovisioned). Sample sizes (in parentheses) refer to mean values for each individual and breeding phase. Means with the same letter are not significantly different (Student-Newman-Keuls tests).

	Males		Females	
	Mass $\bar{x} \pm SD (n)$	Size-corrected $\bar{x} \pm SD (n)$	Mass $\bar{x} \pm SD (n)$	Size-corrected $\bar{x} \pm SD (n)$
<b>Year</b>				
1985	a 23.5 ± 1.6 (12)	a 0.78 ± 0.05 (12)	a 25.2 ± 2.6 (23)	a 0.85 ± 0.08 (23)
1986	b 24.2 ± 1.3 (21)	b 0.81 ± 0.05 (14)	a 25.8 ± 2.9 (36)	a 0.87 ± 0.09 (29)
1987	b 24.3 ± 1.0 (41)	ab 0.79 ± 0.04 (23)	a 25.8 ± 3.0 (42)	a 0.86 ± 0.10 (42)
<b>Treatment</b>				
Prov.	a 24.4 ± 0.8 (42)	a 0.81 ± 0.04 (18)	a 26.9 ± 3.0 (53)	a 0.90 ± 0.10 (47)
Unprov.	b 23.7 ± 1.5 (32)	a 0.78 ± 0.05 (31)	b 24.3 ± 1.8 (48)	b 0.82 ± 0.06 (47)
<b>Phase</b>				
P	a 23.5 ± 1.1 (26)	a 0.77 ± 0.04 (20)	ab 25.2 ± 2.4 (22)	ab 0.85 ± 0.08 (20)
L	a 24.2 ± 0.6 (8)	a 0.80 ± 0.04 (3)	d 30.6 ± 1.8 (9)	d 1.03 ± 0.07 (8)
I	a 25.0 ± 1.1 (10)	a 0.83 ± 0.04 (5)	c 27.9 ± 2.1 (16)	c 0.93 ± 0.08 (15)
B	a 24.2 ± 1.4 (9)	a 0.80 ± 0.04 (5)	bc 26.2 ± 1.8 (18)	bc 0.87 ± 0.06 (17)
N	a 24.4 ± 1.4 (15)	a 0.81 ± 0.05 (13)	a 23.5 ± 1.4 (28)	ab 0.79 ± 0.05 (27)
F	a 24.1 ± 0.5 (5)	a 0.80 ± 0.03 (3)	a 23.1 ± 1.0 (6)	a 0.77 ± 0.04 (5)

corrected incubation mass ( $F = 18.06, P < 0.01$ , and  $F = 9.79, P < 0.05, n = 9$  respectively).

DISCUSSION

Studies of avian breeding have often noted the marked differences between sexes with respect to mass changes. While males usually maintain relatively constant body masses throughout the breeding effort (Petersen 1955, Haukioja 1969, Morton et al. 1973, Silverin 1981, Ricklefs and Hussell 1984, Biermann and Sealy 1985), females frequently undergo significant changes for different reasons. Gonadal growth and egg production leads to body mass increments of between 7 and 30% up to a peak before the beginning of laying (Petersen 1955, Haukioja 1969, Dowsett-Lemaire and Collette 1980, Jakober and Stauber 1980, Ricklefs and Hussell 1984,

Wijnandts 1984, Alonso 1985). There usually follows an abrupt decline while the clutch is being laid. This decline is continued during incubation in anseriforms and galliforms (Breitenbach and Meyer 1959, Redfield 1973, Korschgen 1977, Ankney and MacInnes 1978), while it ceases in passerines and raptors to be substituted by constancy or even increases (Nice 1937, Petersen 1955, Dowsett-Lemaire and Collette 1980, Askenmo 1982, Ricklefs and Hussell 1984, Wijnandts 1984, Newton 1986).

It is only after hatching that body mass decreases further in females of these species to reach a new period of stability at the end of the nestling period. There is increasing evidence that females keep previously stored body reserves throughout incubation (Newton 1972, Morton et al. 1973, Jones and Ward 1976, Ricklefs and Hussell 1984,

TABLE 6. Masses (g) and size-corrected masses (mass/tarsus length (mm)) of females during the late nestling phase (N) according to year and treatment (provisioned vs. unprovisioned). Sample sizes (in parentheses) refer to mean values for each individual and breeding phase. Means with the same letter are not significantly different (Student-Newman-Keuls tests).

