

VARIATION IN DAILY ENERGY EXPENDITURE IN NESTING NORTHERN WHEATEARS (*OENANTHE OENANTHE*)

JUAN MORENO¹

Department of Animal Ecology, University of Uppsala, Box 561, S-751 22 Uppsala, Sweden

ABSTRACT.—The field metabolic rate (FMR) of 19 adult Northern Wheatears (*Oenanthe oenanthe*) feeding nestlings was measured with the doubly labeled water $D_2^{18}O$ technique (DLW) over three seasons. The energy expenditures of four almost fully grown nestlings were also measured with DLW (average consumption = 52 kJ/day). Adult wheatears expended on average 87.4 kJ/day, with no difference between females and males. This was 2.2 times the basal metabolic rate (BMR). Energy expenditure was 10% below that predicted for their body size. Parents collect three times as much energy to supply an average-sized brood of nearly grown nestlings than they need for self-maintenance. I found no difference in metabolic rate or metabolic intensity (multiples of BMR) between females brooding and feeding ectothermic chicks of 1–4 days of age and females that fed endothermic nestlings of 9–13 days of age. Brooding females had lower feeding rates and spent less time flying, so the similarity in FMR should be due to the energetic costs of brooding itself. Feeding rates correlated positively with FMR for late nestling females; proportion of active time spent in flight had no apparent effect. Brood size was unrelated to energy expenditure of females that fed large nestlings. I detected no effect of brood manipulations. Female condition (body mass divided by tarsus) varied positively with brood size. Females that cared for large broods had energy expenditures equal to those feeding small broods, but were apparently in better physical condition. Received 25 January 1988, accepted 16 July 1988.

ENERGY shortage has been proposed to be a critical constraint in avian life histories (Drent and Daan 1980). Lack (1954) proposed that the capacity of the parents to supply food to the nestlings limits the reproductive rates of nidicolous birds (see Klomp 1970, Murphy and Haukioja 1986). The doubly labeled water (DLW) technique has been used to study avian energetics (Lifson and McClintock 1966, Nagy 1980). The technique is useful in comparisons of parental expenditure between related species (Westerterp and Bryant 1984), between different reproductive phases (Bryant and Westerterp 1980, Westerterp and Drent 1985), between sexes (Ricklefs and Williams 1984) and between temperate and tropical regions (Bryant et al. 1984). It is accurate enough to detect individual variation (Bryant and Westerterp 1982), in a manner which energy budget calculations based on time budgets cannot (Williams and Nagy 1984, Weathers et al. 1984, Buttemer et al. 1986).

The DLW technique has also been applied to

the study of reproductive rates in birds. Hails and Bryant (1979) showed that male House-Martin (*Delichon urbica*) metabolism increased with increased mass of the nestling brood. Bryant and Westerterp (1983a) documented decreases in net energy balance with brood size in the same species. In one study of the Savannah Sparrow (*Passerculus sandwichensis*), parents that raised two and three nestlings respectively had similar rates of energy expenditure (Williams and Nagy 1985). In another study, mass-independent metabolism was positively affected by brood size (Williams 1987). Ricklefs and Williams (1984) found no relationship between energy expenditure and either brood size or brood mass in the European Starling (*Sturnus vulgaris*).

To document the sources of variation in energy expenditure of Northern Wheatears while they fed nestlings, I measured the field metabolic rates (FMR) of parents during this allegedly critical breeding period. The Northern Wheatear is a widespread insectivorous passerine (Cramp 1988), that breeds in open habitats. Due to its conspicuous appearance and behavior, the species is particularly well-suited for

¹ Present address: Museo Nacional de Ciencias Naturales, J. Gutierrez Abascal 2, 28006 Madrid, Spain.

detailed behavioral observations. I wanted to determine if trends in parental energy expenditure were related to nestling age and brood size. DLW measurements were also made on a few almost fully grown nestlings to estimate the total energy needs that parents must supply at this time.

