THE EFFECT OF SUPPLEMENTAL FOOD ON TIME BUDGET AND BODY CONDITION IN THE BLACK REDSTART *PHOENICURUS OCHRUROS*

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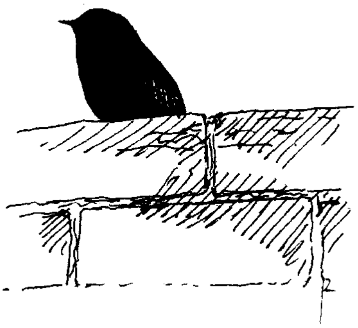

We studied the effect of supplementary food on time allocation, breeding success and parental body condition in Black Redstarts *Phoenicurus ochruros* in the Alps, NW. Italy. Time budgets of both ♂♂ and ♀♀ were significantly affected: individuals provided with supplementary food spent less time foraging and more time preening and vigilant. In accordance with predictions on the difference between sexes in parental investment, ♂♂ increased the time spent singing by 5 to 26% and reduced the number of feeds to nestlings from 5.4 to 2.0 h^{-1}. Females showed a higher rate of nestling feeding wich offset reduced provisioning of nestlings by the ♂♂. The breeding success of control and supplemented pairs was similar. The mass of adults was monitored using electronic balances placed near the nest cavity. Control pairs decreased in mass while adults given supplementary food showed an increase. The difference between control and fed adults was greater in ♂♂ than ♀♀. The hypothesis of an adaptive reduction in mass by all individuals due to programmed anorexia is not supported. We discuss the alternative hypothesis of a cost of reproduction utilizing estimates of energy expenditure from time budgets.

Key words: *Phoenicurus ochruros* - breeding energetics - mass loss - mating system - reproductive stress

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INTRODUCTION

Mating systems are thought to be the outcome of potentially conflicting interests of the sexes (Davies 1991). In birds occasional polygyny has been observed in 39% of 122 well-studied biparental European passerines which are normally monogamous (Møller 1986). In these altricial species, relative parental investment may be influenced by the availability and distribution of breeding resources such as nest sites or food (Emlen & Oring 1977, Gwynne 1990). When food is abundant, the relative value of male parental care to offspring survival decreases, and ♂♂ should invest relatively less in parental care if ♀♀ are able to feed the young (Orians 1969). Defecting ♂♂ might benefit by remating and initiating a second breeding attempt shortly after desertion or by having free time for extra-pair copulations. Thus food availability may influence competition for mates as the number of available ♂♂ increases and the operational sex ratio becomes skewed towards ♂♂.

Experimental food provisioning represents a simple way to assess the effect of food abundance on altricial birds. Previous studies have focused on life-history, physiological and behavioural consequences. The effects of (natural or experimental) food variation on life-history traits like survival, date of laying, number of breeding attempts and breeding success have recently been considered (Simons & Martin 1990, Nilsson 1991, Richner 1992) and reviewed (Boutin 1990). The physiological changes after food provisioning deal mainly with body mass variation in nestlings and parents. In adults there is typically a decrease in mass during reproduction which is usually seen as an indication of reproductive stress (Bryant 1979, Drent & Daan 1980, Cucco & Malacarne 1995a), although an hypothesis of programmed anorexia also has been proposed (Freed 1981, Norberg 1981) and this explains the observed mass variation in some species (Merkle & Barclay 1996). ♂♂ and ♀♀ can differ in the extent of mass variation, with food-provisioning experiments showing a greater effect on ♀♀ (Moreno 1989b, Garcia *et al.* 1993).

Behavioural studies relying on food variation also indicate male-female differences. In accordance with Orians' (1969) prediction, abundant resources cause ♀♀ to increase feeding frequency while the ♂♂ reduce or abandon paternal care (Ewald & Rohwer 1982, Davies & Lundberg 1984, Hochachka & Boag 1987, Arcese & Smith 1988, Simons & Martin 1990, Whittingham & Robertson 1994).

