

1 Opinion piece

2 *Keeping slim when food is abundant: what energy mechanisms could be at play?*

3 Lewis G. Halsey

4 University of Roehampton, London SW15 4JD U.K.

5 l.halsey@roehampton.ac.uk

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7 Keywords: activity, bird, digestive efficiency, energy expenditure, metabolic rate,

8 mitochondria, obesity

9 Running title: Body weight control

10 **Abstract**

11 The obesity epidemic in humans is juxtaposed by observations of passerine birds
12 exhibiting fine-scale body mass regulation. The ecology literature is replete with research
13 into why these animals regulate body weight, citing trade-offs between competing
14 pressures such as emaciation and predation. Yet studies on the underlying mechanisms of
15 mass regulation in these animals are scarce. Maintaining or decreasing weight is obviously
16 achieved by limiting food intake. However, there are numerous reasons why an animal may
17 not control ingestion precisely. This review investigates the plausibility of possible
18 behavioural and physiological mechanisms to adaptively maintain or decrease body mass in
19 birds and other animals. Candidate behavioural mechanisms include exercising, and
20 fidgeting, while physiological mechanisms could include reducing digestive efficiency or
21 mitochondrial efficiency.

22 **Teaser:** Passerine birds exhibit fine-scale weight regulation. Why they do this has been
23 widely studied, but little is known about how. Evidence for a plethora of possible
24 behavioural and physiological mechanisms is reviewed.

25 Many people who have unfettered access to food become progressively fatter [1]. Passerine
26 birds, in contrast, do not. My analysis of recently published data show that birds living in
27 close proximity to feeders, providing them with an almost limitless food supply, nonetheless
28 maintain very consistent body weights (Figure 1A). Yet while body weight control is
29 documented for a number of wild species [e.g. 2], there has been relatively little research
30 into how they achieve this feat. The aphorism that weight can only be lost when your
31 energy intake is lower than your energy expenditure may be sage advice for the dieter [c.f.
32 3] but belies the plethora of mechanisms that could manipulate the body's energy stores
33 and thus play a role for those species, and those individuals, that stay slim in a food-rich
34 environment. In this essay, I consider these mechanisms and the possibility that they are
35 involved in the impressive weight consistency, and even regulated weight reduction,
36 exhibited by certain birds and other species.

37 **Birds and other animals staying slim**

38 The life of a bird can be cut short by starvation [4], with an unpredictable cold snap both
39 reducing food availability and increasing energy expenditure [5, 6]. Succumbing to disease
40 can be equally insidious by restricting foraging [7]. Yet even when food is available *ad*
41 *libitum*, passerine birds do not store copious amounts of adipose tissue to guard against
42 such misfortunes – they do not get fat (Figure 1 A and B). Rather, they control their body
43 weight carefully, trading off fat stores between the countering demands of enduring the
44 winter (or surviving disease) and escaping predation. They put on a limited amount of extra
45 fat when predicting food scarcity and remove that fat when predation pressure mounts [8-
46 13]. This trade-off occurs because extra adipose tissue probably decreases a bird's capacity
47 to accelerate when fleeing a predator [14-16]. For example, Zimmer et al. [10] argue that

48 the loss of mass exhibited by tufted ducks *Aythya fuligula* and teal *Anas crecca* in response
49 to predatory pressures afforded them a more favourable wing loading and increased their
50 flight power by 7-10%, probably enhancing their flight performance (cf. [17]).

51 How did the ducks accomplish this reduction of their body weight to a lower homeostatic
52 set point? Zimmer et al. [10] interpret the mass lost as entirely due to a voluntary reduction
53 in foraging. However, greenfinches *Carduelis chloris* appear to employ a physiological,
54 rather than behavioural, mechanism to achieve the same ends. Lilliendahl [18] observed
55 that greenfinches stopped foraging and sat motionless for 20 minutes when a mock hawk
56 was flown overhead. During these periods the greenfinches lost body mass, as would be
57 expected, but at a much higher rate than during the night or even at the end of the day
58 once foraging ceased. This suggests that they lost mass adaptively. The two conceivable
59 mechanisms to accomplish this are an increase in metabolic rate or an emptying of the
60 digestive tract.

