



ARTICLES

Daily routines of body mass gain in birds: 1. An exponential model

VICENTE POLO & LUIS MIGUEL BAUTISTA

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

(Received 28 July 2004; initial acceptance 15 November 2004;
final acceptance 18 September 2005; published online 31 July 2006; MS. number: 8224R)

Small birds show the greatest rates of body mass gain at dawn and before dusk. Some environmental and internal factors may change the intensity and duration of the first period of body mass gain relative to the second one, and thus may change the shape of daily fattening trajectories. A frequent problem for researchers is setting the periods of the day when each of the main environmental factors operates, because its effects usually decay or increase smoothly from dawn to dusk. We solved this problem by fitting the body mass to time of day with a model generated with a differential approach. This model shows the typical bimodal pattern of daily fattening routines in small birds and allows calculation of the inflexion point, that is, the time of day when the trajectory ends the decelerated period of body mass gain and starts the accelerated increase in body weight. A delay or advance in the inflexion point can be related to environmental stress that may otherwise pass unnoticed. We calculated a mean delay of 10% in the inflexion point in a sample of studies with limited food availability, and a mean advance of 6% in a sample of studies with increased predation risk. The change in the shape of daily trajectories of body mass between stressful and nonstressful conditions was inversely correlated with body mass at dawn.

© 2006 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Small birds follow a variety of daily mass gain routines in response to several environmental factors (Houston et al. 1993; Witter & Cuthill 1993; Koivula et al. 2002). The rates of body mass gain are frequently bimodal, with a first burst after dawn and a smaller second one before dusk (Bednekoff & Houston 1994a; McNamara et al. 1994; Pravosudov & Grubb 1997a; Macleod et al. 2005). This pattern has exceptions and, depending on what factors are working, the first burst may be absent, because morning reserves, flight costs, predation risk, social status or food availability are high (Polo & Carrascal 1997; Olsson et al. 2000; Pravosudov & Lucas 2001), and body mass should increase exponentially during the day (Fig. 1a). On the other hand, food unpredictability, foraging interference, low morning reserves or low social status foster body mass gain in the first part of the day, decreasing or

cancelling the second burst (McNamara et al. 1990; Lilliendahl et al. 1996; Cresswell 1998), even in small hoarding birds (Brodin 2000), and body mass should follow a Bertalanffy trajectory (Fig. 1b).

The shape of most daily fattening routines reflects a trade-off between different environmental stressors and body mass. The common bimodal pattern reported in most field and laboratory studies of body mass trajectories can arise by means of an additive combination of previous exponential and Bertalanffy models (i.e. the double exponential model; Fig. 1c; Appendix 1).

Although several body mass trajectories have been described, the bimodal pattern prevails in nature (Pravosudov & Grubb 1997a). This pattern shows a special moment when the first, decelerated, period of body mass gain ends and the second, accelerated, starts (inflexion point; Fig. 1c). The inflexion point may be delayed or advanced by any of the factors previously cited, and thus it may easily characterize the relative timing of different strategies of body mass gain. The computation of the inflexion point does not require previous identification of the time boundaries of the bimodal pattern, in contrast to most studies on diurnal trajectories of body mass (e.g. body mass measures at just three times per day, dawn,

* PII of Part 2 of this article S0003-3472(06)00175-8. doi:10.1016/j.anbehav.2005.09.025

Correspondence: V. Polo, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal 2, E-28006, Madrid, Spain (email: v.polo@mncn.csic.es).

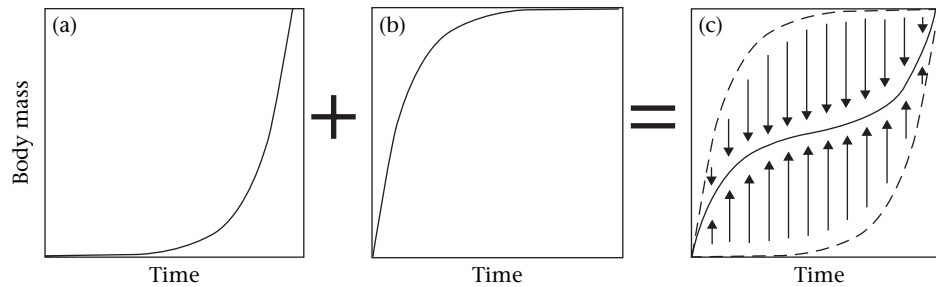


Figure 1. Hypothetical diurnal trajectories of body mass when birds are constrained by (a) mass-dependent costs only (exponential trajectory), (b) starvation risk only (Bertalanffy trajectory) and (c) both circumstances (double exponential trajectory).

noon and dusk: Koivula et al. 2002; Lange & Leimar 2004; five times a day: Dall & Witter 1998; Macleod et al. 2005; up to once an hour: Lilliendahl 2002; continuously during the foraging period: Bednekoff & Krebs 1995; Cresswell 1998; van der Veen 1999; Cuthill et al. 2000).

In this study, we generated a model by using a differential approach to describe the daytime trajectory of body mass of small birds. We examined the changes in the inflexion point of the trajectories in relation to different environmental factors. We also discuss the potential utility of the inflexion point by calculating it from some of the published studies on body mass trajectories. This literature review aims to illustrate the potential advantages of the inflexion point as a new index to manage the variability across body mass trajectories, experimental conditions and levels of stress.

We predicted that inflexion point would be delayed more or less depending on some physiological, morphological or ecological limits for each bird species. Among other limits, body mass of a species may be one of the suitable variables with which to explore the trajectory changes across species, because it has clear allometric implications for metabolism and physiological costs and other foraging behaviours (McMahon 1973; McMahon & Bonner 1983). Therefore, we also explored the relation between inflexion point delays and body mass across species.

METHODS

Model Description

If survival depends only on starvation risk, the differential increase in body mass should be proportional to the difference between the current body mass (W) and the body mass required to survive during the night (R):

$$dW \propto k_1(R - W)dt \quad (1)$$

where k_1 is a positive parameter. The solution of equation (1) is a decelerated function of daytime (t):

$$W = R + (W_0 - R)e^{-k_1 t} \quad (2)$$

where W_0 is the body mass at dawn (Fig. 1b).

When mass-dependent cost is the main environmental stress on daily fattening, the change in body mass should be proportional to itself. Thus, body mass accelerates

towards the end of the day (Fig. 1a):

$$dW \propto k_2 W dt \quad (3)$$

where k_2 is a positive parameter. The solution of equation (3) is an accelerated exponential function:

$$W = W_0 + B(e^{k_2 t} - 1) \quad (4)$$

where B is a positive adjusting parameter.

When both starvation and mass-dependent cost are present, there is a general solution by means of an additive combination of equations (2) and (4) into a double exponential curve (Fig. 1c):

$$W = a + b(e^{k_2 t} - 1) + c(1 - e^{-k_1 t}) \quad (5)$$

where a represents the body mass at dawn. Parameters b and c are constants of proportionality for the accelerating ($e^{k_2 t} - 1$) and decelerating ($1 - e^{-k_1 t}$) exponential terms of the body mass function. A simplified version of equation (5) is enough to describe the shape of most daily body mass trajectories, in which both exponential exponents are the same ($k_1 = k_2 = k$):

$$W = a + b(e^{kt} - 1) + c(1 - e^{-kt}) \quad (6)$$

However, for more general purposes in studies on daily body mass regulation, equation (5) should be used rather than the simplified version, equation 6.

The first derivative of body mass function with respect to time of day (t) provides the bimodal function of the rate of body mass gain (r):

$$r = \frac{\partial W}{\partial t} = k(b e^{kt} + c e^{-kt}) \quad (7)$$

In this bimodal function (Fig. 2), rates of body mass gain at the beginning ($r_t = 0$) and at the end ($r_t = T$) of the foraging period may be higher than at the inflexion time (r_{inf}). The time of day when the decelerating trajectory of body mass becomes accelerating can be calculated as:

$$t_{\text{inf}} = \frac{1}{2k} \ln\left(\frac{c}{b}\right) \quad (8)$$

We refer to this time as the inflexion point (Appendix 1). The delay or advance in the inflexion point may characterize the changes in the shape of daily body mass gain and in the rate of body mass gain in relation to food availability (Fig. 2).