In this study we performed a food supplementation experiment on the Black Redstart *Phoenicurus ochruros*, a small dimorphic passerine that is reported to be monogamous, with rare instances of bigamy (Cramp 1988). The aim of the study was (1) to test Orians' prediction that ♂♂ reduce investment when food is abundant; (2) to evaluate the consequence of reproductive effort on body mass of breeding adults. We compared the adaptive anorexia hypothesis, which predicts an adaptive decrease in mass in both control and food-supplemented parents during reproduction, and the cost of reproduction hypothesis, according to which the experimental parents would lose less mass than controls.

METHODS

The research was conducted in the Alps (Susa Valley, NW. Italy) during the breeding season (June and July) in 1993 and 1994. Our study area contains two mountain villages (Sauze d'Oulx at 1500 m above sea level and Grand Villard at 1550 m a.s.l.) where Black Redstarts established their territories (Cucco & Malacarne 1995b). The nests were built in cavities in the external walls of buildings. Nests were reached using a ladder for inspection and ringing operations.

After their arrival from the wintering quarters, adult birds were captured by mist-nets or spring traps baited with a single mealworm, and individually colour-ringed. In this study we did not consider subadult ♂♂ entering their second year of life, which are clearly distinguishable from adult ♂♂, the former having dull brown and the latter black plumage. Although subadults regularly breed, we considered only pairs with adult ♂♂ to avoid possible confounding effects on behavioural analyses due to lack of experience in subadults. We considered only broods of the commonest size (five young) to avoid confounding effects of brood-size on the reproductive effort of adults.

We placed electronic balances (accurate to 0.1 g) on the ground 5-15 m from the nest to allow repeated weighing of the breeding birds. Adults were induced to perch on the top of the balance by mealworm(s) placed on the plate. The birds visiting the balances usually remained on the plate long enough (> 2 s) for the measured mass value to stabilize. Only in a few cases could no mass be obtained due to the bird's movements or wind. Mass values were automatically read and stored by portable computers connected via the RS232 serial interface. The identity of perched adults was ascertained from their colour-ring combination observed at a distance (about 30-40 m, with 10× binoculars). We did not measure the growth of nestlings because chick handling causes precocious fledging or falling of birds from the nest.

The behaviour of parents was described by analysis of their time budget during two hours of observations each morning. Fed birds were watched for two hours during the four-hour period of experimental manipulation (see below). Time of observation did not differ between experimental and control nests (t_{15} = 0.06, P = 0.95). Times spent in different behaviours were assigned to six categories: (1) flight, the parent flies (more than 3 s), approaching the nest cavity with the prey in its beak, moving away after nestling feeding or moving between song posts; (2) foraging, the parent walks, inspecting the ground in search of food; some jumps or flights of a few meters can briefly (< 3 s) interrupt the terrestrial locomotion; (3) preening, the perching parent preens its plumage; (4) vigilance, from a prominent point the perching parent looks around without singing; (5) singing, always performed while perched on a pre-eminent point, only by ♂♂; and (6) absence, the parent moved far from the visual field of the observer. In most cases, when a second researcher was able to follow the bird, it was typically seen foraging, with little preening or vigilance and no singing. No other behaviours were recorded so that the six categories made up 100% of the time budget.

In the statistical analysis, for each individual we averaged the times it was observed in the various activities on different days, thus obtaining a single value for each parent. Percentages were arcsine transformed before *t*-test application. Where multiple comparisons were made, i.e. in the case of the six behavioural categories which are not independent of one another, the significance level was corrected according to the Bonferroni method, thus $P < 0.008$ (= 0.05/6) was used to reject the null-hypothesis.

Experimental manipulation

In order to detect the effect of food abundance on the behaviour and body condition (mass) of parents we considered two adult categories: adults with food supplementation and a control group. For eight pairs with food supplementation, each morning during the chick-rearing period (14 days) we placed Wax Moth caterpillars *Galleria mellonella* in a large quantity (100 individuals) on the balance platform. Caterpillars had an average mass of 0.3 g and parents were allowed to capture them freely for four hours each day. Usually the parents flew to the nest with two or three caterpillars in the beak. Occasionally they took only one caterpillar and very rarely more than four (maximum six). Like control birds, experimental parents were weighed at their first landing on the balance plate. In the control group (nine pairs), each morning we started by placing one caterpillar on the balance platform in order to attract and weigh the first of the two parents. After the capture of the caterpillar, another one was set in place only when the second parent was seen to approach the nest (typically less than a minute was required for the adults to detect the caterpillar). No other caterpillars were given to control pairs.

