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Daily routines of body mass gain in birds: 2. An experiment with reduced food availability

VICENTE POLO & LUIS MIGUEL BAUTISTA

Department of Evolutionary Ecology, National Museum of Natural History, CSIC

Theoretical models predict that small birds should adjust daily patterns of body mass gain in response to environmental and internal factors. In a companion paper, we described a model on daily fattening that allows the analysis of precise changes in the shape of hourly patterns of body mass. In this study, we tested one of the main predictions of the model: the inflexion point of the body mass trajectory should be delayed in response to a decrease in food availability, increasing body mass as soon as possible when food is scarce. This effect might be stronger in subordinate than in dominant birds. We tested both predictions with four pairs of coal tits, *Periparus ater*, kept in cages where food was delivered at high and low rates. Daytime increase in body mass was 1 g in both treatments. As predicted by the model, the tits increased body mass as soon as possible when food was delivered at a low rate, and the inflexion point of the body mass trajectory was 16.7% delayed compared to the high food delivery rate. However, dominance rank had no significant effect on the shape of daily body mass increase. To our knowledge, this is the first precise estimate of the change in the shape of body mass trajectories. Our findings have important implications for the analysis of daily patterns of body mass and for the design of studies of body mass in small birds.

In small birds the rates of body mass gain during the day are frequently bimodal, with a first burst after dawn and a smaller second one before dusk (Bednekoff & Houston 1994; McNamara et al. 1994; Pravosudov & Grubb 1997). Thus, the shape of most daily fattening routines reflects a trade-off between different stressful factors and body mass. Food unpredictability and foraging interference may change this bimodal balance by fostering body mass gain in the first part of the day and decreasing or cancelling the second burst (McNamara et al. 1990; Lilliendahl et al. 1996; Cresswell 1998).

In our companion paper (Polo & Bautista 2006), we proposed a double exponential model to explore body mass changes during the daytime. In this study, we experimentally tested a theoretical fattening model, generated with a differential approach, to describe the daytime trajectory of body mass of pairs of coal tits, *Periparus ater*. We examined the changes in the inflexion point of the trajectories in relation to food availability and social status within pairs. In small forest Mediterranean species, such as the

coal tit, body mass gain is delayed to the end of the day when food is abundant (e.g. Polo & Carrascal 1997), and thus the shape of the trajectory is mainly accelerated and the point of inflexion appears early in the day. This basic trajectory could be modified and become decelerated when food is scarce (McNamara et al. 1990), or when social status is low in small bird species (see dynamic game by Clark & Ekman 1995). The inflexion point then appears late in the day. Therefore, we predicted an advance in the inflexion point when food availability was experimentally increased.

METHODS

Housing and Operant Schedules

We caught eight coal tits at 'El Ventorrillo' field station in December 1997. They were colour-ringed and housed in pairs in small cages (0.5 × 0.3 m and 0.4 m high). The four pairs of birds were kept in the same room, visually but not acoustically isolated. During the experiment the birds lived in a closed economy (Collier 1983), obtaining all their food through the experimental schedule. The light:dark cycle was 9:15 h, with lights on from 0915 hours to 1815 hours. The change from light to dark was gradual and lasted 15 min at the beginning and end of

the daily cycle. Fresh drinking water was always available in bottles at the base of the cage. For a 2-month period we trained the birds to obtain all their food through the food hopper in the experimental cages. During this period they had an ad libitum supply of food and water.

Each cage had an operant panel in the centre of the back wall with a coloured light, 2 cm on the right of a central food hopper. The coloured light was used as the discriminative stimulus signalling that a food reward was ready to be delivered on request. The food hopper had a pecking key attached and connected to a pellet dispenser (Campden Instruments, Loughborough, U.K.). The pellet dispenser was filled with dry kitten cookies ground and sieved to an even size. One unit of food averaged 0.041 g and took 1 s to deliver. An Acorn RiscPC-600 microcomputer running the Arachnid experimental control language (Fray 1990) controlled the stimulus events and response contingencies, and also recorded some of the data. To train the birds, we used an autoshaping procedure (Staddon 1983).

Between 0930 hours and 1800 hours (8.5 h of foraging) birds obtained pellets of food in sequential foraging trials. A trial began with the light flashing for 12 s. If the pecking key was pressed while the light was flashing, a pellet was delivered in the hopper (with a probability of 0.60 or 0.14, see below), and the program waited 30 s before a new trial was started. If the pecking key was not pressed while the light was flashing, the program deactivated the pecking key and the flashing light, and an interval of 30 s elapsed before the next trial started.