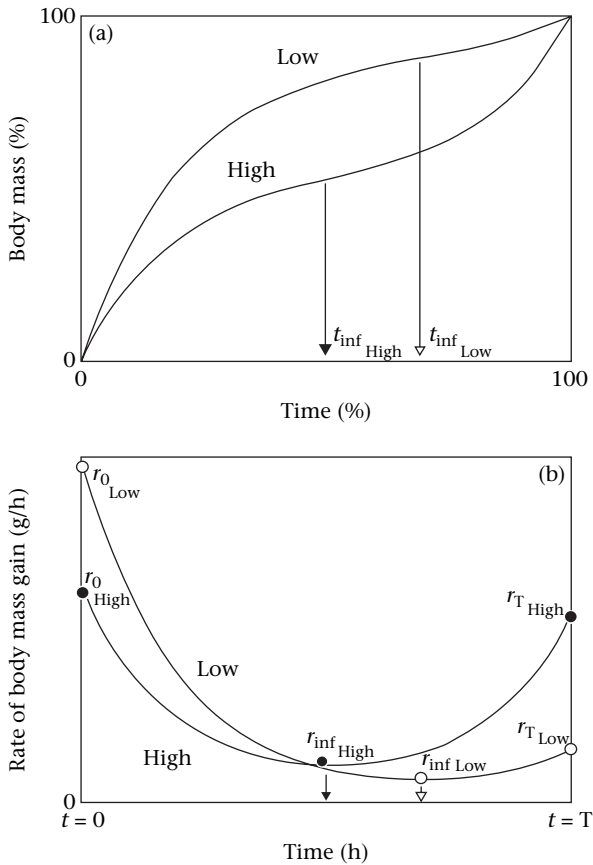


Figure 2. Diurnal trajectories of (a) body mass (BM; calculated as $100 \times (BM_{time = t} - BM_{initial}) / (BM_{last} - BM_{initial})$) and (b) the rate of body mass gain (g/h) predicted by a double exponential function, for two levels of food availability: Low and High. There are four meaningful parameters in these Low and High trajectories: (1) the time of day when the trajectory changes from decelerated to accelerated (the inflexion point, t_{inf} ; a); (2) the rates of body mass gain at the start, at the end and at the inflexion time (r_0 , r_T and r_{inf} , respectively, for both Low and High). When the trajectory is most decelerated, t_{inf} is achieved later in the day, r_0 is higher and r_T is smaller than on days when the trajectory is mainly accelerated.

Review of the Literature

We reviewed the literature on field and laboratory studies on daily body mass routines, and we found 52 body mass daytime routines with 14 ± 5 data points per trajectory ($\bar{X} \pm SD$). Most studies published mean values across subjects and days as figures or tables. Data were extracted from the published figures with the software Datathief II, version 1.1.0 (<http://www.datathief.org>). We transformed body mass and time of day to percentages to allow between-species comparisons and we calculated the inflexion point of the trajectories after fitting the model described above. We calculated the standard error for the parameter estimates after rescaling the mean square error to one, which is recommended for maximum likelihood estimates (Statsoft 2001). Mean inflexion times when environmental stress was present and absent as percentages with respect to the total foraging time. The delay

or advance in the inflexion time between treatments was calculated as the difference of percentages.

Some studies were difficult to analyse because they published pooled results and only a few data points were available. Pooled results were published in tables or figures with, for example, two (e.g. Krams 2000; Rands & Cuthill 2001), three (e.g. Koivula et al. 2002) or four (Bednekoff & Krebs 1995) data points. These studies were not included in our review.

Two studies included only one treatment (control or stress), allowing the computation of an inflexion point (Owen 1954; Lilliendahl 2002, Figs A1 and A2 in Appendix 2), but not the comparison of inflexion points between pairs of treatments. In those studies that included stressful and nonstressful treatments, the double exponential model was not suitable in a few of them (e.g. Cresswell 1998; Cuthill et al. 2000) because the unusual sigmoid trajectories reported in these studies cannot be fitted by an antisigmoid model.

Eleven studies of eight small bird species were eligible for the analyses presented here (Table 1). Eight studies included a stressful treatment with changes in time or energy budgets without any change in predation risk. We included in this group nearly as many studies as different ways to impose a stressful treatment were used. The changes were obtained by direct manipulation of food resources (Hurly 1992; Dall & Witter 1998; Pravosudov & Grubb 1998; Thomas 2000; Pravosudov & Lucas 2000; Polo & Bautista 2006), competition (Ekman & Lilliendahl 1993) or air temperature (Lilliendahl et al. 1996). Food availability was reduced mainly by decreasing the amount of food supplied, but also by increasing the temporal variation in food supply (Hurly 1992) or replacing solid food items with powder to prevent hoarding behaviour (Pravosudov & Grubb 1998).

Three studies included predation risk as a stressful treatment (Lilliendahl 1998; van der Veen 1999; van der Veen & Sivars 2000). Predation risk is expected to delay the increase in body mass towards the second part of the day (Bednekoff & Houston 1994a; McNamara et al. 1994), and advance the inflexion time of the trajectory instead of delaying it.

A detailed explanation and comments on how we dealt with each of the 11 studies included in our review are given in Appendix 2.

Statistics

We used Spearman correlation to analyse the change in the inflexion time between stressful and nonstressful treatments as a function of body mass at dawn in nine bird species. Experiments were classified in two groups: stress caused by predation risk, which predicted an advance in the inflexion point ($N = 3$ studies; this group was not included in the calculation of the Spearman correlation) and stress caused by food availability, food variability, competition or air temperature manipulations, which predicted a delay in the inflexion point ($N = 8$ studies).

Table 1. Mean inflexion times for nine bird species when environmental stress was present and absent

| Species | Environmental stress | Inflexion time* (%) | | Body mass† (g) | Type‡ | Source |
|---|-------------------------|---------------------|---------------|----------------|--------|---|
| | | Stress present | Stress absent | | | |
| Marsh tit, <i>Poecile palustris</i> | Variable food supply | 43.97 | 23.15 | 10.22§ | Lab | Hurly 1992 |
| Willow tit, <i>Poecile montanus</i> | Flock size change | 49.82 | 31.05 | 11.60 | Field | Ekman & Lilliendahl 1993 |
| Great tit, <i>Parus major</i> | Temperature decrease | 78.69 | 70.03 | 16.22 | Lab | Lilliendahl et al. 1996 |
| Zebra finch, <i>Taeniopygia guttata</i> | Food supply decrease | 51.19 | 49.23 | 12.60 | Lab | Dall & Witter 1998 |
| Tufted titmouse, <i>Baeolophus bicolor</i> | Uncachable food | 42.10 | 40.42 | 22.51** | Aviary | Pravosudov & Grubb 1998 |
| European robin, <i>Erithacus rubecula</i> | Food supply decrease | 58.75 | 55.24 | 21.07 | Field | Thomas 2000 |
| Carolina chickadee, <i>Poecile carolinensis</i> | Food supply decrease | 59.41 | 51.59 | 11.17 | Lab | Pravosudov & Lucas 2000 |
| Coal tit, <i>Periparus ater</i> | Food supply decrease | 69.25 | 52.53 | 8.70 | Lab | Polo & Bautista 2006 |
| Yellowhammer, <i>Emberiza citrinella</i> | Predation risk increase | 56.21 | 62.15 | 26.49 | Lab | Lilliendahl 1998; van der Veen 1999; van der Veen & Sivars 2000 |

*Percentage of the active foraging period.

†Mean body measured at the start of the day in stressful treatments, obtained from figures and tables.

‡Lab: laboratory experiment; aviary: aviaries in natural conditions; field: free-flying birds.

§A. Hurly (personal communication).

**V. Pravosudov (personal communication).

RESULTS

The inflexion point was calculated for 11 published studies when environmental stress was present and absent (Table 1). Figure 3 shows the shape of the adjustment with one of the studies. All trajectories are available in Appendix 2.

Overall, the inflexion point was delayed by 10.0% when sources of environmental factors other than predation risk were present (Table 1). Predation risk advanced the inflexion point by 5.9%. There was a significant decrease between inflexion time delay and body mass across species when all sources of environmental stress except predation risk were considered ($\ln \text{delay} = 7.5 - 2.1 \ln \text{body mass}$; $F_{1,6} = 6.9$, $P = 0.04$; Fig. 4). Therefore, the higher the body mass, the smaller the change in the shape of daily trajectory of body mass gain.

DISCUSSION

Daily Body Mass Trajectory

The trajectories of body mass in most empirical studies on various species (tufted titmice, *Baeolophus bicolor*: Pravosudov & Grubb 1997b; zebra finch, *Taeniopygia guttata*: Dall & Witter 1998; yellowhammer, *Emberiza citrinella*: Lilliendahl 1998) showed the typical bimodal fattening pattern, with the greatest increases in body weight at the start and the end of the foraging period, and the lowest increases in body weight at noon (i.e. at the inflexion time). Although other daytime trajectories that are approximately linear have been found (e.g. Lilliendahl

et al. 1996; Lange & Leimar 2004), these trajectories have been predicted only for special circumstances (McNamara et al. 1990, 1994; see also sigmoid trajectories in Gosler 1996; Cuthill et al. 2000).