METHODS

A population of wheatears was studied 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 with scattered junipers (*Juniperus communis*). It forms part of the Stora Alvaret, whose climate, topography and vegetation were described by Rosen (1982). Approximately 30 pairs of wheatears bred in the study area, the number fluctuates only slightly from year to year. Individuals were captured throughout the season and individually color-banded. The breeding phenology was monitored by repeated checks of the nests which were usually found during nest construction or egg laying.

Wheatears arrive at the study area during the second half of April and begin to nest in early May. Mean ($\bar{x} \pm$ SD) will be presented throughout) clutch size was 6.2 ± 0.7 ($n = 70$) eggs and mean brood size 5.6 ± 1.1 ($n = 54$) young. Males neither incubate nor feed the female during incubation. Both parents feed the young, but only the females brood during the first week (Moreno 1987a). Nestlings fledge after 2 weeks in the nest (Moreno 1987b) and become independent 2 weeks after fledging (Moreno 1984a).

I captured nesting adults in mist nets during the evening in the vicinity of the nest. After capture, I injected 0.15 ml of a mixture that contained 5 g of 51.60 AP H₂¹⁸O and 1.29 g of 99.95 AP D₂O intraperitoneally. Birds were kept in a dark box for 1 h to allow complete equilibration of the isotopes in the body water. Blood was sampled from a brachial vein and stored in flame-sealed capillary tubes until analysis. The labeled birds were weighed, measured, and released. Of 34 labeled individuals, 12 did not appear at the nest the following morning (although they returned later), and 3 deserted. Of 19 birds which behaved naturally in the morning, 13 were recaptured the following evening (after 0.99 ± 0.03 days) and 6, more than a day after initial capture (1.36 ± 0.12 days). Five chicks older than 10 days (2 in 1985, 3 in 1986) were injected and the blood was sampled in the same manner as adults, except that they remained in the nest during the hour after injection. Wheatear chicks barely increase in mass after the age of 10 days (Moreno 1987b), and I assumed a constant body water volume during the day of measurement (see Nagy 1980 for assumptions of the DLW method). To obtain background values I took blood samples

from a few individuals without previous injection. Blood samples were analyzed for ¹⁸O and D concentrations at the Center for Isotope Research (C.I.O.) of the University of Groningen, Netherlands.

The DLW technique is fully described by Lifson and McClintock (1966), Mullen (1973) and Nagy (1980). It has been repeatedly validated in the laboratory, showing errors of less than 10% (Williams and Prints 1986). CO₂ production was calculated with the formula (Lifson and McClintock 1966):

$$r_{\text{CO}_2} = \frac{N}{2.08} (K_{18} - K_2) - 0.015K_2N \text{ mols/day}$$

where N = body water volume (mols); K_2 = fractional turnover rate of deuterium per day; K_{18} = fractional turnover rate of ¹⁸O per day. Water turnover rate was calculated as: $r_{\text{H}_2\text{O}} = K_2 \cdot N$ mols/day.

Body water volume in the Wheatear was $63 \pm 4\%$ ($n = 6$) of body mass. The field metabolic rate (FMR in kJ/day) was calculated with the conversion factor 25 kJ/l CO₂ produced, which is intermediate between that derived for insectivorous nestling Savannah Sparrows (24.6; Williams and Prints 1986) and that in the insectivorous lizard (*Uta stansburiana*; 25.75; Nagy 1983). I termed field metabolic rate divided by basal metabolic rate (FMR/BMR) as metabolic intensity (MI) (Westerterp and Bryant 1984). For BMR, I used the value of 3.39 ml O₂/(g·h) determined in respirometry measurements of captive wheatears.

For the 6 individuals which were bled a second time 2 nights or more after injection, I calculated their nighttime metabolism from the equation:

$$\text{MR} [\text{ml O}_2/(\text{g}\cdot\text{h})] = 5.71 - 0.12T_n (\text{°C}),$$

derived from laboratory measurements of captive wheatears (Moreno in press) and the nighttime temperatures recorded. Nighttime CO₂ production was calculated assuming an RQ of 0.8 and subtracted from the total CO₂ production. The CO₂ production/h of daytime was calculated by dividing the rest by the hours of daylight between samplings. The CO₂ production used to estimate FMR for these individuals was derived by subtracting the values for the second night and the extra hours of daylight the following morning from the total CO₂ production measured. This produced parity between this group of birds and those recaptured after approximately 24 h.