Each pair experienced two treatments, High and Low, which lasted 12 days each, but only the last 10 days were used in the analyses. We used a balanced design with half of the birds experiencing the High treatment first and the other half experiencing the Low treatment first. The probability of food delivery was programmed to be 0.60 or 0.14 (treatments High or Low). The food delivered in treatments High and Low could reach up to 29.3 g and 6.7 g, respectively, per session and pair of birds. These amounts were six and 1.5 times higher, respectively, than the mean daily intake measured for the four pairs of caged coal tits living with food ad libitum (4.6 ± 0.2 g/day; $N = 4$), and kept with the same light:dark cycle.

Data Collection and Analysis

We recorded samples of activity through a one-way window. For 10 min in each hour, we counted the hops of two birds, each from a different pair, and their visits to the drinking bottle and to the food hopper. These figures were extrapolated to calculate the food and water intake rates (number of visits to the food hopper and to the drinking bottle/h) and the hopping rate (hops/h). Overall, each bird was sampled twice an hour for each treatment (i.e. $N > 20$ for each bird and treatment).

To determine the dominance rank in each pair of birds, we counted the attacks per 10 min and the outcome of the attacks. Displacements from the feeder box and the identity of the loser were recorded as attacks because physical aggression was seldom observed. The size of the food

hopper allowed the birds to forage together, but most of the time ($>95\%$) it was used by one bird only.

Birds were weighed 10 times per day, the first time at 0930 hours, the second time at 1000 hours, and thereafter every hour until 1800 hours. To weigh a bird we caught it by hand and put it in a small plastic box. It took less than 9 min to weigh all the birds. Repeated trapping is likely to reduce any detrimental effect of trapping on body condition or survival (Gosler 2001). The birds resumed foraging immediately after the last bird was released into its cage. Although the coal tits might have been stressed by the weighing procedure, and thus we cannot discount some effect of disturbance on the shape of body mass trajectories, different levels of stress should not explain the changes in the body mass trajectory, because birds were weighed with the same protocol in all treatments.

To analyse the shape of the trajectories of body mass during the daytime, we used the double exponential model proposed in our companion paper (Polo & Bautista 2006). The hourly pattern of body weight in this model is described in terms of the additive combination of two exponential, accelerating and decelerating, functions. The inflexion point of the double exponential model characterizes precisely the changes in the shape of the trajectories. We used the delay or advance in the inflexion point of the fitted body mass trajectories (Polo & Bautista 2006) to characterize the change in the shape of daily body mass gain in relation to the food availability experiment.

Ethical Note

We chose coal tits for this experiment because they are the least aggressive species of the Paridae (Cramp & Perrins 1993). Although birds were housed in small cages, because of limited space in the laboratory, we did not observe detrimental effects of the rearing conditions on behaviour and body mass (the coefficients of variation of body mass for the 10 days used in the analysis were less than 1%). However, we were not happy with the size of these experimental cages and we recommend using larger ones if similar studies are repeated in the future. The food delivery rate in the Low treatment constituted a mild foraging stress. We monitored the birds when we recorded activity, and also on some occasions before we weighed them, to ensure that there was no severe competition or aggression during the experiment (i.e. when a subordinate bird could not get access to the feeder for a 10-min period if the dominant bird prevented it). Approximately 90% of agonistic interactions were displacements or short chases near the feeder. No severe acts of aggression were observed and subordinate birds could always escape from the dominants. Should it have been necessary, we were ready to remove any individual quickly with minimal disturbance, but this was never necessary.

Birds were used for a subsequent study, where they lived, in pairs, for 2.5 months in a large outdoor aviary at El Ventorrillo field station. The aviary was divided into large cages of 10.5 m³ (1.75×3 m and 2 m high), separated by a thick, green, plastic net, with pine branches and nesting cages, and ad libitum access to food, water

and vitamins. Once this study was finished, the individuals were not disturbed and spent an additional month in the aviary, but the cages were opened and they were allowed to use all the cages of the aviary. The birds were finally released to the wild after this period of acclimation. They were gently chased in the aviaries and trained to fly away from humans before we released them. Two of the eight coal tits were observed at El Ventorrillo field station during the following winter. This proportion is typical for coal tits that are recaptured in the same area.

The capture of birds and the experiments were licensed by the consejería de Medio Ambiente y Desarrollo de la Comunidad de Madrid, Spain.