	Mass $\bar{x} \pm SD (n)$	Size-corrected mass $\bar{x} \pm SD (n)$
1985	a 23.7 ± 0.9 (10)	ab 0.80 ± 0.02 (10)
1986	a 23.9 ± 1.6 (10)	a 0.82 ± 0.06 (9)
1987	a 22.8 ± 1.4 (8)	b 0.76 ± 0.05 (8)
Provisioned	a 23.5 ± 1.4 (6)	a 0.78 ± 0.06 (5)
Unprovisioned	a 23.5 ± 1.4 (22)	a 0.80 ± 0.05 (22)

TABLE 7. Mean monthly values for daily mean, maximum, and minimum temperatures, and wind speed at 13:00, and total monthly precipitation during the breeding seasons of 1985–1987 in Southern Öland, Sweden.

	Mean temp. °C	Max. temp. °C	Min. temp. °C	Wind speed m/sec	Precip. mm
May 1985	7.8	10.9	5.3	7.0	8.0
June 1985	12.8	16.4	10.3	5.4	32.5
May 1986	8.2	10.8	6.2	6.0	27.4
June 1986	14.0	17.3	11.4	5.1	24.7
May 1987	6.8	9.5	4.9	7.2	42.3
June 1987	10.4	13.0	8.5	6.6	72.7

Jones 1987), which can later be mobilized in order to sustain the breeding effort. The Northern Wheatear is another example of this sexual difference in reserve storage and use of body mass. Males do not store nor mobilize reserves, and have thus no scope for significant mass changes. Females store reserves which they use for laying and as an energy buffer during incubation. This reserve is depleted during the first week after hatching, when females brood the chicks and cooperate with the male in feeding them (Moreno 1987). After this decrease the scope for further mass declines appears exhausted and mass stabilizes at the prelaying level.

Variation exists around the typical pattern. Higher temperatures lead to higher masses in males and incubating females, probably due to improved feeding conditions. Date has a negative influence on female incubation masses. This seasonal effect could be related to the negative trend in clutch size and brood size with laying date (Moreno, unpubl.). As we will argue below, large broods may require larger prehatching reserves than small broods. The negative effect of date on female masses during N could be due to lower prehatching mass levels. The positive effect of date on masses of provisioned males again points out the different strategies of males and females. More interesting is the positive effect of brood size on both male and female masses. Declines in body mass of birds feeding nestlings have been used as evidence for reproductive stress or as a good measure of reproductive costs (Husell 1972, De Steven 1980, Yom-Tov and Hilborn 1981, Westerterp et al. 1982, Nur 1984). If that is so, the present results imply that females raising large broods experience less stress or are subjected to smaller costs than those rearing

smaller broods. On the other hand, if we assume that clutch size is adjusted to the phenotypical quality of the parents (Perrins and Moss 1975, Drent and Daan 1980, Högstedt 1980), we would not normally expect any clutch-size dependent trends in reproductive stress nor in body mass. However, phenotypical differences due to age or some other factor could also be large enough to explain the positive trend.

Food provisioning had no effect on males, while it was associated with larger female masses. However, this effect on females did not show after the posthatching mass loss. All females attained the same mass levels during N. This result indicates that the 14% of body mass lost while brooding is not a symptom of physiological stress. One possible reason for this lack of effect of provisioning is that females could use the extra food to change their resource allocation in favor of their offspring. Incubating females increased their nest attentiveness along with increasing food supplements (Moreno, unpubl.). Later, when the chicks became sufficiently large to consume mealworms (2–3 days), parents began to deliver almost all of them to the young (it was impossible to quantify exactly the amounts consumed by adults and delivered to young as the observer had to concentrate on reading the display of the balance). Nonprovisioned females probably experience a similar voluntary reduction in energy intake after hatching of the young. The reserves of the female are in this way indirectly transferred to the young in order to speed up their growth. Greater reserves could mean faster growth. The proportion of incubation mass lost by female wheatears after their chicks hatch is positively correlated with the mass level attained at the end of incubation. Females in good condition at hatching are apparently willing to lose proportionally more mass in order to care properly for their young.

Norberg (1981) has discussed this transference of body reserves as one of the advantages of post-hatching mass losses. This advantage can explain why females of many passerines and raptors with uniparental incubation maintain their reserves until hatching. Lifjeld and Slagsvold (1986) have shown that the mass of Pied Flycatcher (*Ficedula hypoleuca*) females during incubation is positively correlated with fledgling size and condition. The importance of keeping reserves until hatching is shown by incubating female sparrowhawks, *Accipiter nisus* (Newton 1986), and swal-

lows, *Hirundo rustica* (Jones 1987), which desert when falling below a certain threshold of mass, even if they normally attain the same level when feeding large nestlings.