61 In general, an animal striving to maintain, or reduce, its body mass in the face of high food
62 availability has, at least in theory, a number of behavioural and physiological levers it could
63 pull. Most obviously, it could reduce foraging time [19] and consequently ingest no more
64 calories than it would do during times when food availability is lower. This behavioural
65 strategy could also serve to reduce exposure time to predators [20-22]. Specifically, foraging
66 time could be reduced either by decreasing the period during which foraging attempts are
67 made [23] or spending less time at feeding sites [24], or by ingesting less food per visit to
68 the feeding site [25]. Sometimes, however, it may be the case that animals are unable to
69 resist the lure of easily available, attractive food [26] due to a deep-seated drive to eat
70 whenever possible as an adaptation to an unpredictable environment [27]. They may opt to

71 binge-feed during windows of opportunity when predators are absent [22], or when the
72 commuting distance back to their territory is long [28], or if they are young, unconfident
73 foragers [28]. Alternatively, an animal may be obliged to keep feeding beyond an energy
74 optimum if its diet is nutrient poor [29; in particular, their Figure 7d]. Moreover, given the
75 plethora of influences on foraging behaviour, it is unclear that feelings of satiation moderate
76 feeding behaviour sufficiently accurately to absolutely maintain target body weight. For
77 these reasons, it is likely that other behavioural mechanisms, and quite possibly
78 physiological mechanisms, form part of the capacity of some animals to control against
79 weight gain.

80 While the ecology literature is abound with studies observing weight control by animals in
81 order to trade off against competing threats, studies on the mechanisms that animals
82 employ to achieve this are scarce. The remainder of this essay explores this knowledge gap,
83 by investigating the plausibility of possible behavioural and physiological mechanisms to
84 correct for over-feeding (Figure 2).

85 **Adjusting activity and posture**

86 People seeking to control their weight are advised to increase their exercise levels [30, 31].
87 Animals may also enact this strategy. In endotherms, activity that is sustainable for minutes
88 to hours can increase metabolic rate up to around 10-fold [32], and bursts of exercise
89 incorporating intermittent rest periods can support power outputs considerably higher [33,
90 34]. Possibly apart from shivering [35, 36], activity affords the most rapid way to reduce
91 weight through the reduction of tissue mass. There is little evidence that animals go for the
92 equivalent of a jog. Rather, if indeed animals undertake exercise to control their weight they
93 perhaps incorporate this in involuntary tasks, for example by spending more time

94 interacting with conspecifics, or moving to a new location at an energetically sub-optimal
95 speed or via more energetically demanding routes [37-39]. Perhaps for this reason, as yet
96 there is little direct evidence of animals undertaking activity for the purposes of 'keeping in
97 good physical shape' [40], though there is indirect evidence building [41-43]. Nonetheless,
98 animals including mice, rats and frogs were recorded running on a wheel in the wild when
99 one was made available [44]; an unnatural context but one that demonstrates the capacity
100 of animals to undertake activity of their own volition and of a type not directly for the
101 purpose of foraging, socialising or reproducing.

102 Subtler adjustments to activity, but enacted over extended periods, can also serve to
103 substantially increase overall energy expenditure. Protracted fidgeting is one example,
104 though its effects on weight control have only been investigated in humans [45]. Chronic
105 differences in body posture is another; standing rather than sitting is energetically more
106 expensive in a range of morphologically diverse animals including people [46, 47], broiler
107 chickens *Gallus gallus domesticus* [48], canaries *Serinus canaria* [49] and barnacle geese
108 *Branta leucopsis* [50]. Sometimes, the same activity can incur different energy costs without
109 apparently differing itself. For example, in volant animals, increased body mass increases
110 wing loading and thus the power costs to fly [51, 52]. In theory, then, for volant species,
111 greater weight from feeding may result in heightened flight energy costs serving as a
112 negative feedback mechanism to weight gain.

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115

117 Text box: Singing away supper

118 Could singing, an activity undertaken by many animals, serve as a form of weight-control
119 exercise? The energy costs to sing have only rarely been measured in humans [53], and are
120 low. Nonetheless, in species for which singing is a key element of their ecology, this activity
121 might be employed to increase levels of daily energy expenditure. Direct measurements of
122 singing energy costs in birds have been obtained for canaries and pied flycatchers *Ficedula*
123 *hypoleuca*, which experience an increase in metabolic rate equivalent to that required to
124 stand, representing a 2.5-fold increase in metabolic rate during sleep [49, 54]. Thus if birds
125 commit to chorus for a considerable portion of the day it could substantially increase their
126 daily energy expenditure and reduce their body weight.