Statistics

Statistical requirements of normality and homoscedasticity were fulfilled for all variables in the parametric analyses after we applied a Box–Cox transformation to the daily body mass gain and to the rates of body mass gain and visits to the food hopper and to the drinking bottle, and a logarithmic transformation to the time of inflexion. The double exponential function was fitted to body mass with the simplex-quasi-Newton method included in the nonlinear estimation procedure (Statsoft 2001).

Birds lived in pairs during the experiment, so 'cage' was defined as a nested factor to control for the cage effect. Only the hopping rate differed between cages (repeated measures ANOVA: $F_{3,4} = 14.0$, $P < 0.02$). There was no significant cage effect in the rest of the variables analysed (all tests: $F_{3,4} < 3.1$, $P > 0.15$).

A linear regression was fitted first to the trajectories of body mass to check the benefits of using a more complex model such as the double exponential four-parameters function. We used the Akaike Information Criterion (AIC) to decide which was the more parsimonious model (Quinn & Keough 2002). We calculated AIC values for 160 regressions (8 birds × 10 days × 2 treatments) for each model. Overall, there were 153 double exponential cases (lower AIC), and in only seven cases was the double exponential model not different from a linear model (higher AIC). Overall, the double exponential model was the best model (−40.83 versus −50.88 AIC, linear versus double exponential model). The trajectory of body mass was better fitted by the exponential than by a simple linear function (96.6 versus 88.5% variance explained in exponential versus linear models; repeated measures ANOVA of the mean variance explained in the High and Low treatments within individuals, with cage defined as a fixed factor: $F_{1,4} = 57.8$, $P < 0.01$), and the variance explained by the double exponential model did not change between treatments (High: 96.7%; Low: 96.5%, $F_{1,4} = 0.1$, $P = 0.76$, power $= 0.80$), but decreased from 93.8% in the High treatment to 83.1% in the Low treatment when a linear model was used ($F_{1,4} = 36.1$, $P < 0.01$). In addition, we used the AIC to discard other, more general, five-parameters models with two different k parameters (see Appendix 1 in Polo & Bautista 2006).

The hourly patterns of hopping, drinking and foraging during the day were tested for each bird with two-way ANCOVAs with time of day defined as a covariate, the treatment (High or Low) defined as a fixed factor and the cage defined as a random factor. The combined significance level of treatment for all birds was obtained in two steps. First, we calculated the significance level within birds as described with one-way ANCOVAs. Second, the eight significance levels from each cage were combined again to determine the significance effect of the treatment in the experiment (combined probability test, Sokal & Rohlf 1981). Time of day was included as time (hour), time^2 (hour^2) and time^3 (hour^3) in these analyses to include the cubic nonlinear effects on the hourly activity patterns because of the cubic nonlinear effects of time.

RESULTS

Diurnal Trajectory of Body Mass

Coal tits increased body mass continuously, with maximum rates of body mass gain in the first 30 min of the day and the last hour of the foraging period. Daytime increase in body mass was approximately 1 g in both treatments (Table 1). These results agree with the trajectories of body mass gain fitted with a double exponential model to each bird, day and treatment (Fig. 1). The fitted model explained 96.6% of the variance (range 93.7–98.3% between birds and treatments; Table 2).

The inflexion point (t_{inf}) was delayed 1.43 h (16.7%) in the Low treatment relative to the High treatment (Table 3). The body mass increase before t_{inf} was greater than afterwards, and greater in the Low than in the High treatment. Body mass increased faster at dawn in the Low treatment, but it increased faster at the end of the foraging period in the High treatment (Table 3). In addition, the most important period of the day to forage was the morning because the inflexion time was later than half the foraging period (i.e. 4.25 h; combined probability of Student's t tests within birds, comparing mean values with respect to 4.25; $\chi^2_8 > 80$, $P < 0.01$ in both treatments; Table 3). In summary, coal tits increased body mass as soon as possible when food was scarce, but later when food was plentiful, and gained

Table 1. Body mass (g, $\overline{X} \pm$ SE) at the start and at the end of the foraging period in the Low and High treatments (see Methods)

	Rate of food delivery		Difference between treatments	
	Low	High	$F_{1,4}$	P
Start	8.70±0.20	8.97±0.19	104.7	<0.01
End	9.72±0.21	9.98±0.20	101.5	<0.01
Body mass gain*	1.01±0.03	1.01±0.04	0.5	0.51