Energy calculations

To calculate the allocation of resources in the parents, we needed an estimate of the energy spent per hour in each behaviour. We used the equation in Aschoff & Pohl (1970) to estimate the basal metabolic rate (1 *BMR*) of parents. In order to account for the variation of mass during the rearing period, we considered different *BMR* values for each sex, treatment (control/supplemented) and day (1 to 14). The initial *BMR* of ♂♂ was 1.024 kJ h^{-1} (mean mass = 16.7 g) and of ♀♀ 1.011 kJ h^{-1} (16.4 g). In the subsequent days the mass values utilized in the Aschoff & Pohl equation were modified according to the observed variation, as reported in the results section. Following Goldstein (1988) we estimated active flight at 11 *BMR*, terrestrial locomotion (foraging) at 5 *BMR* and active perching (preening/vigilance activities) at 2 *BMR*. The singing requirement was estimated at 5 *BMR* (Eberhardt 1994). The periods of absence were assigned a value of 5 *BMR* since inspecting was the main activity in these periods (see above). A sensitivity analysis found that increasing or decreasing the Goldstein (1988) and Eberhardt (1994) coefficients by 50% resulted in changes to our total energy estimates from +31% to -16%. At night the parents were considered to be resting, with an estimated 1 *BMR* energy requirement. Martins & Wright (1993) fully discuss some sources of bias when estimating energy costs, such as differences in adult body mass, assimilation of insects, and metabolic conversion of food or fat into energy. The energy value of caterpillars was estimated at 8.54 kJ g^{-1} (McCance & Widdowson 1991) and assimilation efficiency at 65% (Kacelnik 1984), thus pairs supplied with 100 caterpillars saved 167 kJ day^{-1} and a total of 2338 kJ in the 14 days of the experiment.

RESULTS

Time budget

The time budget of supplemented pairs was considerably different from control pairs. Experimentally fed ♂♂ (Fig. 1A) spent less time flying (t_{15} = 5.6, $P < 0.001$) and inspecting around the nest foraging (t_{15} = 20.9, $P < 0.001$). Instead, the fed ♂♂ spent more time singing near the nest, in preening and vigilant activities, and were out-of-sight more frequently (t_{15} = -23.9, -5.0, -8.6, -5.4 respectively; all $P < 0.001$). Of the eight fed ♂♂, two deserted (two and four days before the young fledged), while the others remained with the ♀♀. During all the time-budget sessions and supplementary inspections in the study area we did not detect remating nor did we find any cases of bigamy in our control or experimental ♂♂ (indeed there was only one case of bigamy in another 22 territories not subjected to mass and time budget checks).

Manipulated ♀♀ (Fig. 1B) increased the time spent flying (t_{15} = 3.9, P = 0.001. Bonferroni corrected P values for acceptance < 0.01) and vigilant (t_{15} = 7.6, $P < 0.001$), while they reduced their foraging activity (t_{15} = -4.8, $P < 0.001$). There was no difference between supplemented and control ♀♀ in the time spent preening (t_{15} = 0.59, P = 0.54).

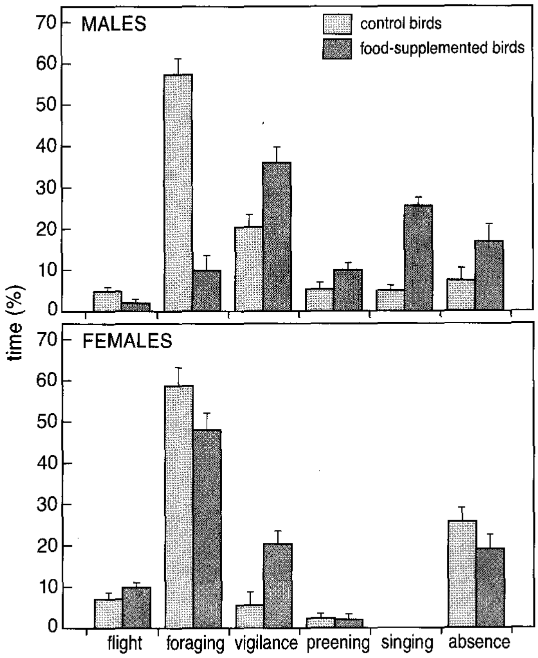

Fig. 1. Time budget during the nestling rearing period in male and female Black Redstarts (mean + SD).