I constructed time budgets for 13 labeled individuals observing their activity as closely as possible throughout the day between blood samplings. The following activities were recorded continuously on an EPSON portable computer: flight, perching, time in nest, stationary time on the ground, and running on the ground (see Moreno 1984b for a description of wheatear foraging behavior). Simultaneously I recorded the frequency of visits to the nest with food. For 9 of the birds, 6 h or more of recorded observations were obtained by continuous coverage. The different coverage for various individuals was due to

TABLE 1. CO₂ production, field metabolic rate (FMR), metabolic intensity (MI = FMR/BMR) and water turnover rate of Northern Wheatears rearing nestlings in Oland.

Sex	Mass (g)	Tarsus length (mm)	Age (days)	Brood size ^a	Brood mass (g)	Temperature		CO ₂ production (ml/h)	FMR (kJ/d)	MI	H ₂ O turnover (ml/d)
						\bar{x} (°C)	Min. (°C)				
F	27.3	29.6	1	6	24.5	13.3	8.0	151.0	93.6	2.1	20.1
F	27.8	29.6	2	4r	34.5	11.5	10.0	161.2	96.8	2.1	19.1
F	25.6	29.5	3	6	56.4	16.6	10.7	138.8	83.3	2.0	15.5
F	26.1	30.2	3	8e	84.9	12.1	8.1	150.2	93.4	2.2	20.3
F	24.0	29.7	4	6	53.8	9.2	7.8	145.1	87.0	2.2	21.7
F	26.1	30.4	4	5	52.9	9.2	7.2	174.7	104.8	2.5	28.8
F	23.5	29.8	9	5	110.0	16.1	10.1	156.2	93.7	2.4	16.0
F	23.2	29.5	9	5	115.9	14.1	11.1	146.4	87.9	2.3	16.3
M	26.7	30.3	9	7	—	11.6	8.7	121.7	73.0	1.7	21.6
F	23.0	28.4	9	—	—	14.6	10.7	158.7	95.2	2.5	22.9
F	24.4	30.1	9	6	106.1	15.5	10.4	147.0	88.2	2.2	22.6
F	22.0	28.6	9	3r	64.7	18.6	12.9	145.2	87.1	2.4	18.3
F	23.0	28.4	9	7e	162.9	18.6	12.9	122.5	73.5	2.0	16.1
F	25.0	29.7	9	7e	146.8	10.3	6.3	161.6	96.9	2.4	24.1
M	24.7	30.4	10	8e	187.0	9.6	8.3	114.0	68.4	1.7	20.8
F	21.8	28.6	10	5	115.0	16.3	12.7	122.0	73.2	2.0	17.9
F	21.3	30.3	12	4	76.0	9.7	8.5	116.7	70.0	2.0	24.1
F	22.6	30.1	12	5	103.1	11.3	8.7	146.6	88.0	2.4	23.0
M	24.1	29.6	13	4	—	12.7	9.5	177.8	106.7	2.7	17.7

^ae = enlarged broods; r = reduced broods.

weather and territory topography. For other individuals, activity was sampled throughout the day in 20-min blocks, to obtain 3 h of recorded observations. In total 78.4 hours of observations were analyzed. To determine whether birds cared for their young normally after being held captive for 1 h, I compared the pattern of nest visitation of injected and recaptured birds with that of undisturbed birds in the same area.

Nestlings of the injected parents were weighed during the day of measurement. A few nests were not accessible for this purpose, even though the chicks could be seen and counted. In others, the number of chicks could not be determined exactly due to their location in inaccessible crevices. Some nestlings of the same age (day 0 being that on which the majority of the clutch hatched) were added or removed for experimental purposes at the time of the initial capture of the parent. I obtained daily mean, maximum and minimum temperatures (°C), precipitation (mm), and mean wind speed (m/s) during the day of measurement from the Meteorological Station of Ottenby, 40 km south of the study area.