Why is it only females that transfer body reserves to their young? The answer lies probably in the accumulation of reserves prior to laying. Once these reserves have been collected for the purpose of egg production, it is easier to maintain them throughout a low activity phase such as incubation. Males which have become liberated from the presumably ancestral condition of joint incubation (Kendeigh 1952, Skutch 1957) are active and therefore conspicuous to predators during incubation. In cavity nesters such as the Northern Wheatear, they are vulnerable to predators because they remain outside of nest cavities throughout incubation. Male wheatears are also very active in trying to attract other females or roaming around neighboring territories during this time (Carlson et al. 1985 and pers. observ.). They need to be lean in order to fly and escape predators or rival males and display to females in spectacular display flights. Here the ideas of Freed (1981) and Norberg (1981) regarding minimization of flight costs would apply in full force. The absence of effects of provisioning on male mass also indicates that males are unwilling to put on reserves. Only females have the capacity for keeping and transferring reserves to the young, a process which is typical of altricial and semialtricial species with role separation between the sexes.

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#### LITERATURE CITED

- ALONSO, J. C. 1985. Schwankungen des Körpergewichts beim Weidensperling (*Passer hispaniolensis*). J. Ornithol. 126:195–205.
- ANKNEY, C. D., AND C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 95:459–471.
- ASKENMO, C. 1982. Clutch size flexibility in the Pied Flycatcher *Ficedula hypoleuca*. Ardea 70:189–196.
- BIERMANN, G. C., AND S. G. SEALY. 1985. Seasonal dynamics of body mass of insectivorous passerines breeding on the forested dune ridge, Delta Marsh, Manitoba. Can. J. Zool. 63:1675–1682.
- BREITENBACH, R. P., AND R. K. MEYER. 1959. Effect of incubation and brooding on fat, visceral weights and body weight of the hen pheasant. Poul. Sci. 38:1014–1026.
- CARLSON, A., L. HILLSTRÖM, AND J. MORENO. 1985. Mate guarding in the Wheatear *Oenanthe oenanthe*. Ornis Scand. 16:113–120.
- CARPENTER, F. L., D. C. PATON, AND M. A. HIXON. 1983. Weight gain and adjustment of feeding territory size in migrant hummingbirds. Proc. Natl. Acad. Sci. USA 80:7259–7263.
- CRICK, H. Q. P., AND C. H. FRY. 1986. Effects of helpers on parental condition in red-throated bee-eaters (*Merops bullocki*). J. Anim. Ecol. 55:893–906.
- DE STEVEN, D. 1980. Clutch size, breeding success, and parental survival in the tree swallow (*Iridoprocne bicolor*). Evolution 34:278–291.
- DOWSETT-LEMAIRE, F., AND P. COLLETTE. 1980. Weight variations of adult Marsh Warblers (*Acrocephalus palustris*) during the breeding cycle. Vogelwarte 30:209–214.
- DRENT, R. H., AND S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252.
- FREED, L. A. 1981. Loss of mass in breeding wrens: stress or adaptation? Ecology 62:1179–1186.
- HAUKIOJA, E. 1969. Weights of Reed Buntings (*Emberiza schoeniclus*) during summer. Ornis Fenn. 46:13–21.
- HÖGSTEDT, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territorial quality. Science 210:1148–1150.
- HUSSELL, D. J. T. 1972. Factors affecting clutch size in arctic passerines. Ecol. Monogr. 42:317–364.
- JAKOBER, H., AND W. STAUBER. 1980. Flügelängen und Gewichte einer südwestdeutschen Population des Neuntötters (*Lanius collurio*) unter Berücksichtigung der geschlechtsspezifischen Arbeitsteilung während der Brutperiode. Vogelwarte 30:198–208.
- JONES, G. 1987. Time and energy constraints during incubation in free-living swallows (*Hirundo rustica*): an experimental study using precision electronic balances. J. Anim. Ecol. 56:229–245.
- JONES, P. J., AND P. WARD. 1976. The level of reserve protein as the proximate factor controlling the timing of breeding and clutch-size in the Red-billed Quelea *Quelea quelea*. Ibis 118:547–574.
- KACELNIK, A. 1984. Central place foraging in starlings (*Sturnus vulgaris*). I. Patch residence time. J. Anim. Ecol. 53:283–299.
- KENDEIGH, S. C. 1952. Parental care and its evolution in birds. Ill. Biol. Monogr. 22:1–356.
- KORSCHGEN, C. E. 1977. Breeding stress of female Eiders in Maine. J. Wildl. Manage. 41:360–373.
- LIFJELD, J. T., AND T. SLAGSVOLD. 1986. The function of courtship feeding during incubation in the pied flycatcher *Ficedula hypoleuca*. Anim. Behav. 34:1441–1453.
- MCCAUCE, R. A., AND E. M. WIDDOWSON. 1960. The composition of foods. H.M.S.O., London.
- MORENO, J. 1984. Parental care of fledged young, division of labor, and the development of foraging techniques in the Northern Wheatear (*Oenanthe oenanthe*). Auk 101:741–752.