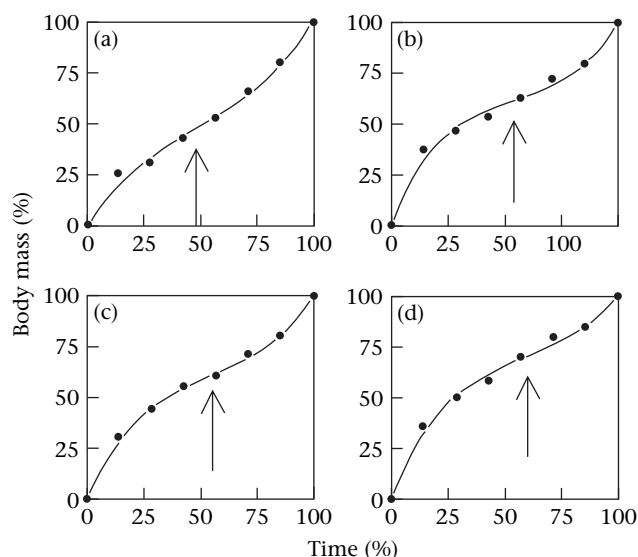


Figure 3. Body mass trajectories of (a, b) subordinate and (c, d) dominant yellowhammers on days when a stuffed sparrowhawk was (a, c) concealed or (b, d) displayed. The stressful treatment (sparrowhawk displayed; c, d) delayed the inflexion point. Adapted from figure 1 in Lilliendahl (1998). Solid lines show the trajectories predicted by the double exponential model. Vertical arrows show the inflexion time.

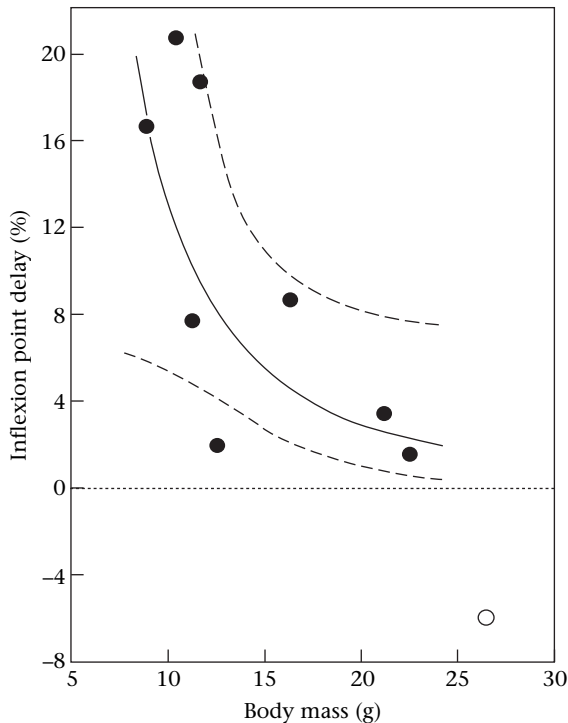


Figure 4. Inflexion time delay between stressful and nonstressful treatments as a function of body mass measured at dawn in nine small bird species. Experiments were classified into two groups: stress caused by simulated predation risk (○), and stress caused by other factors such as food availability, food variability, competition or air temperature manipulation (●: see details in Table 1 and Appendix 2). Continuous line shows the regression analysis of delay on body mass for all sources of environmental stress factors except predation risk. Dashed lines show the 95% confidence interval for the regression line. Spearman correlation: $r_s = -0.74$, $N = 8$, $P = 0.037$.

The daily pattern of body mass showing a double exponential shape is the result of a trade-off in energy management. Fat deposits are generally smaller than the maximum possible (Blem 1976), suggesting that there must be constraints on maintaining and carrying large fat reserves (Bednekoff & Houston 1994b; reviewed in Witter & Cuthill 1993; Pravosudov & Grubb 1997a). The large increase in body mass at dawn may be explained by the decrease in fat and water reserves of birds during the night. Body reserves should be recovered with an increase in intake at the start of the next foraging period (Kendeigh et al. 1969), thus decreasing the risk of starvation during the morning when fat reserves are lowest. However, there is a cost of putting on weight too early in the day because of an increased risk of predation caused by a decrease in flight manoeuvrability (Witter et al. 1994). Thus, a second peak in foraging activity at dusk should permit birds to put on enough fat for the next nocturnal period while minimizing the body mass-dependent costs during the day (reviewed in Witter & Cuthill 1993).

On the basis of the results from previous studies (Appendix 2) it appears that a proportion might be well

represented as a straight line. For instance, data in studies such as that by Cresswell (1998) would be best represented as a single exponential function. However, even if this is a better description of the data than a bimodal function, the double exponential model is still superior to either a single linear or exponential model, so the approach in this paper remains valid.

Factors Shaping Daily Trajectories

The double exponential model was able to predict the shape of the body mass trajectory in the studies we reviewed. This description of diurnal fattening complements previous analyses of energy maximization strategies on foraging decision obtained by dynamic programming (McNamara & Houston 1990; Bednekoff & Houston 1994a; McNamara et al. 1994). Furthermore, it allows us to make several quantitative estimates, such as the delay or advance at the inflexion point as a function of food availability or other sources of environmental stress, and the quantification of very different trajectories of body mass gain: purely accelerated, purely decelerated or mixed. Thus, the model offers a common ground for a new array of analyses on body mass regulation.

Birds may use various strategies to ensure survival when food is scarce and/or unpredictable. First, birds might increase their mean daily rate of body mass gain to deal with short-term drops in food availability (Ekman & Hake 1990; Bednekoff & Krebs 1995; Witter et al. 1995; Gosler 1996; Lilliendahl et al. 1996; Witter & Swaddle 1997). However, this strategy could not be the only one used to deal with food shortage, because scarcity of food per se might impose a limit on the mean rate of body mass gain. Second, birds might save energy by decreasing their activity in the first half of the day because there is an energetic cost to being active associated with body mass (Witter & Cuthill 1993; Houston et al. 1997, and references therein), and the circadian flight activity pattern peaks at dawn and descends thereafter (Aschoff 1966). Third, birds could modify the diurnal trajectory of body mass gain by advancing the fattening to earlier hours of the day when food is scarce, because the daily routine of body mass gain is probably the result of an equilibrium between costs and benefits linked to the level of reserves and the risks of starvation and predation (McNamara et al. 1994). Our literature review supports this third strategy for small birds, because the smaller the bird species, the greater is the change in the inflexion point.

Most studies on daily body mass regulation have been done indoors, under highly controlled and artificial conditions (Ekman & Hake 1990; Bednekoff & Krebs 1995; Bateson & Kacelnik 1996; Cuthill et al. 1997; Fransson & Weber 1997; Witter & Swaddle 1997; Bautista et al. 1998), in which food availability was decreased, food unpredictability was increased or both factors were changed simultaneously. Foraging stress for the subordinate male was relaxed in one study by removing the dominant male from the flock (Ekman & Lilliendahl 1993) and in another by decreasing air temperature during the night

(Lilliendahl et al. 1996). In one study food items were ground up to make them uncachable (Pravosudov & Grubb 1998), with the aim of stressing the birds by not allowing them to build daily caches. Overall, in the eight studies that we reviewed, there was a 10% delay in the inflexion point of the daily body mass trajectories in these stressful treatments (Table 1).

We also calculated a mean 5.9% advance in the inflexion point from the three studies of body mass trajectories under increased predation risk (Table 1). However, yellowhammers varied their body mass trajectories in various ways (Figs A11–A13 in Appendix 2), and the results of our analysis were contradictory: depending on the study, the inflexion point was advanced (van der Veen 1999; van der Veen & Sivars 2000) or was delayed (Lilliendahl 1998). This contradiction may reflect differences in the perceived risk of predation by birds between these experimental studies. Another explanation is that the experimental birds considered the predation event to be a reduction in food availability (Rands & Cuthill 2001; Macleod 2006) and, in this situation, birds should delay the inflexion time. Further experiments are required to clarify the usefulness of the double exponential model for the study of body mass trajectories under predation risk. We cannot report a statistical significance of the delays calculated for any experiment reviewed (Table 1) except for the one calculated in our companion paper (Polo & Bautista 2006), because the data from the literature were pooled as figures and tables. Thus, we present this review as an illustrative report, not a conclusive analysis.