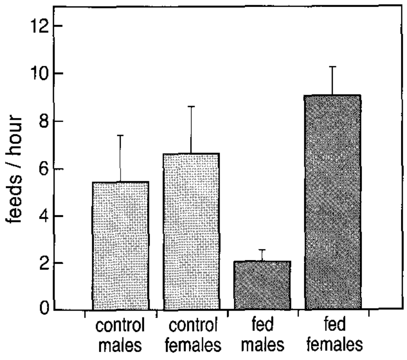

Fig. 2. Contribution of ♂♂ and ♀♀ to nestling feeding (mean number of feeds h-1 + SD).

Feeding of nestlings and breeding success

The ♂♂ fed the nestlings slightly but not significantly less frequently than the ♀♀ in control pairs (t_{16} = 1.24, P = 0.205). The difference between sexes was increased (t_{14} = 15.0, $P < 0.001$) by food supplementation (Fig. 2). The provisioned ♀♀ delivered significantly more food to the nestlings than control ♀♀ (t_{15} = 2.96, P = 0.029), while the reverse was found in ♂♂ (t_{15} = -4.43, P = 0.003). The decreased provisioning by

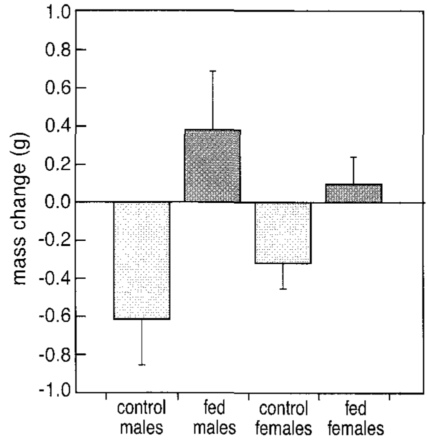

Fig. 3. Mass change of male and female Black Redstarts in the nestling rearing period (mean + SD).

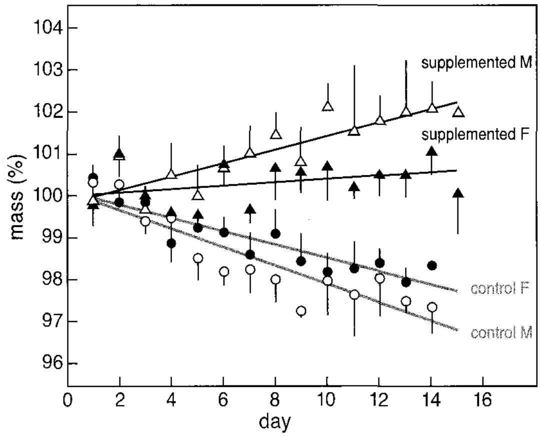

Fig. 4. Mass variation pattern (mean ± SE) for supplemented and control Black Redstarts. The mass of each individual was standardized to a value of 100% in the first day of the nestling rearing period.

♂♂ was compensated by the increased effort of ♀♀, thus the total number of feedings provided to nestlings by each pair was similar in control and experimental nests ($t_{15} = 0.633$, $P = 0.54$). Fledging success of control (4.0 ± 1.32) and fed pairs (4.25 ± 0.71 young per nest) was not significantly different ($t_{15} = 0.45$, $P = 0.63$).

Body condition and energy budget

Food supplementation influenced the variation in mass of adults during the nestling rearing period (Fig. 3). There was a significant difference between experimentally fed and control individuals both in ♀♀ ($t_{15} = 5.71$, $P < 0.001$) and ♂♂ ($t_{15} = 6.9$, $P < 0.001$). The ♂♂ were more affected by the availability of extra food, and the mean gain of experimental subjects with respect to control individuals (+0.38 g *versus* -0.61 g; total 0.99 g) represented 5.9% of a 16.7 g adult, while in the ♀♀ the gain (+0.10 g compared to -0.31 g; total 0.41 g) was 2.5 percent.