- MORENO, J. 1987. Parental care in the Wheatear *Oenanthe oenanthe*: effects of nestling age and brood size. *Ornis Scand.* 18:291-301.
- MORENO, J. 1989. Variation in daily energy expenditure in nesting Northern Wheatears (*Oenanthe oenanthe*). *Auk* 106:18-25.
- MORTON, M. L., J. L. HORSTMANN, AND C. CAREY. 1973. Body weights and lipids of summering mountain White-crowned Sparrows in California. *Auk* 90:83-93.
- MROSOVSKY, N., AND D. F. SHERRY. 1980. Animal anorexias. *Science* 207:837-842.
- NEWTON, I. 1972. *Finches*. Collins, London.
- NEWTON, I. 1986. *The Sparrowhawk*. T. & A.D. Poyser, Berkhamsted.
- NICE, M. M. 1937. The biological significance of bird weights. *Bird-Banding* 9:1-11.
- NORBERG, R. A. 1981. Temporary weight decrease in breeding birds may result in more fledged young. *Am. Nat.* 118:838-850.
- NUR, N. 1984. The consequences of brood size for breeding blue tits. I. Adult survival, weight change and the cost of reproduction. *J. Anim. Ecol.* 53:479-496.
- PEHRSSON, O. 1987. Effects of body condition on molting in Mallards. *Condor* 89:329-339.
- PERRINS, C. M., AND D. MOSS. 1975. Reproductive rates in the Great Tit. *J. Anim. Ecol.* 44:695-706.
- PETERSEN, A. J. 1955. The breeding cycle in the Bank Swallow. *Wilson Bull.* 67:235-286.
- REDFIELD, J. A. 1973. Variations in weight of Blue Grouse (*Dendragapus obscurus*). *Condor* 75:312-321.
- RICKLEFS, R. E. 1974. Energetics of reproduction in birds, p. 152-291. In R. A. Paynter [ed.], *Avian energetics*. Nuttall Ornithol. Club, Cambridge, MA.
- RICKLEFS, R. E., AND D.J.T. HUSSELL. 1984. Changes in adult mass associated with the nesting cycle in the European Starling. *Ornis Scand.* 15:155-161.
- ROSÉN, E. 1982. Vegetation development and sheep grazing in limestone grasslands of South Öland, Sweden. *Acta Phytogeogr. Suec.* 72:1-104.
- SHERRY, D. F., N. MROSOVSKY, AND J. A. HOGAN. 1980. Weight loss and anorexia during incubation in birds. *J. Comp. Physiol. Psychol.* 94:89-98.
- SIBLY, R., AND R. H. MCCLEERY. 1980. A balance for weighing ground-nesting birds. *J. Appl. Ecol.* 17:323-327.
- SILVERIN, B. 1981. Reproductive effort, as expressed in body and organ weights, in the Pied Flycatcher. *Ornis Scand.* 12:133-139.
- SKUTCH, A. F. 1957. The incubation patterns of birds. *Ibis* 99:69-93.
- WESTERTERP, K., W. GORTMAKER, AND H. WJUNGAARDEN. 1982. An energetic optimum in brood-raising in the Starling *Sturnus vulgaris*: an experimental study. *Ardea* 70:153-162.
- WIJNANDTS, H. 1984. Ecological energetics of the Long-eared Owl, *Asio otus*. *Ardea* 72:1-92.
- YOM-TOV, Y., AND R. HILBORN. 1981. Energetic constraints on clutch size and time of breeding in Temperate zone birds. *Oecologia (Berl.)* 48:234-243.