We had no prior hypothesis about a possible relation between the inflexion point change caused by the environmental factor and the body mass of the species. Therefore we have no explanation for the finding shown in Fig. 4 as either a causal or an incidental effect of body size on body mass trajectory. None the less, if there were a real effect of foraging stress in the daily trajectory of body mass, we might expect the inflexion point to be delayed more or less depending on some physiological, morphological or ecological limits. Among other variables, body mass of the species may be a suitable variable to explore the trajectory changes across species because it has clear allometric implications for metabolism and physiological costs and other foraging behaviours (McMahon 1973; McMahon & Bonner 1983). For instance, Kacelnik & Bateson (1996) suggested that body mass may determine the result of decision making in risk-sensitive foraging, where smaller bird species are more willing than larger bird species to revert their foraging preferences. This hypothesis may be applied to our study, and it might also be considered in further studies.

In summary, the inflexion point must vary in relation to the level of the stressful treatment (i.e. the higher the level of stress, the later is the inflexion point). Such variation might result from a balance between the antagonistic effects of starvation risk and the costs of maintenance and acquisition of fat reserves. For example, 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 (Blem 1990; McNamara

et al. 1994). Conversely, when food is plentiful, a small increase in body mass at the beginning of the day may induce low costs of maintenance and acquisition of fat reserves (Lima 1986; Metcalfe & Ure 1995; Houston et al. 1997).

Acknowledgments

Luis M. Carrascal, Innes C. Cuthill, John M. C. Hutchinson, Bart Kempenaers, Kristjan Lilliendahl, Ross Macleod, Neil B. Metcalfe, Vladimir V. Pravosudov, Sean Rands, Robert J. Thomas, Ineke T. van der Veen and four anonymous referees made valuable comments on the manuscript. Luis M. Carrascal was a boundless source of statistical advice. Andrew Hurly and Vladimir Pravosudov kindly provided unpublished data. This study was funded by DGCYT project PB95-0102-CO2-01 of the Spanish Ministry of Education & Science (MEC). V.P. was supported with a predoctoral grant and L.M.B. was supported with a postdoctoral contract from MEC. The Biological Station El Ventorrillo provided birds and logistical support.

References

- Aschoff, J. 1966. Circadian activity pattern with two peaks. *Ecology*, **47**, 657–662.
- Bateson, M. & Kacelnik, A. 1996. Rate currencies and the foraging starling: the fallacy of the averages revisited. *Behavioral Ecology*, **7**, 341–352.
- Bautista, L. M., Tinbergen, J. M., Wiersma, P. & Kacelnik, A. 1998. Optimal foraging and beyond: how starlings cope with changes in food availability. *American Naturalist*, **152**, 545–563.
- Bednekoff, P. A. & Houston, A. I. 1994a. Avian daily foraging patterns: effects of digestive constraints and variability. *Evolutionary Ecology*, **8**, 36–52.
- Bednekoff, P. A. & Houston, A. I. 1994b. Optimizing fat reserves over the entire winter: a dynamic model. *Oikos*, **71**, 408–415.
- Bednekoff, P. A. & Krebs, J. R. 1995. Great tit fat reserves: effects of changing and unpredictable feeding day length. *Functional Ecology*, **9**, 457–462.
- Blem, C. R. 1976. Patterns of lipid storage and utilization in birds. *American Zoologist*, **16**, 671–684.
- Blem, C. R. 1990. Avian energy storage. In: *Current Ornithology*. Vol. 7 (Ed. by D. M. Power), pp. 59–113. New York: Plenum.
- Brodin, A. 2000. Why do hoarding birds gain fat in winter in the wrong way? Suggestions from a dynamic model. *Behavioral Ecology*, **11**, 27–39.
- Cresswell, W. 1998. Diurnal and seasonal mass variation in blackbirds *Turdus merula*: consequences for mass-dependent predation risk. *Journal of Animal Ecology*, **67**, 78–90.
- Cuthill, I. C., Hunt, S., Cleary, C. & Clark, C. W. 1997. Colour bands, dominance, and body mass regulation in male zebra finches (*Taeniopygia guttata*). *Proceedings of the Royal Society of London, Series B*, **264**, 1093–1099.
- Cuthill, I. C., Maddocks, S. A., Weall, C. V. & Jones, E. K. M. 2000. Body mass regulation in response to changes in feeding predictability and overnight energy expenditure. *Behavioral Ecology*, **11**, 189–195.
- Dall, S. R. X. & Witter, M. S. 1998. Feeding interruptions, diurnal mass changes and daily routines of behaviour in the zebra finch. *Animal Behaviour*, **55**, 715–725.

- Ekman, J. B. & Hake, M. K. 1990. Monitoring starvation risk: adjustments of body reserves in greenfinches (*Carduelis chloris* L.) during periods of unpredictable foraging success. *Behavioral Ecology*, **1**, 62–67.
- Ekman, J. B. & Lilliendahl, K. 1993. Using priority to food access: fattening strategies in dominance-structured willow tit (*Parus montanus*) flocks. *Behavioral Ecology*, **4**, 232–238.
- Fransson, T. & Weber, T. D. 1997. Migratory fuelling in blackcaps (*Sylvia atricapilla*) under perceived risk of predation. *Behavioral Ecology and Sociobiology*, **41**, 75–80.
- Gosler, A. G. 1996. Environmental and social determinants of winter fat storage in the great tit *Parus major*. *Journal of Animal Ecology*, **65**, 1–17.
- Houston, A. I., McNamara, J. & Hutchinson, J. M. C. 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society of London, Series B*, **341**, 375–397.
- Houston, A. I., Welton, N. J. & McNamara, J. 1997. Acquisition and maintenance costs in the long-term regulation of avian fat reserves. *Oikos*, **78**, 331–340.
- Hurly, T. A. 1992. Energetic reserves of marsh tits (*Parus palustris*): food and fat storage in response to variable food supply. *Behavioral Ecology*, **3**, 181–188.
- Kacelnik, A. & Bateson, M. 1996. Risky theories: the effects of variance on foraging decisions. *American Zoologist*, **36**, 402–434.
- Kendeigh, S. C., Kontogiannis, J. E., Maza, A. & Roth, R. 1969. Environmental regulation of food intake by birds. *Comparative Biochemistry and Physiology*, **32**, 941–957.
- Koivula, K., Orell, M. & Lahti, K. 2002. Plastic daily fattening routines in willow tits. *Journal of Animal Ecology*, **71**, 816–823.
- Krams, I. 2000. Length of feeding day and body weight of great tits in a single- and a two-predator environment. *Behavioral Ecology and Sociobiology*, **48**, 147–153.
- Lange, H. & Leimar, O. 2004. Social stability and daily body mass gain in great tits. *Behavioral Ecology*, **15**, 549–554.
- Lilliendahl, K. 1998. Yellowhammers get fatter in the presence of a predator. *Animal Behaviour*, **55**, 1335–1340.
- Lilliendahl, K. 2002. Daily patterns of body mass gain in four species of small wintering birds. *Journal of Avian Biology*, **33**, 212–218.
- Lilliendahl, K., Carlson, A., Welander, J. & Ekman, J. B. 1996. Behavioural control of daily fattening in great tits (*Parus major*). *Canadian Journal of Zoology*, **74**, 1612–1616.
- Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology*, **67**, 377–385.
- Macleod, R. 2006. Why does diurnal mass change not appear to affect the flight performance of alarmed birds? *Animal Behaviour*, **71**, 523–530.
- Macleod, R., Barnett, P., Clark, J. A. & Cresswell, W. 2005. Body mass change strategies in blackbirds *Turdus merula*: the starvation-predation risk trade-off. *Journal of Animal Ecology*, **74**, 292–302.
- McMahon, T. A. 1973. Size and shape in biology. *Science*, **179**, 1201–1204.
- McMahon, T. A. & Bonner, J. T. 1983. *Size and Life*. Princeton, New Jersey: Princeton University Press.
- McNamara, J. & Houston, A. I. 1990. The value of fat reserves and the tradeoff between starvation and predation. *Acta Biotheoretica*, **38**, 37–61.
- McNamara, J., Houston, A. I. & Krebs, J. R. 1990. Why hoard? The economics of food storing in tits, *Parus* spp. *Behavioral Ecology*, **1**, 12–23.
- McNamara, J., Houston, A. I. & Lima, S. L. 1994. Foraging routines of small birds in winter: a theoretical investigation. *Journal of Avian Biology*, **25**, 287–302.
- Metcalf, N. B. & Ure, S. E. 1995. Diurnal variation in flight performance and hence potential predation risk in small birds. *Proceedings of the Royal Society of London, Series B*, **261**, 395–400.
- Olsson, O., Wiklander, U. & Nilsson, S. G. 2000. Daily foraging routines and feeding effort of a small bird feeding on a predictable resource. *Proceedings of the Royal Society of London, Series B*, **267**, 1457–1461.
- Owen, D. F. 1954. The winter weights of titmice. *Ibis*, **96**, 299–309.
- Polo, V. & Bautista, L. M. 2006. Daily routines of body mass gain in birds: 2. An experiment with reduced food availability. *Animal Behaviour*, **72**, 517–522.
- Polo, V. & Carrascal, L. M. 1997. The winter diurnal cycle of body weight in a wild population of *Parus cristatus* in Central Spain. *Ardeola*, **44**, 215–224.
- Pravosudov, V. V. & Grubb, T. C. 1997a. Energy management in passerine birds during the nonbreeding season: a review. In: *Current Ornithology*. Vol. 14 (Ed. by V. Nolan), pp. 189–234. New York: Plenum.
- Pravosudov, V. V. & Grubb, T. C. 1997b. Management of fat reserves and food caches in tufted titmice (*Parus bicolor*) in relation to unpredictable food supply. *Behavioral Ecology*, **8**, 332–339.
- Pravosudov, V. V. & Grubb, T. C. 1998. Management of fat reserves in tufted titmice (*Parus bicolor*): evidence against a trade-off with food hoards. *Behavioral Ecology and Sociobiology*, **42**, 57–62.
- Pravosudov, V. V. & Lucas, J. R. 2000. The effect of social dominance on fattening and food-caching behaviour in Carolina chickadees, *Poecile carolinensis*. *Animal Behaviour*, **60**, 483–493.
- Pravosudov, V. V. & Lucas, J. R. 2001. Daily patterns of energy storage in food-caching birds under variable daily predation risk: a dynamic state variable model. *Behavioral Ecology and Sociobiology*, **50**, 239–250.
- Rands, S. A. & Cuthill, I. C. 2001. Separating the effects of predation risk and interrupted foraging upon mass changes in the blue tit *Parus caeruleus*. *Proceedings of the Royal Society of London, Series B*, **268**, 1783–1790.
- Statsoft, I. 2001. *STATISTICA 6.0*. Tulsa, Oklahoma: StatSoft Inc.
- Thomas, R. J. 2000. Strategic diel regulation of body mass in European robins. *Animal Behaviour*, **59**, 787–791.
- van der Veen, I. T. 1999. Effects of predation risk on diurnal mass dynamics and foraging routines of yellowhammers (*Emberiza citrinella*). *Behavioral Ecology*, **10**, 545–551.
- van der Veen, I. T. & Sivals, L. E. 2000. Causes and consequences of mass loss upon predator encounter: feeding interpretation, stress or fit-for-fight? *Functional Ecology*, **14**, 638–644.
- Witter, M. S. & Cuthill, I. C. 1993. The ecological costs of avian fat storage. *Philosophical Transactions of the Royal Society of London, Series B*, **340**, 73–92.
- Witter, M. S. & Swaddle, J. P. 1997. Mass regulation in juvenile starlings: response to change in food availability depends on initial body mass. *Functional Ecology*, **11**, 11–15.
- Witter, M. S., Cuthill, I. C. & Bonser, R. H. C. 1994. Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. *Animal Behaviour*, **48**, 201–222.
- Witter, M. S., Swaddle, J. P. & Cuthill, I. C. 1995. Periodic food availability and strategic regulation of body mass in the European starling, *Sturnus vulgaris*. *Functional Ecology*, **9**, 568–574.