RESULTS

CO₂ production, FMR values, and water turnover rates (Table 1) did not statistically differ for all individuals among the breeding seasons of 1985, 1986, and 1987 (Kruskal-Wallis test). Wheatears caring for nestlings produced CO₂ at 145.1 ± 18.6 ml/h and metabolized energy at 87.4 ± 11.3 kJ/day (Table 1). Water turnover

averaged 20.4 ± 3.5 ml/day. The average MI was 2.2 ± 0.3 . Males had slightly lower FMR than females (82.71 ± 20.90 vs. 87.40 ± 11.34 kJ/day). The mean FMR for brooding females was only 1% lower than the value predicted for birds that are not specialized for foraging in flight (Walsberg 1983) and 4.7% lower than that predicted by Bryant et al. (1985). Similarly, the mean FMR of late nestling females was only 2.2% lower than predicted (Walsberg 1983), and 4.3% lower than Bryant et al.'s (1985) prediction. The mean FMR was 10% lower than the value (97.2 kJ) predicted from the allometric equation for passerines derived by Nagy (1987) from DLW measurements.

I distinguished two periods with respect to the age of the nestlings: brooding (1–4 days after hatching of the majority of the brood) and late nestling (9–13 days after hatching). During brooding (Moreno 1987a), chicks increased rapidly in mass (Moreno 1987b). During late nestling, chicks were not brooded, their growth rate slowed markedly (Moreno 1987b), and feeding rates reached a plateau (Moreno 1987a). Brooding females had FMRs comparable to those females caring for late nestlings (Table 2). This was surprising as brood mass, feeding rates, and proportions of active time spent in flight were only half that among the brooders (Table 2). The lack of differences in FMR values between

TABLE 2. Field metabolic rate (FMR), metabolic intensity (MI), brood mass, feeding rate, and percentage of active time spent flying for brooding females, and males and females during the late nestling period ($\bar{x} \pm SD$). Sample sizes are in parentheses. Probabilities associated with Mann-Whitney *U*-tests are presented between groups tested.

	Brooding females	<i>P</i>	Late nestling period		
			Females	<i>P</i>	Males
FMR (kJ/day)	93.1 ± 7.5 (6)	0.329	85.4 ± 9.7 (10)	0.499	82.7 ± 20.9 (3)
MI (×BMR)	2.2 ± 0.2 (6)	0.448	2.3 ± 0.2 (10)	0.398	2.0 ± 0.6 (3)
Brood mass (g)	51.2 ± 20.8 (6)	0.002	108.9 ± 29.7 (10)		
Feedings/h	6.1 ± 1.6 (5)	0.003	14.4 ± 2.3 (8)		
% of active time in flight	5.2 ± 1.5 (5)	0.003	10.6 ± 2.0 (8)		

categories of females cannot be due to lower temperatures or more severe weather in general, as there was no significant difference between periods in any climatic variable (Mann-Whitney *U*-tests, $P > 0.05$). The similarity in FMR was not a result of larger average body mass of brooding females, as there were no differences in metabolic intensity (MI) between periods (Table 2). MI scaled to mass as BMR, and thus corrects for the differences in metabolism due to differences in mass. Males and females had similar metabolic rates during the late nestling period (Table 2), although the sample of males was small.

Nestling feeding rates of brooding females and late nestling males and females (Table 2) did not differ from the feeding rates of uninjected birds in the study area (Mann-Whitney *U*-test: $P > 0.10$, $n = 15$ for brooding; $P > 0.10$, $n = 23$ for late nestling). There was no apparent effect of injection and handling of the birds. Brood manipulations had no effect on FMR, feeding rates, time budgets, or size-corrected masses (Kruskal-Wallis tests for all data and for the late-nestling period comparing enlarged, unmanipulated and reduced broods, $P > 0.10$). On June 19, 1986, 2 young of the same age were transferred from a brood of 5 to another in the neighboring territory after labeling both females. Both females fed their nestlings throughout the next day, although I had an accurate time budget for only one due to visibility problems in the other territory. The female that fed the enlarged brood had the lower FMR; in fact, one of the lowest recorded for late nestling females. The feeding rate was normal, and all the chicks increased in mass that day. As brood manipulations had no apparent effects on parental behavior or metabolism, data for manipulated and unmanipulated broods were pooled in further analyses.