The mass variation in the 14 days of rearing was gradual (Fig. 4). In a subset of experimental and control individuals (four ♂♂ and four ♀♀) that were monitored daily, a linear regression significantly represents the variation in mass with time in control ♂♂ ($r_{14} = 0.89$, $P < 0.01$), control ♀♀ ($r_{14} = 0.90$, $P < 0.01$) and supplemented ♂♂ ($r_{15} = 0.87$, $P < 0.01$). In supplemented ♀♀ there was no significant trend ($r_{15} = 0.38$, $P = 0.11$, N.S.).

Estimates of energy expenditure

An estimate of the energy expenditure from the time budgets (Fig. 1) in control and experimental individuals is provided in Table 1. We did not regularly collect behavioural data outside of the four hours of food supplementation. Even if sporadic observations indicate that the time budget outside of the feeding sessions was similar in experimental and control pairs, we calculated the energy requirement of supplemented birds under two extreme hypotheses. The first hypothesis (hypothesis 1) emphasizes the differences observed in the four hours of food supplementation by assuming that the time budget of the experimental parents remained unchanged in the following hours. The second one (hypothesis 2) reduces the difference between fed and control birds by assuming that at the end of each experimental session the parents utilized the time budget of control pairs. On the whole, the provisioned individuals spent less time in energetically costly activities and, even if they weighed more, their calcu-

Table 1. Total energy requirements (KJ) over the 14 day nestling rearing period, estimated from time budgets of control and food-supplemented Black Redstarts. Hypotheses 1 and 2 represent two extreme scenarios for supplemented birds, as reported in the text. The energy requirements of different activities were estimated as multiples of *BMR* as reported in 'Methods'. The total requirement was calculated for the fourteen days during which there were young in the nest and when food was supplemented. The amount of metabolizable energy obtainable from 1 g of fat is 37.7 kJ according to Blem (1990).

Behaviour	♀♀			♂♂		
	Control	Supplemented		Control	Supplemented	
		hypoth. 1	hypoth. 2		hypoth. 1	hypoth. 2
Flight	162.3	228.9	180.5	112.8	51.7	98.3
Foraging	621.8	511.3	594.1	608.3	106.6	484.3
Vigilance	23.9	86.8	40.7	87.0	155.4	106.6
Preening	10.5	9.2	10.2	21.9	42.6	27.8
Singing	-	-	-	51.3	276.5	112.1
Absence	272.3	202.8	254.5	77.8	182.5	107.0
Rest	126.5	126.9	127.0	127.3	130.1	130.1
Total	1217.3	1165.9	1207.0	1086.4	945.4	1066.2
Difference Supplemented-Control		51.4	10.3		141.0	20.2
Observed mean mass difference		0.41 g			0.99 g	
body fat equivalent to		15.5 kJ			37.3 kJ	

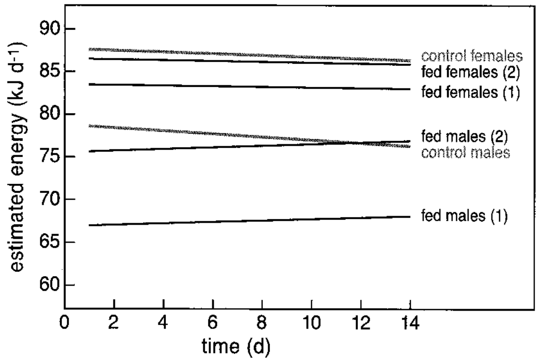

Fig. 5. Estimated energy expenditure for Black Redstart parents in the 14 days of nestling rearing. The negative slopes indicate a decrease of estimated energy expenditure due to body mass decrease during reproduction, while the reverse is indicated by positive slopes. Hypotheses 1 and 2 represent two extreme scenarios for supplemented birds, as reported in the text.

lated energy expenditure was lower than that of controls (Table 1). During the 14 days of nestling rearing there was a reduction in the estimated energy consumption of both ♀♀ (ranging from 51.4 kJ under hypothesis 1 to 10.3 kJ under hypothesis 2) and ♂♂ (range from 141.0 kJ to 20.2). The ranges of values obtained encompass the energy equivalents of the measured body mass differences (15.5 kJ in ♀♀ and 37.3 kJ in ♂♂; Table 1).