Data are the mean of eight coal tits measured 10 days in each treatment ($N = 80$). Tests are two-way repeated measure ANOVAs of the differences between the two treatments within birds with the cage defined as a fixed factor. There were no significant differences between cages when both treatments were compared ($F_{3,4} = 4.5$, $P > 0.09$).
*Mean of individual differences.
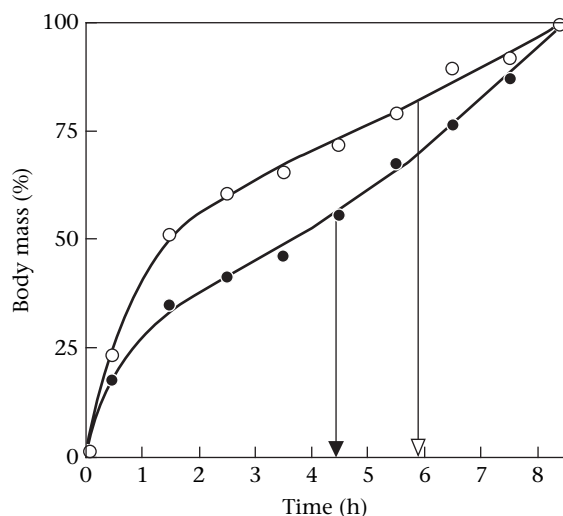
Figure 1. Mean percentage of body mass gain during the day when food was delivered at low (○) and high (●) rates. Each symbol shows the mean body mass (%) of eight coal tits calculated for the last 10 days of each treatment. Solid lines are the trajectories predicted by the double exponential model, fitted independently to each day and the parameters averaged. Vertical arrows show the mean inflexion time in each treatment.

most of their body mass in the first part of the day, although the size of this increase differed between treatments.

Dominance rank had no significant effect on the shape of daily body mass increase, and on the relevant parameters of the model fitted to body mass trajectories (repeated measure ANOVA of the parameters within birds in each treatment comparing dominant versus subordinate birds: $2.41 > F_{1,6} > 0.02$, $0.17 < P < 0.88$).

Behaviour of Birds During the Day

Coal tits adjusted their locomotive activity with time of day to a cubic model, regardless of food availability (combined probability test: $R^2 = 49.09\%$, $\chi^2_8 > 40$, $P < 0.01$). Birds were more active before the inflexion time, decreasing the hopping rate afterwards (Fig. 2), and they moved more in the High than in the Low treatment (25.4 versus 18.0 hops/min, repectively; $\chi^2_8 > 40$, $P = 0.03$). The decrease in activity rate in the Low treatment relative to the High treatment was more intense in the more active phase of the day (i.e. at dawn; combined probability test with the results of individual tests of parallelism between treatment and covariates: $\chi^2_8 = 15.66$, $P = 0.047$; Fig. 2). The most active birds showed the

Table 3. Three attributes ($\overline{X} \pm SE$) of body mass trajectories calculated with parameters of the double exponential regression fitted to body mass (see Methods)

	Food availability treatment			
	High	Low	$F_{1,4}$	P
t_{inf} (h)*	4.465 ± 0.068	5.886 ± 0.155	118.5	<0.01
BM_{before} (g)†	0.603 ± 0.015	0.844 ± 0.017	192.0	<0.01
BM_{after} (g)†	0.407 ± 0.014	0.170 ± 0.021	163.5	<0.01
$r_{t=0}$ (g/h)‡	0.265 ± 0.011	0.484 ± 0.014	24.7	<0.01
$r_{t=t_{inf}}$ (g/h)‡	0.064 ± 0.002	0.039 ± 0.002	15.5	0.01
$r_{t=T}$ (g/h)‡	0.230 ± 0.015	0.136 ± 0.009	53.8	<0.01

The differences between food availability treatments were tested with two-way repeated measure ANOVAs within birds where the cage was defined as a fixed factor.
*Inflexion time in the trajectory of body mass.
†Increase in body mass predicted by the regression model before (BM_{before}) and after (BM_{after}) the inflexion time.
‡Rates of body mass gain predicated by the regression analysis at the start ($r_{t=0}$), inflexion ($r_{t=t_{inf}}$) and end ($r_{t=T}$) of the foraging period.