Brood size had no significant effect on FMR

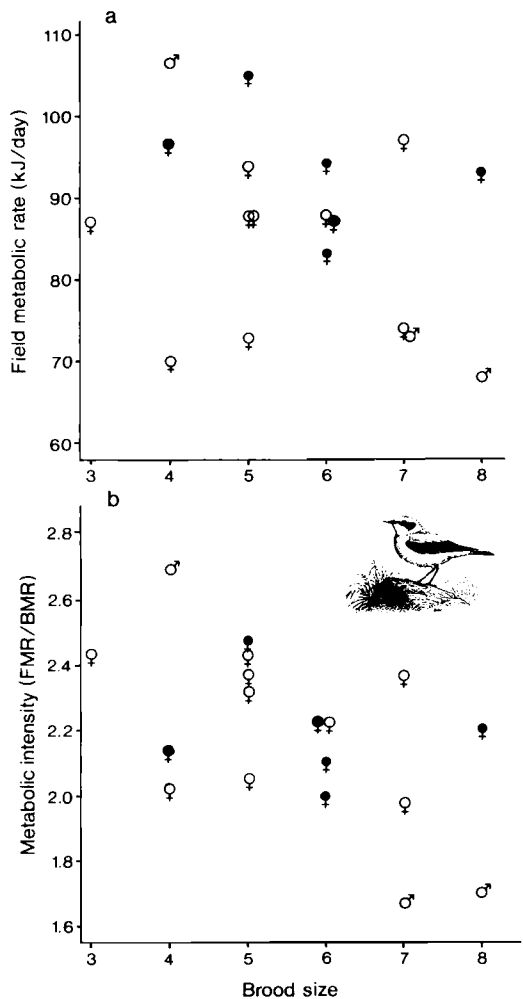


Fig. 1. (a) Field metabolic rates of parent Northern Wheatears (*Oenanthe oenanthe*) in relation to size of brood being fed and (b) metabolic intensities (expressed as multiples of BMR) of parent Northern Wheatears in relation to brood size. Filled symbols denote brooding; open symbols, late nestling.

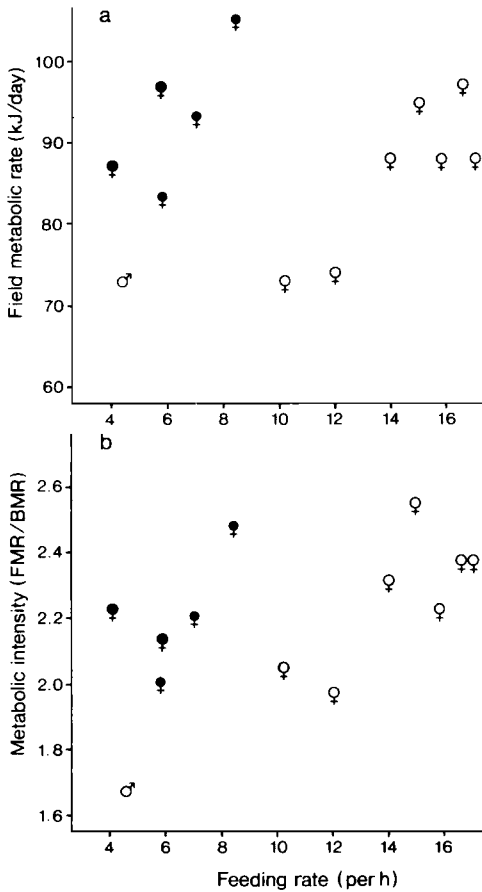


Fig. 2. (a) Field metabolic rates of parent Northern Wheatears (*Oenanthe oenanthe*) in relation to hourly rate of food deliveries, and (b) metabolic intensities of parent Northern Wheatears in relation to hourly rate of food deliveries. Symbols as in Fig. 1.