Figure 5 allows a comparison of the two contrasting effects of food supplementation, i.e. (1) the mass variation of parents in the rearing period implies a related variation of energy expenditure, revealed by the different slopes of the lines; the fed birds had higher mass day after day than controls; (2) a difference between control and fed parents related to the different time budgets (fed birds performed less expensive activities). The variation of parental mass during reproduction represented a difference ranging from -0.3 and -0.7% (fed and control ♀♀) to +0.8 and -1.3% (fed and control ♂♂) of the initial energy expenditure. The effect related to the different time budgets of experimental and control individuals was more marked (two to ten-fold). According to hypothesis 1 fed ♀♀ saved 4.2% of energy and ♂♂ 13.0%; according to hypothesis 2 the former saved 0.8% and the latter 1.9%.

The magnitude of extra energy provided by food supplementation (2338 kJ) was two orders greater than the saved energy. Indeed the supplementary food was almost completely delivered to the nestlings and we very rarely observed a parent swallowing it. Usually parents, after collecting some caterpillars from the balance platform, flew straight to the nest to feed the nestlings.

DISCUSSION

Time budget and mating system

In this study the provision of food during the rearing period changed the time budget of both male and female parents. In agreement with Orians'(1969) prediction, ♂♂ considerably decreased their parental effort, while ♀♀ compensated for this by increasing chick feeding. Males with extra food did not change their territory, but had more spare time in which to rest or sing to attract other ♀♀. However, we did not detect successful remating of deserting ♂♂, nor extra-pair copulations. In the Dunnock *Prunella modularis*, similar results were observed in ♂♂ (Davies & Lundberg 1984), but there the availability of feeders reduced the territories of ♀♀, leading to a change in the mating system (from polyandry to polygynandry) and to an increase of male mating success. Among the few other studies evaluating the influence of food on parental roles, the involvement of ♂♂ in nestling feeding decreased in the Red-winged Blackbird *Agelaius phoeniceus* (Whittingham & Robertson 1994), while there was a reduction in feeding rate or desertion by both sexes in the Snail Kite *Rostrhamus sociabilis* (Beissinger & Snyder 1987) and in the Penduline Tit *Remiz pendulinus* (Persson & Öhrström 1989). Why ♂♂ are more prone than ♀♀ to abandon offspring is debated (Krebs & Davies 1991). However, it is likely that ♂♂ have more to gain from desertion since they can potentially fertilize eggs at a faster rate and with a lower energy cost per offspring than a ♀ can lay them.

In our study area the potential for polygyny in the Black Redstart population was not utilized. Male songbirds readily desert to gain extra ♀♀ if given a chance, for example by removal of a neighbouring ♂ (Davies 1991), but strong competition among ♂♂ may make it difficult for a ♂ to gain a second ♀. Such strong male competition is likely to occur in our study area: the operational sex ratio of the population could be unbalanced since first-year ♂♂ with ♀-like plumage have been observed in high proportions and regularly breed (Cucco & Malacarne 1995b).

Reproductive success

The reproductive success of the Black Redstart was not affected by food provisioning. Since we did not weigh nestlings (to avoid precocious fledging), we are not able to assess whether body condition in supplemented broods was better (higher body mass) than in control broods. Even if it can be hypothesized that chick mass was not greatly affected by the experiment, given that the total number of feedings per nest (♀ + ♂) was very similar in supplemented and control broods, caution must be taken because the load and the number of prey carried in each trip could have been higher in the experimental pairs. The extra food was almost completely delivered to the nestlings and the energy provided by food supplementation (167 kJ day^{-1}) likely represented a significant percentage of the requirement of a brood of five (for the closely related, 22.8 g Northern Wheatear *Oenanthe oenanthe*, a consumption of 52 kJ day^{-1} per nestling was reported, Moreno 1989c).