Appendix 1

If survival depends on starvation risk and on mass-dependent costs, there is a general solution between the current body mass (W) and time of day (t) by means of a double exponential function:

$$W = a + b(e^{k_2t} - 1) + c(1 - e^{-k_1t}) \quad (A1)$$

where a represents the body mass at dawn, parameters b and c are constants of proportionality for the accelerating ($e^{k_2t} - 1$) and decelerating ($1 - e^{-k_1t}$) exponential terms of the body mass function, and parameters k_1 and k_2 represent the rate of body mass gain for these accelerating and decelerating parts. A simplified version of equation (A1) is enough to describe the shape of most daily body mass trajectories, in which both exponential exponents are the same ($k_1 = k_2 = k$):

$$W = a + b(e^{kt} - 1) + c(1 - e^{-kt}) \quad (A2)$$

The first derivative of body mass function with respect to time of day provides the bimodal function of the rate of body mass gain (r):

$$r = \frac{\partial W}{\partial t} = k(be^{kt} + ce^{-kt}) \quad (A3)$$

In this bimodal function, rates of body mass gain at the beginning ($r_{t=0}$) and at the end ($r_{t=T}$) of the foraging period may be higher than at the inflexion time ($r_{t_{inf}}$).

The time of day when the curvature of the function changes from convex to concave is the inflexion point of the body mass function W . To obtain the inflexion point (t_{inf}), the second derivative of body mass with respect to time t should be set to zero:

$$\left[\frac{\partial^2 W}{\partial t^2} \right]_{t=t_{inf}} = k^2 (be^{kt_{inf}} - ce^{-kt_{inf}}) = 0; \text{ where } t_{inf} = \frac{1}{2k} \ln\left(\frac{c}{b}\right) \quad (A4)$$

The relative position of t_{inf} in the foraging period shows the main foraging period of the day. If $t_{inf} < T/2$, the body mass gain takes place mainly in the first part of the day (i.e. high b). When $t_{inf} > T/2$, the body mass gain increases mainly at the end of the day (i.e. low b). At time t_{inf} , we may also obtain the body mass, W_{inf} , and the minimum value of body mass gain rate, r_{inf} with the following equations:

$$W_{inf} = a - b + c \quad (A5)$$

$$r_{inf} = 2k\sqrt{bc} \quad (A6)$$

We can rewrite the daily body mass (equation A2) and the daily body mass rate (equation A3) functions in terms of W_{inf} , r_{inf} and t_{inf} as:

$$W = W_{inf} + \frac{r_{inf}}{k} \sinh[k(t - t_{inf})] \quad (A7)$$

$$r = r_{inf} + \cosh[k(t - t_{inf})] \quad (A8)$$

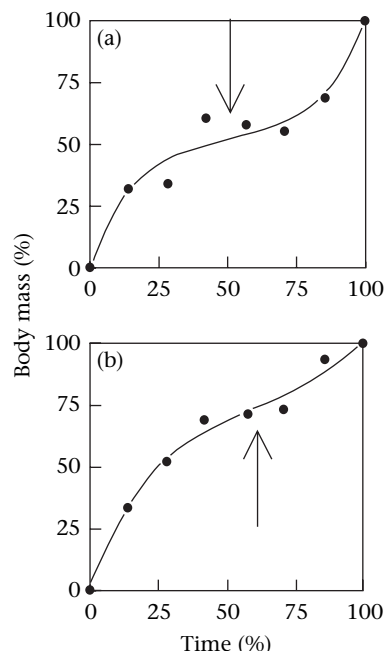


Figure A1. Body mass trajectories of (a) great tits and (b) blue tits. Adapted from figures 1 and 2 in Owen (1954). Solid lines show the predicted trajectories by a double exponential model. Vertical arrows show the inflexion time.

The body mass function (equation A7) is an odd function with respect to $W = W_{inf}$ and $t = t_{inf}$. The rate of body mass gain (equation A8) is an even function with respect to $t = t_{inf}$. As body mass is a positive increasing function and $\cosh^2 x - \sinh^2 x = 1$, it is possible to relate the body mass gain from t_{inf} to t with the rate of body mass gain in these times, r_{inf} and r :

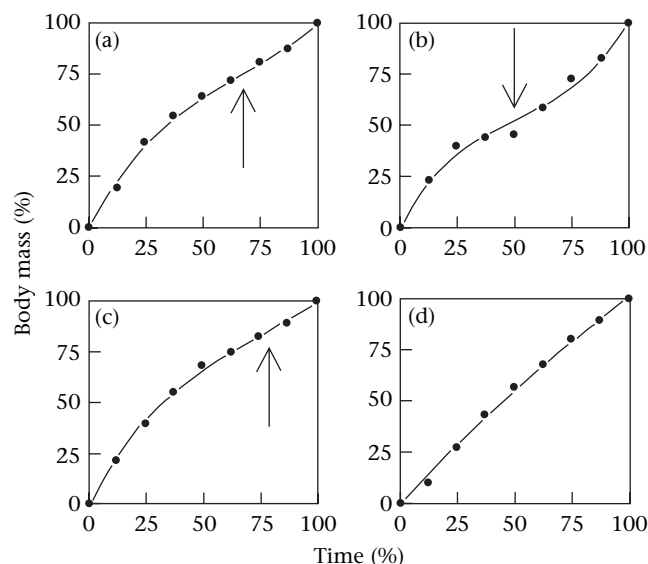


Figure A2. Body mass trajectories of (a) European nuthatches, (b) marsh tits, (c) willow tits and (d) great tits. An inflexion point cannot be calculated for great tits. Adapted from figure 2 in Lilliendahl (2002). Lines and arrows explained in Fig. A1.