(Fig. 1), but correlated negatively with MI for all adult individuals ($r_s = -0.52$, $P = 0.028$, $n = 18$) and for late nestling measurements ($r_s = -0.64$, $P = 0.025$, $n = 12$; see Fig. 1). The trends in MI were explained by the positive correlations of brood size and brood mass with size-corrected body mass (mass/tarsus length) of late nestling parents ($r_s = 0.65$, $P = 0.016$, $n = 13$ for brood size, $r_s = 0.64$, $P = 0.035$, $n = 11$ for brood mass). Parents that fed large broods were relatively heavier for their size, which leads to higher estimates of BMR and lower estimates of MI.

Feeding rate correlated positively with FMR and MI for late nestling parents ($r_s = 0.83$, $P = 0.010$ and $r_s = 0.78$, $P = 0.021$ [respectively], $n = 8$), but not for brooding females (Fig. 2). No

component of the time budget was correlated significantly with FMR or MI in any period. The proportion of time spent in flight was not significantly correlated with feeding rate. Mean, maximum and minimum temperatures were correlated negatively with MI for brooding females ($r_s = -0.93$, $P = 0.008$, $r_s = -0.83$, $P = 0.042$ and $r_s = -0.83$, $P = 0.042$ [respectively], $n = 6$). Relative humidity and precipitation correlated negatively with FMR for the late nestling period ($r_s = -0.62$, $P = 0.024$, $n = 13$ and $r_s = -0.64$, $P = 0.019$, $n = 13$ [respectively]).

I analyzed blood samples from 4 chicks. All were 11–12 days old, weighed 22.8 ± 1.4 g (97% of adult mass at this stage of breeding) and increased only 0.5 g during 24 h. They produced CO_2 at 86.45 ± 7.17 ml/h and metabolized 51.8 ± 4.3 kJ/day, 60% of the adult rate. Their daily energy expenditure corresponded to a MI of 1.4 according to the BMR obtained for adults in laboratory trials (Moreno MS) or 1.7 according to the prediction from Aschoff and Pohl's (1970) allometric equation for the resting period. Water flux was 11.13 ml/day, only 55% of adult water turnover.

DISCUSSION

Wheatear parents feeding nestlings had 10% lower field metabolic rates than expected from their body size (Nagy 1987). They also had relatively low MIs when compared to other passerines (Utter 1971). Extrapolations from time budgets suggest values around $2 \times \text{BMR}$ in species much less dependent on flight than the wheatear (Mugaas and King 1981, Biedenweg 1983, Finch 1984). The reasons for the relatively low energy expenditures in the wheatear are not clear. Using the 20% lower BMR value predicted by Aschoff and Pohl's (1970) allometric equation for passerines at rest, instead of the measured value, the average MI value would increase to 2.7. This is well below the maximum sustained working level predicted by Drent and Daan (1980). There is clearly a great deal of variation in levels of energy expenditure, even within the order of passerine birds. Species that fly extensively, like hirundines (Bryant et al. 1984, Westerterp and Bryant 1984), have high MIs relative to ground-foraging Savannah Sparrows (Williams and Nagy 1985, Williams 1987), mockingbirds (Utter 1971), and perch-hunting wheatears. In this small sample of species I found no relationship between MI and flight time.

Wheatears spend a large proportion of their active time in flight (10% during the late nestling period) as do starlings which have a higher MI (Ricklefs and Williams 1984, Westerterp and Drent 1985).