Since our experimental procedure did not involve broods of different size, we cannot reject the possibility of an effect of supplementation on fledging success, particularly in large broods.

Food availability and breeding success covaried in studies of the House Martin *Delichon urbica* (Bryant 1979), Darwin's Finch *Geospiza fortis* (Price 1985), Capricorn Silvereye *Zosterops lateralis* (Catterall *et al.* 1982) and Red-winged Blackbird (Whittingham & Robertson 1994), and food supplementation increased breeding success in the European Starling *Sturnus vulgaris* (Crossner 1977), Magpie *Pica pica* (Hochachka & Boag 1987), Song Sparrow *Melospiza melodia* (Arcese & Smith 1988) and Cactus Wren *Campylorhynchus brunneicapillus* (Simons & Martin 1990).

In our study the ♀ contributed more than the ♂ to the reproductive success of the brood, both in natural and experimental conditions. Females of many passerine species can raise the brood in an extreme situation such as male removal (Gowaty 1983, Lyon *et al.* 1987, Dunn & Robertson 1992). Only when food is scarce can male removal cause the impairment of reproductive success (Greenlaw & Post 1985, Lyon *et al.* 1987, Wolf *et al.* 1990, Whittingham & Robertson 1994).

Body mass variation

Food provisioning allowed both parents to maintain a higher mass than controls. In ♂♂ the gain was probably related to the increased spare time and the lower engagement in energetically expensive activities such as flying or terrestrial locomotion. The gain in mass of provisioned ♀♀ was lower, probably because they increased the flights for nestling feeding and reduced to a lesser extent the inspecting activity. Estimates of energy expenditure from time-budget are likely to be reliable. Actually, the estimated values encompass the energy equivalents of the measured body mass differences (15.5 kJ in ♀♀ and 37.3 kJ in ♂♂).
Parental differences in mass changes during reproduction have been observed in other avian species. In passerines, ♀♀ generally gain mass prior to laying, maintain mass during incubation, and lose mass while rearing the young (Moreno 1989a). Contrary to our finding, food supplementation experiments revealed in both the Northern Wheatear and Mountain Bluebird *Sialia currucoides* that ♂♂ maintain constant body mass throughout the season (Moreno 1989b, Merkle & Barclay 1996). Also in captive Zebra Finches *Poephila guttata* with different feeding conditions ♀♀ showed a more marked mass variation than ♂♂ (Skagen 1988). However, the high variability in food-supplementation experiments should be mentioned. Researchers on the Mountain Bluebird, after obtaining remarkable differences concerning nestling growth and parental mass in experiments using two different schedules (Garcia *et al.* 1993, Merkle & Barclay 1996), stressed the importance to consider when supplementation commences. In Merkle & Barclay (1996) supplementation began on the first day of incubation, thus food appeared to be a predictable source during the reproductive cycle. In Garcia *et al.* (1993) and our study, supplementation did not begin until the nestling period, and probably the food appeared to be unpredictable, a situation in which passerines are known to add body mass (Ekman & Hake 1990, Hurly 1992).

Estimates of energy expenditure

Patterns of body mass change in breeding birds have frequently been viewed as evidence for the presence of reproductive stress (Moreno 1989a). Mass loss in particular has been used as an index of reproductive costs. However, mass changes could be adaptive (Freed 1981, Norberg 1981) or be an outcome of compromises among different selective factors (Moreno 1989a). Many experimental studies on mass change support the cost of reproduction hypothesis (Nur 1984, Dijkstra *et al.* 1990, Johnson *et al.* 1990, Martins & Wright 1993, Cucco & Malacarne 1995a), while others favour the adaptive hypothesis of the decreased cost of flight (Gaston & Jones 1989, Croll *et al.* 1991, Curlee & Beissinger 1995, Merkle & Barclay 1996). The cost of reproduction hypothesis predicts that supplemented birds will not lose mass or will lose less than control birds. According to the adaptive hypothesis, all birds would lose mass in a similar pattern because there is an optimal body mass for flight. The results of our study of the Black Redstart support the cost of reproduction hypothesis.