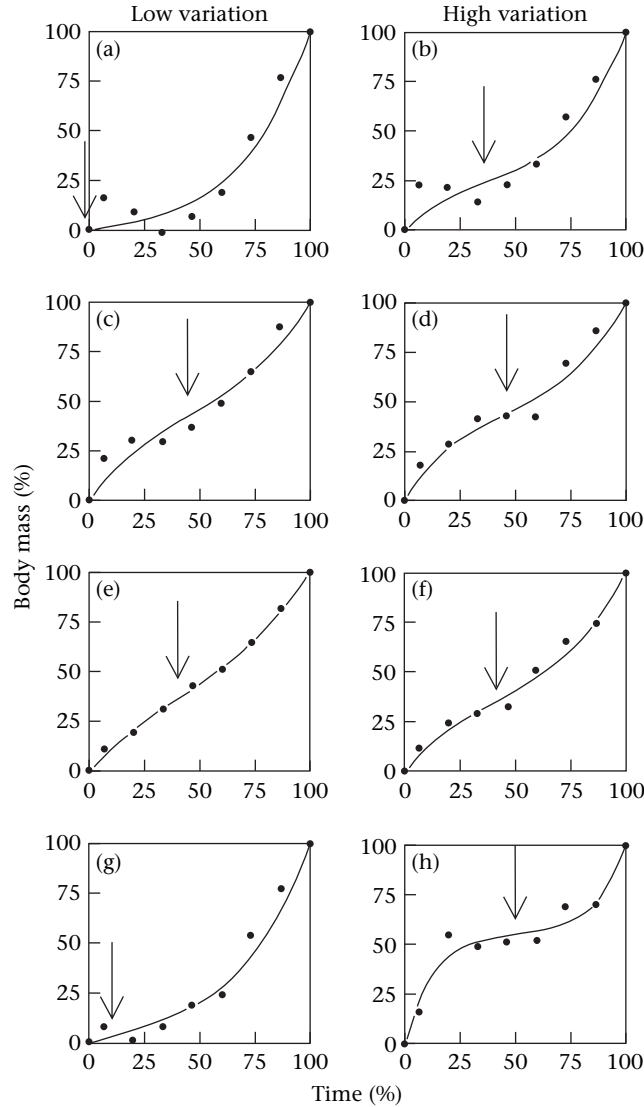


Figure A3. Body mass trajectories of four marsh tits when variation in food availability was low and high (the same bird is shown in each row). Adapted from figure 7 in Hurly (1992). Lines and arrows explained in Fig. A1.

$$W - W_{\text{inf}} = \pm \frac{1}{k} \sqrt{r^2 - r_{\text{inf}}^2} \quad (\text{A9})$$

where the plus sign is used when $t > t_{\text{inf}}$ and the minus sign when $t < t_{\text{inf}}$. Body mass gain from t_{inf} is also an odd function.

Appendix 2

Here we show the process and the results of fitting a double exponential regression model to 13 studies. An explanation and a figure with the line fitted to the published data points are included for each study.

Figures A1 and A2 show the trajectories fitted to body masses recorded during winter (Owen 1954) and autumn (Lilliendahl 2002) as a sample of observational studies.

These figures show the typical trajectory of body mass for small birds. As in most field studies, there were no experimental treatments, and therefore it was not possible to calculate the delay in the inflexion time caused by a change in stressful conditions. Figures A3–A10 show the trajectories fitted to a sample of studies that included a stressful treatment with changes in time or energy budgets, and without any change in predation risk. Next we comment on each study to show how we dealt with them.

Hurly (1992) studied body mass trajectories of four marsh tits, *Poecile palustris*, when temporal variation in food availability was low and high (figure 7 in Hurly 1992). Hundreds of weights for each bird were recorded each day, but they were grouped into nine periods when published as body mass trajectories. With nine data points per bird and per treatment, we calculated a mean delay of 20.82% in the inflexion point caused by a stressful

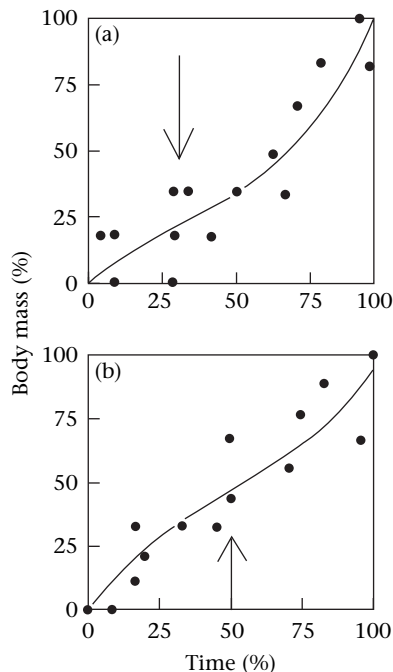


Figure A4. Body mass trajectories of a subordinate willow tit (a) before and (b) after removal of the dominant bird. Adapted from figure 3 in Ekman & Lilliendahl (1993). Lines and arrows explained in Fig. A1.

treatment of high temporal variation in the food supply (Fig. A3). The size of the delay varied from less than 2% in two birds to nearly 40% in another two birds.

Ekman & Lilliendahl (1993) studied body mass trajectories of five subordinate willow tits, *Poecile montanus*,

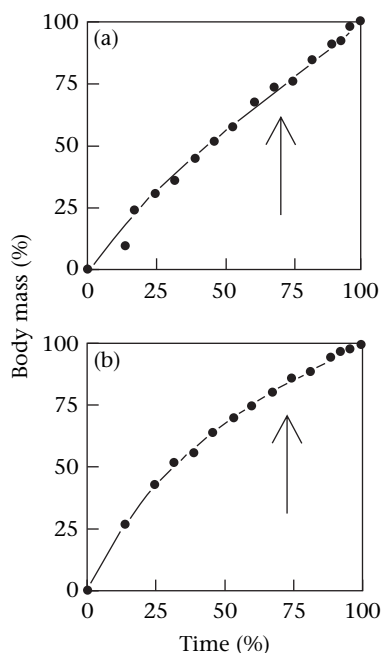


Figure A5. Body mass trajectories of great tits (a) before and (b) after the air temperature was decreased during the night. Adapted from figure 3 in Lilliendahl et al. (1996). Lines and arrows explained in Fig. A1.

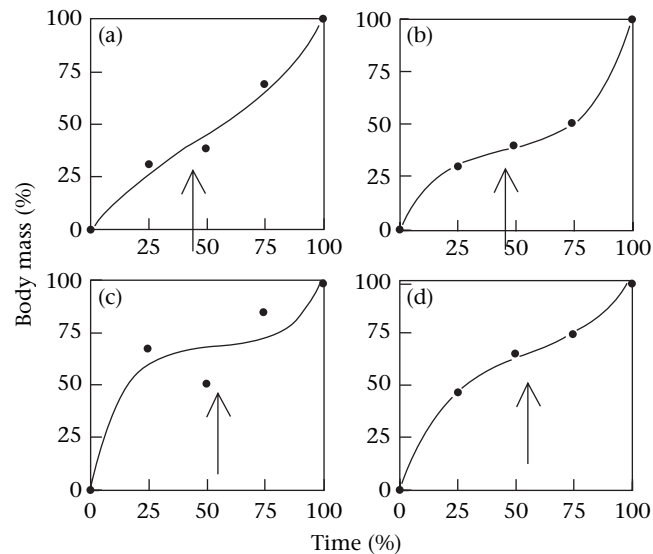


Figure A6. Body mass trajectories of (a, b) male and (c, d) female zebra finches on days (a, c) before and (b, d) after feeding was interrupted for 2 h a day. Adapted from Table 1 in Dall & Witter (1998). Lines and arrows explained in Fig. A1.

foraging in dominance-structured flocks (figure 3 in Ekman & Lilliendahl 1993). Competition for food was relaxed by removing the dominant bird from each flock. It is unknown whether the same level of stress would appear when the dominant bird was returned to its flock, and therefore the length of the delay in the inflexion point may depend on whether the dominant bird is removed or returned. Subordinate birds were weighed before and after the removal. One data point per day and per subordinate bird was recorded at various times of day for several days. Because this study was done in field conditions, data records between treatments do not match in the timescale. We used data points from only one bird (bird a, see figure 3a in Ekman & Lilliendahl 1993), because in that bird the weighing period was 92% the same for both treatments, and also because the overlap between treatments was centred: 4% of the time was left out at each side of the day. We calculated a delay of 18.77% in the inflexion point (Fig. A4) caused by a stressful factor for the subordinate bird, such as the presence of a dominant bird in the flock. In the other four experimental birds (figure 3b–e in Ekman & Lilliendahl 1993), the weighing period overlapped only 66–82% between treatments, and the overlap was not evenly distributed between treatments. We did not calculate the inflexion point for these birds.