greatest decrease in activity rate from the High to the Low treatment ($R^2 = 76.5\%$, $r = 0.87$, $P = 0.05$, power = 0.91).
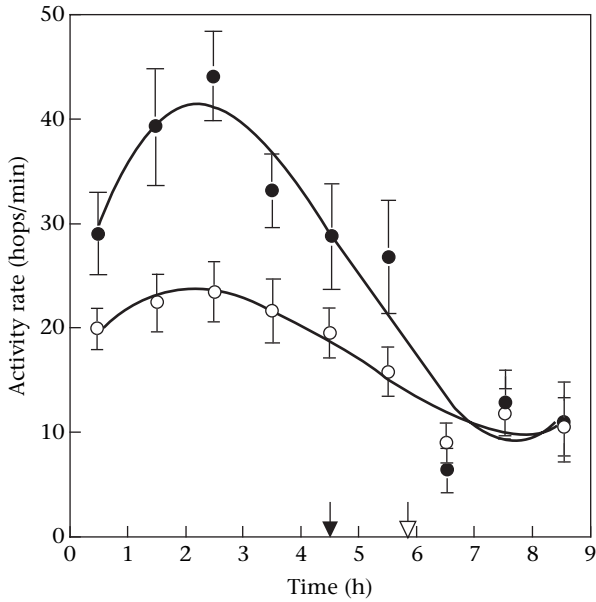
Birds requested food on most, but not all of the foraging trials in the Low treatment (83.4%; Fig. 3), suggesting that food delivery rate did not constrain the body mass trajectories. In contrast, birds requested food on only 43.4% of trials in the High treatment (comparing the two treatments: $F_{1,4} = 176.9$, $P < 0.01$). The circadian pattern of food requested differed in the two treatments (test of parallelism between covariates and treatment: $F_{2,711} = 4.6$, $P = 0.01$; Fig. 3). Thus, there was an increase in foraging towards dusk only in the High treatment. Birds visited the food hopper more often in the Low than in the High treatment (0.75 versus 0.34 times/min, respectively; $F_{1,4} = 7.1$, $P < 0.05$). Birds visited the drinking bottle 0.17 times/min in the High treatment and 0.15 times/min in the Low treatment ($F_{1,4} = 1.8$, $P = 0.25$). The rate of aggressive encounters did not differ between treatments (High: 0.11 attacks/min; Low: 0.10 attacks/min: $F_{1,4} = 0.2$, $P = 0.72$).

DISCUSSION

## Shape of Daily Body Mass Trajectory

Coal tits increased body mass continuously during the day. However, even in the High treatment, this increase was bimodal, not linear. This is in agreement with the general predictions of dynamic programming models on

Table 2. Parameters ($\overline{X} \pm SE$) of the double exponential regression model $W = a + b(e^{kt} - 1) + c(1 - e^{-kt})$ (Polo & Bautista 2006) fitted to diurnal body mass trajectory for the last 10 days of each food availability treatment

Treatment	a (g)	b ($\times 100$)	c	k	R^2 (%)
High	9.03 ± 0.21	0.21 ± 0.06	0.56 ± 0.03	0.46 ± 0.05	96.7 ± 0.44
Low	8.71 ± 0.20	0.30 ± 0.02	0.84 ± 0.03	0.59 ± 0.05	96.5 ± 0.53

Each day was fitted independently and the parameters were averaged for all birds.

Figure 2. Activity rate during the day estimated as hops/min ($\overline{X} \pm$ SE, $N = 8$ birds) when food was delivered at high (●) and low (○) rates. Mean rates ± 1 SE were calculated with at least two data points per bird and hourly period (i.e. $N > 16$ in each point). Arrows show the inflexion time for high (■) and low (□) rates.

daily body mass regulation (e.g. Bednekoff & Houston 1994), and may arise because our feeding regimes delivered the food probabilistically and pairs might have experienced some environmental stochasticity (parameter $p > 0$ in figure 1 in Bednekoff & Houston 1994). The trajectory of body mass showed the typical bimodal fattening pattern, with the greatest increases in body weight at the start and end of the foraging period, and the lowest increases in body weight at noon (i.e. at the inflexion
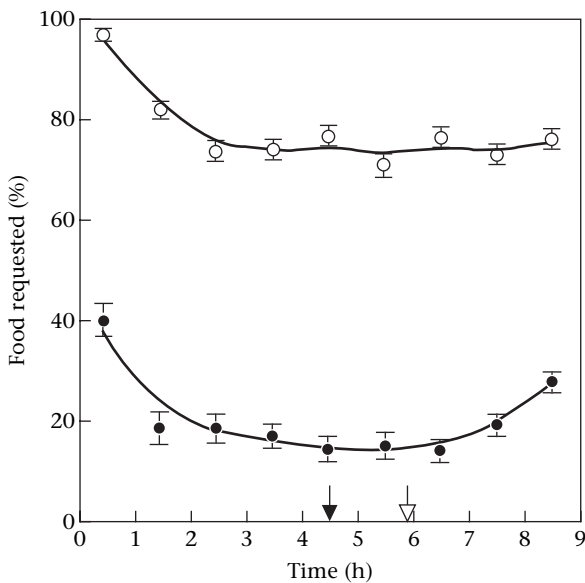
Figure 3. Bimodal foraging routine. Percentage ($\overline{X} \pm$ SE) of trials on which birds requested food during the day when food was delivered at high (●) and low (○) rates. Arrows show the inflexion time for high (■) and low (□) rates.