Nevertheless, we must be cautious before rejecting the adaptive hypothesis. In food-supply experiments the conditions of experimental and control birds is not exactly the same, because fed birds face a better situation than controls. A different version of the adaptive hypothesis would predict that only birds with less food would adaptively lose mass, while birds with food abundance would not benefit from losing weight since they fly less. Their optimal strategy might be to put on fat. In all adaptive versions, the energy saved by mass decrease should reach a significant value. For example, in the study of Norberg (1981), a 10% mass decrease was employed in the calculation of energy consumption. In our study on the Black Redstart the energy saved by control birds was low (maximal 1.3% in ♂♂) on account of their mass decrease, while the energy saved by experimental birds engaged in less expensive activities was two (hypothesis 2) to ten-fold (hypothesis 1) greater. Thus, in order to save the same amount of energy, the control birds should have lost a larger amount of mass than they actually did.

In conclusion, our results are more in line with the energetic stress hypothesis. Control and fed birds had different patterns of mass variation, thus there is not an absolute optimal mass for flight. Moreover, we calculated that the energy saved by the load reduction in control parents was much less than the energy saved by fed parents by behavioural changes of the time budget. The present predictions of energy consumption in birds exposed to different situations could be a good point of departure for a future validation utilizing direct measurements (e.g. by doubly labelled water) of energy consumption.

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SAMENVATTING

Het grootbrengen van een nest vol jongen is zwaar werk en bij zangvogels gaat dit proces vaak gepaard met gewichtsverlies van de ouders. Dit gewichtsverlies wordt vaak gezien als een indicatie voor de stress die de ouders doormaken: ze zouden onvoldoende voedsel voor zowel de jongen als zichzelf kunnen vergaren. De ouders investeren (tijdelijk) veel energie in hun nageslacht, ten koste van zichzelf. Een alternatieve verklaring voor het optreden van gewichtsverlies in de nestjongen-periode is, dat dit is voorgeprogrammeerd. Ten behoeve van het grootbrengen van de jongen moeten de ouders vele voedselvluchten uitvoeren en een (tijdelijk) lager gewicht is hiervoor gunstig omdat de vliegkosten dan lager zijn. Om uit te maken welke van deze twee hypothesen geldig is, is een experiment gedaan met Zwarte Roodstaarten *Phoenicurus ochruros*. Een aantal broedparen kreeg tijdens de jongenfase extra voedsel bij het nest aangeboden, terwijl een controle groep geen extra voedsel kreeg. Het gedrag van de oudervogels werd dagelijks onderzocht, het broedsucces bij beide groepen werd bepaald en het gewichtsverloop van de ouders werd gevolgd. Dit laatste werd gedaan door het aangeboden voedsel (100 rupsen per nest van vijf jongen per dag) te presenteren op een electronische weegschaal. Vogels uit de controlegroep werden gewogen door dagelijks één rups per ouder op een weegschaal aan te bieden. Zoals verwacht, namen de vogels uit de controle groep langzaam in gewicht af. De bijgevoerde vogels daarentegen, namen zelfs iets in gewicht toe, ook al werden de aangeboden rupsen vrijwel niet door de ouders gegeten, maar meest aan de nestjongen gevoerd. Door het extra voedselaanbod konden de ouders bezuinigen op - energetisch kostbaar - foerageergedrag. De gegevens van deze vogels zijn in overeenstemming met de hypothese dat stress tijdens het broedseizoen ertoe leidt, dat de oudervogels niet op gewicht kunnen blijven. Interessant is ook het verschil in gedrag tussen de sexen bij aanbod van extra voedsel. De ♂♂ gingen de jongen minder voeren en spendeerden meer tijd aan zingen en rondkijken, mogelijk in een poging om de kansen op het bevruchten van eieren bij een tweede ♀ te vergroten. De ♀♀ compenseerden het gedrag van hun partner en gingen meer voer naar het nest brengen, waardoor de jongen in controle nesten en nesten met extra voer uiteindelijk evenveel voedsel kregen. Het aantal uitgevlogen jongen per nest verschilde niet tussen controle en bijgevoerde nesten.

(MFL)

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