Lilliendahl et al. (1996) studied body mass trajectories of 10 great tits, *Parus major*, kept alone in cages. The stressful treatment was a decrease in the air temperature in the cage during the night before the body mass was recorded. Fifteen data points per day and bird were recorded at fixed times for each treatment (cold and warm nights), although body masses were pooled across birds for publishing (figure 3 in Lilliendahl et al. 1996). We calculated a delay of 8.65% in the inflexion point (Fig. A5) caused by a stressful factor.

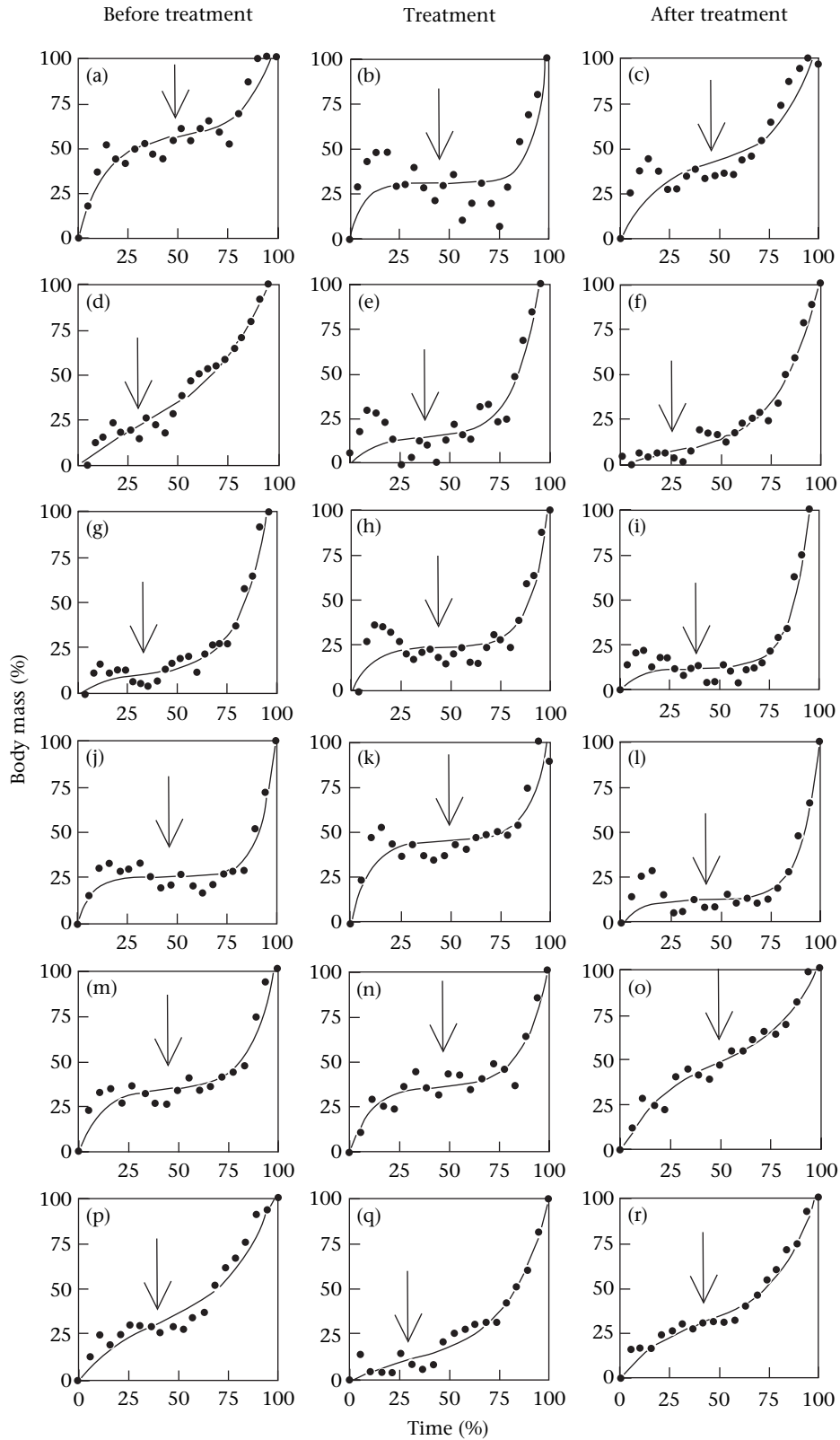


Figure A7. Body mass trajectories of tufted titmice before, during and after food access was limited (the same bird is shown in each row). Adapted from figure 2 in Pravosudov & Grubb (1998). Lines and arrows explained in Fig. A1.

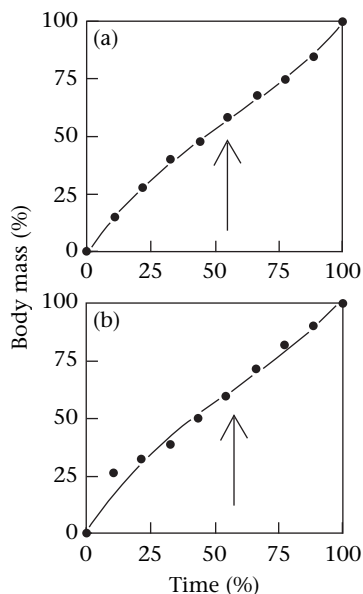


Figure A8. Body mass trajectories of European robins (a) before and (b) after food ad libitum food was removed for 1 day. Adapted from figure 1 in Thomas (2000). Lines and arrows explained in Fig. A1.

Dall & Witter (1998) studied body mass trajectories of 24 zebra finches, *Taeniopygia guttata*, kept in 12 cages as female and male pairs. Food was provided ad libitum. Each bird was removed from its cage once per day, and body mass and other variables were recorded. This procedure was repeated for 5 days at various times to gather five data points per bird before the stressful treatment took place. During the stressful treatment, food was randomly removed for 2 h a day for six pairs, while the other six pairs were used as a control for manipulation. After the stressful treatment finished, the procedure for measuring body masses at various times for 5 days was repeated. Body masses were pooled by sex for publishing (Table 1 in Dall & Witter 1998). We calculated a delay of 1.95% in the inflexion point before and after feeding was interrupted (Fig. A6).

In the study of Pravosudov & Grubb (1998), six tufted titmice, *Baeolophus bicolor*, were fed a diet of uncachable sunflower seed powder for 6 days. This slightly stressful treatment was preceded and followed by control treatments during which they were fed with cachable sunflower seeds. We calculated the inflexion time for each treatment, and the mean inflexion time with the two control treatments for each bird. Although our model does not account for partially decreasing trajectories of body mass, the model still describes well the overall pattern of the data, so it can be compared between treatments. We calculated an arithmetic difference for each bird between the inflexion time for the experimental treatment and the mean inflexion time for the control treatments. Finally, the mean of the six differences, one per bird, was calculated as a delay of 1.68% in the inflexion time (Fig. A7) between the experimental and the control treatments. A stronger stressful treatment was used by Pravosudov & Grubb (1997b) with the same experimental set-up, where food availability and food temporal predictability were decreased. As a consequence, body mass trajectory