Parents have to satisfy the energy needs of the young as well as their own. If we assume an energy content in nestling tissue of 6.3 kJ/g wet mass (Ricklefs 1974), and that nestlings older than 10 days only increase daily in body mass by 0.5 g I measured, then a single nestling of that age each day metabolizes 52 kJ and invests 3 kJ into production of body tissue, for a total of 55 kJ. Six nestlings of that age would require 330 kJ of metabolizable energy each day from their parents. If parents share equally in feeding the brood, each adult would have to gather about 3 times as much food each day as needed for self-maintenance ($[165 + 87]/87$). This value is an underestimate because parents would expend less energy when only caring for themselves. Still, this value was higher than the 1.75 estimated for House Finches (*Carpodacus mexicanus*; Gettinger et al. 1985) or 1.75 – 1.87 calculated for Savannah Sparrows (Williams 1987).

The lack of differences in FMR between brooding and late nestling parents was unexpected. Brooding by both parents in seabirds is much less costly than rearing endothermic chicks (Adams et al. 1987, Obst et al. 1987). In starlings, where comparatively low metabolic rates were measured in brooding females (Ricklefs and Williams 1984), males contributed to the warming of eggs and chicks during absences by females (Ricklefs and Hussell 1984). In the Savannah Sparrow, on the other hand, the female alone incubated and brooded (Williams 1987), as was the case in wheatears. The FMR for incubating and brooding female Savannah Sparrows (Williams 1987) were not significantly different from those of females tending nestlings older than 4 days, in spite of the increase in feeding rates with nestling age. Because brooding female wheatears were much less active, flew less, and fed the chicks less often than female wheatears in the late nestling phase, the similarity in energy expenditure between these 2 periods may depend on the costs of brooding the chicks in the nest. Also, the negative correlation between ambient temperature and MI for brooding females could indicate increased brooding costs with lower temperatures, although a larger data sample is necessary to confirm this suggestion.

Brooding represents a period of conflict for

single-parent brooders. They must compromise between the heat and food requirements of the chicks and their own food requirements (Moreno 1987a). Brooding in these species is accompanied by marked mass losses (von Haartman 1954, Winkel and Winkel 1976, Freed 1981, Norberg 1981). Ricklefs and Hussell (1984) suggested that the brooding period may imply use of body reserves by singly brooding females due to restrictions in time available for foraging. The relatively high energy requirements I found in wheatears would explain why females cannot maintain their energy balance and lose 14% of prehatching mass during this time (Moreno in press) in spite of the active feeding role taken by males (Moreno 1987a).

Previous studies of birds feeding nestlings have shown weak increases in parental energy expenditures with brood size (Williams 1987) or brood mass (Hails and Bryant 1979). In other cases no clear trends were observed (Bryant and Westerterp 1983a, Ricklefs and Williams 1984, Williams and Nagy 1985). I observed no significant trend in FMR. Feeding rates were positively correlated with FMR during late nestling. However, feeding rate was not related significantly to brood size in wheatears, but this does not imply that chicks in large broods were undernourished (Moreno 1987b). Due to the larger body mass for their size of parents with larger broods, there was a negative trend in MI with late nestling brood size and brood mass. Large brood size apparently had no negative effect on parental condition. Because feeding rates had such a clear effect, the lack of any effect of flight time on FMR was surprising and contrasted with other findings (Westerterp and Drent 1985, Masman and Klaassen 1987). This may be explained by the small variation in flight time observed in the 8 individuals (8.2–13.6% of daylight hours). Humidity and rain presumably reduced metabolism, and the 2 measurements during days with rain yielded the two lowest FMR values (68.4 and 70 kJ). A similar effect was shown among hirundines (Bryant and Westerterp 1983b). Prey availability may be reduced during humid days (Kneis and Lauch 1983), while rain impedes or even prevents wheatear foraging completely (Tye 1980, personal observation).

There is a great deal of unexplained individual variation in FMR (Ricklefs and Williams 1984, Williams 1987). In spite of this variation, I contend that parents with large broods are capable of caring for them at an energetic cost

equivalent to that incurred by parents with small broods. Perhaps because of better foraging abilities or better territories, these birds remain in better condition throughout the nestling period. I concur with the suggestion of Högstedt (1980) and Drent and Daan (1980) that clutch size in the wheatear is adjusted to the favorability of the territory or the phenotypical quality of the parents.

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