time) similar to most empirical studies on other species (see Discussion in Polo & Bautista 2006).

Food Availability and Body Mass Trajectory

As discussed in Polo & Bautista (2006), birds may use various strategies to ensure survival when food is scarce and/or unpredictable. First, they might increase their mean daily rate of body mass gain (Ekman & Hake 1990; Bednekoff & Krebs 1995; Witter et al. 1995; Gosler 1996; Lilliendahl et al. 1996; Witter & Swaddle 1997). Second, they might decrease their activity in the first half of the day (Witter & Cuthill 1993; Houston et al. 1997, and references therein). Third, they might put on weight earlier in the day. The body mass trajectories of the coal tits depended on food availability. When food was less available, the tits reduced their flight activity, and the more active birds decreased their activity the most. However, the total body mass gain during the foraging period was not affected by the experimental scarcity of food. Therefore, our results support the second and third strategies of daily body mass regulation, and contrast with the null effect of foraging interruptions on the body mass trajectory in Dall & Witter's (1998) study on zebra finches. In their experiment, the birds experienced a random 2-h period of food deprivation whereas our coal tits had constant food access. We adjusted individual trajectories for each day and bird, whereas there was only one function adjusted to 5 days before and after the treatment in Dall & Witter's zebra finches. Our experimental procedure offered food at constant intervals, thus time variability, an important factor for increasing body mass in the laboratory and in natural conditions (Kacelnik & Bateson 1996 and references therein), could be eliminated in our experiment.

Coal tits reacted to the decrease in food availability by putting on weight earlier in the day, perhaps as a way to reduce a perceived higher starvation risk during the night or the next morning if birds could not gain enough reserves at the end of the day (Bednekoff & Houston 1994). Thus, birds gained 40% of the total daily body mass in the first 3 h after dawn and 35% in the last 3 h before dusk in the High treatment, and 65% and 18%, respectively, in the Low treatment (for similar results in a wild population of blackbirds, *Turdus merula*, see Cresswell 1998). Therefore, the birds were able to anticipate the gain in body mass to cope with the reduction in food availability: they moved less, but they maintained a constant and high rate of visits to the food hopper during most of the foraging period (Fig. 3).

We predicted that subordinate birds would suffer a larger decrease in daily intake and daily body mass gain than dominant birds when food availability was decreased, because dominant birds could have prevented subordinate birds from gaining access to the food hopper. However, the unknown sex or age of paired birds did not allow us to test this hypothesis. The fact that there was no cage effect does not really help because all the cages might have had the same undefined sex pairing. This would mean no cage effect, as shown in the Results. We do not know whether this information is relevant to same-sex or mixed-sex

pairings, and therefore the effect of dominance rank on the trajectory of body mass cannot be explored with our experiment.

In summary, the double exponential model was able to predict the shape of body mass trajectory in all subjects and for both treatments. The inflexion point must vary in relation to the level of food availability. Such variation might result from a balance between the antagonistic effects of starvation risk and the costs of maintenance and acquisition of fat reserves. When food is scarce, a rapid increase in body mass at the start of the foraging period might be advantageous because the starvation risk decreases (McNamara et al. 1994). Conversely, when food is plentiful, a low increase in body mass at the beginning of the day may incur low costs of maintenance and acquisition of fat reserves (Lima 1986; Metcalfe & Ure 1995; Houston et al. 1997). This description of diurnal fattening complements previous analyses of energy maximization strategies on foraging decisions obtained by dynamic programming (McNamara & Houston 1990; Bednekoff & Houston 1994; McNamara et al. 1994), and allows us to make quantitative predictions for analyses on body mass regulation.

Acknowledgments

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