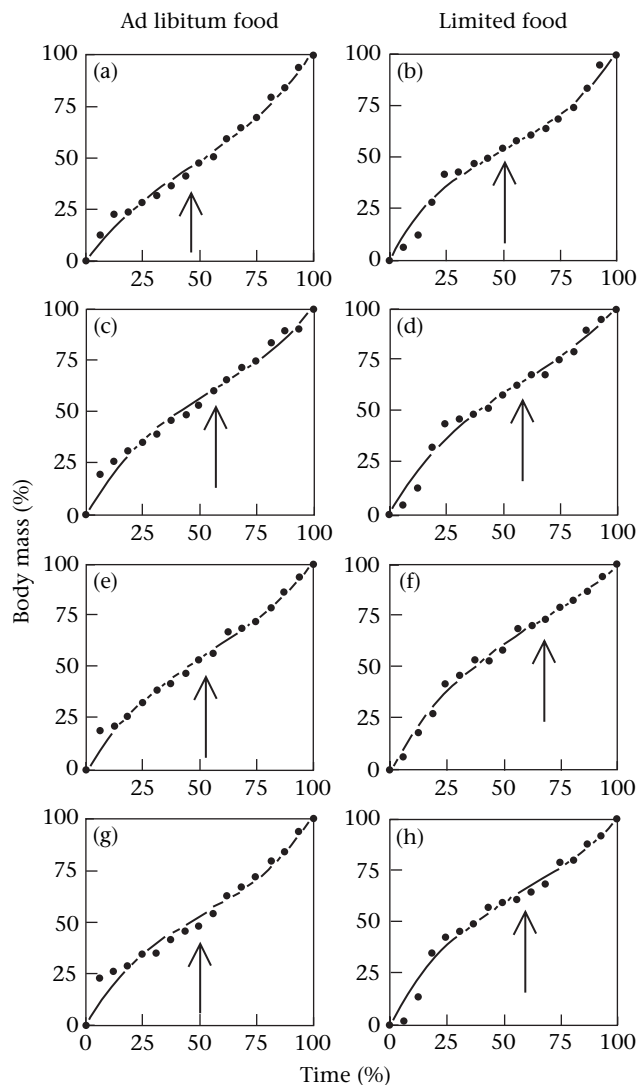


Figure A9. Body mass trajectories of (a, b, c, d) dominant and (e, f, g, h) subordinate Carolina chickadees foraging (a, b, e, f) solitary and (c, d, g, h) in pairs with two levels of food availability: ad libitum and limited (the same birds are shown in each row). Adapted from figure 2 in Pravosudov & Lucas (2000). Lines and arrows explained in Fig. A1.

changed between treatments (figure 3 in Pravosudov & Grubb 1997b). However, we did not calculate the inflexion time delay for this second experiment because data points were grouped in 2-h periods. The first and the last 2-h period may have included changes in body mass, as shown by visual comparison of the two studies (figure 3a in Pravosudov & Grubb 1997b and figure 2 in Pravosudov & Grubb 1998). We are therefore conservative in our analyses, because we included in our review the experiment with a mild stressful treatment.

Thomas (2000) studied body mass trajectories in 10 free-living European robins, *Erithacus rubecula*, that were provided or not with supplementary food. Body masses were measured 10 times per day and bird, although the results were pooled by treatment in the published results (figure 1 in Thomas 2000). We calculated a delay of

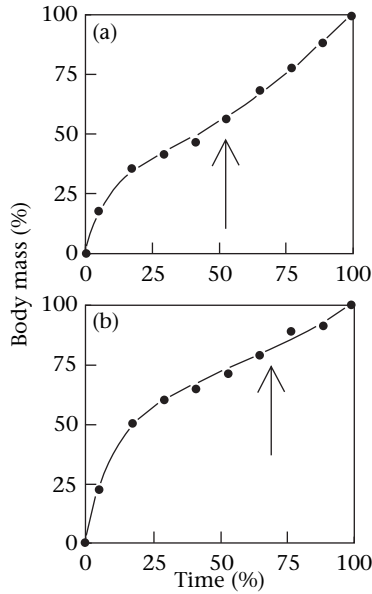


Figure A10. Body mass trajectories of coal tits when food was delivered at (a) high and (b) low rates. Adapted from figure 1 in Polo & Bautista (2006). Lines and arrows explained in Fig. A1.

3.5% in the inflexion time (Fig. A8) on the day after the supplementary food was removed.

Pravosudov & Lucas (2000) studied daily body mass trajectories of 28 Carolina chickadees, *Poecile carolinensis*, foraging alone or in pairs (male and female) with two levels of food availability (ad libitum and limited). We calculated a delay of 7.82% in the inflexion point when food was limited (Fig. A9).

Our companion paper describes a study of daily body mass trajectories of eight coal tits, *Periparus ater*, foraging

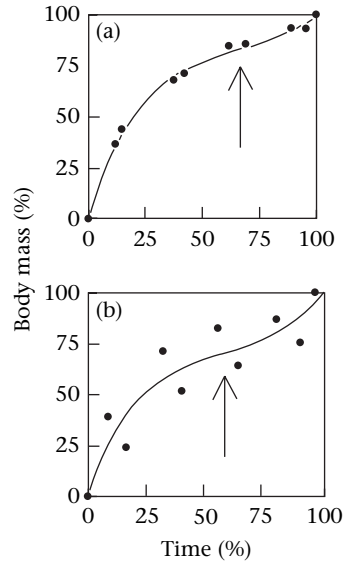


Figure A12. Body mass trajectories of yellowhammers on days (a) before and (b) after a stuffed sparrowhawk was displayed. Adapted from figure 2 in van der Veen (1999). Lines and arrows explained in Fig. A1.

in pairs kept in small cages with two levels of food availability (high and low). We calculated a delay of 16.7% in the inflexion point when food was low (Fig. A10).

Figures A11–A13 show the trajectories fitted to three studies that included predation risk as a stressful treatment (Lilliendahl 1998; van der Veen 1999; van der Veen & Sivars 2000). Predation risk is expected to delay the increase in body mass towards the second part of the day (McNamara et al. 1994; Bednekoff & Houston 1994a), and advance the inflexion time of the trajectory.

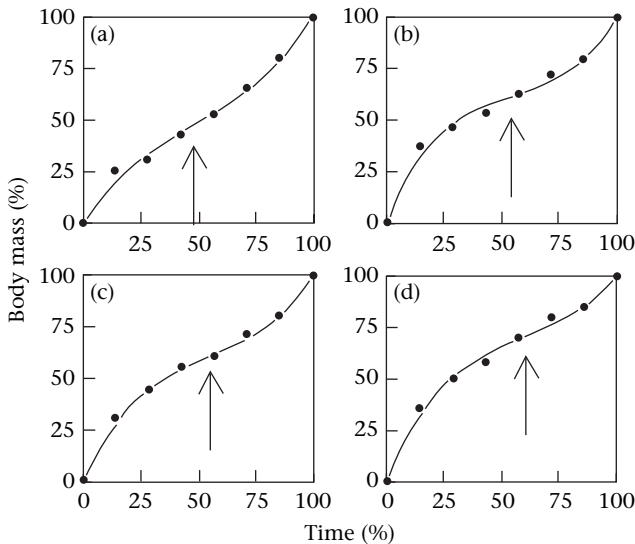


Figure A11. Body mass trajectories of (a, b) subordinate and (c, d) dominant yellowhammers on days when a stuffed sparrowhawk was (a, c) concealed or (b, d) displayed. Adapted from figure 1 in Lilliendahl (1998). Lines and arrows explained in Fig. A1.

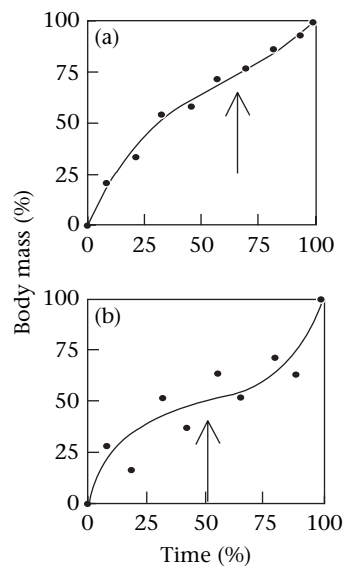


Figure A13. Body mass trajectories of yellowhammers on (a) control days and (b) days when a stuffed sparrowhawk was displayed. Adapted from figure 2a in van der Veen & Sivars (2000). Lines and arrows explained in Fig. A1.

Lilliendahl (1998) studied the effect of predator presence on daily mass trajectories of eight pairs of captive yellowhammers, *Emberiza citrinella*. A stuffed sparrowhawk in a flying position was flown over the cage at the beginning of the morning. The birds received slightly more food than they needed to survive daily. We calculated a delay of 5.26% in the inflexion point when the predator was shown (Fig. A11). This result was not consistent with the expected advance in the inflexion time.

van der Veen (1999) studied the effect of predation risk on daily mass trajectories of 20 captive yellowhammers. A stuffed sparrowhawk was shown perching near the yellowhammers four times per day. The trajectory of body mass was traced with 10 data points recorded at fixed times with an automatic balance, before and after the sparrowhawk was shown, and the body masses were recorded at

the start and the end of the day. Data points were pooled by treatment (figure 2 in van der Veen 1999). We calculated an advance of 6.94% in the inflexion point when the sparrowhawk was shown (Fig. A12). The sign of this result was consistent with an expected advance under predation risk.

van der Veen & Sivars (2000) aimed to distinguish between effects of feeding interruptions and predation risk. They studied 24 yellowhammers under feeding interruptions and under predation risk simulated by a stuffed sparrowhawk and by a dummy (an opaque plastic bottle). Body mass gain was postponed to the end of the day when the stuffed sparrowhawk or dummy was shown. We calculated an advance of 16.1% in the inflexion points between the sparrowhawk and the control treatments (Fig. A13). The sign of this result was consistent with the expected advance under predation risk.