127

128 Adjusting the background costs of existing

129 The idling costs of the body – the on-going metabolic process necessary to maintain
130 functional integrity in the long term – are encompassed in the body's background metabolic
131 rate. Background metabolic rate can represent a substantial, even the majority, proportion
132 of an animal's daily energy costs, both in humans [55] and in other animals [56], so changes
133 in background metabolic rate could have a distinct influence on weight control. Indeed,
134 background metabolic rate is known to vary in response to body condition. Some animals
135 reduce their background levels of oxygen consumption in response to food restriction,
136 either in the laboratory [57, 58] or in a natural context [59, 60], presumably to elongate the

137 period of time before they would reach emaciation. This has also been observed, albeit
138 subtly, in humans [61, 62].
139
140 Background metabolic rate can also increase, during periods of food glut. In rats,
141 background metabolic rate increases in response to overeating [63]. Animals provided a diet
142 of various highly palatable foods consumed 80% more energy yet gained only 27% more
143 mass than control animals, exhibiting around a 30% increase in background metabolic rate
144 [64]. In rodents, it is clear that a key mechanism to upregulate background metabolic rate is
145 brown adipose tissue, which contains uncoupling proteins that can generate heat without
146 the animal being active - non-shivering thermogenesis [64, 65]. Mice employ this
147 mechanism to compensate for overeating, known as adaptive diet-induced thermogenesis;
148 the magnitude of their thermogenesis increases overtime on an obesogenic diet [66]. In
149 humans it is less clear to what extent background metabolic rate can increase in response to
150 overeating [45, 67, 68], however synthetic uncoupling agents were used to treat obesity in
151 the 1930s (until over-zealous prescriptions of this elixir caused severe side effects) [69]. For
152 several decades we have known that humans also have brown adipose tissue [70-72]. The
153 mass of brown adipose tissue in the human body is typically hundreds of grams [70] and its
154 oxidative metabolism can increase at least 10-fold in response to cold exposure resulting in
155 a doubling of whole-body energy expenditure [73], with an even greater increase following
156 acclimation to chronic cold exposure [74]. Direct evidence for a role of brown adipose tissue
157 in the regulation of energy stores in the human body has yet to be forthcoming, however
158 there is indirect evidence for this mechanism in the form of inverse relationships between
159 brown adipose tissue and body mass index. Participants with a higher body mass index are
160 less likely to have brown adipose tissue detected by PET and CT scan [75], and only people

161 who do not exhibit cold-activated brown adipose tissue develop greater visceral fat with age
162 [76].

163

164 Shivering thermogenesis is another major mechanism by which background metabolic rate
165 can be increased [36]. It is a powerful generator of body heat; humans, for example,
166 experience a several-fold increase in metabolic rate during a bout of shivering [35]. While
167 shivering is presumed to have the singular aim of defending the body from hypothermia, at
168 least in theory animals could seek out temperatures below, or even above, their thermal
169 neutral zone [77] to precipitate increases in background metabolic rate due to shivering [36,
170 78] or evaporative heat loss [79], respectively.

171

172 Birds do not have brown adipose tissue but nonetheless have the ability to increase heat
173 generation in a similar fashion to mammals [80]. Juvenile king penguins, for example, exhibit
174 expression of the avian homologue of mammalian uncoupling protein once they have
175 become adapted to cold seawater [81]. During the breeding period, king penguins fast for
176 up to several weeks while guarding their egg or chick, and to reduce the rate that their
177 endogenous energy stores are depleted they decrease their background metabolic rate by a
178 third [60], in part by reducing the abundance of avian uncoupling protein [80]. Levels of
179 non-shivering thermogenesis and metabolic rate return after the penguins have fed for
180 three consecutive days [60] - an example of background metabolic rate increasing in birds in
181 response to food ingestion. Presumably, the reason for this increase in metabolic rate by the
182 penguins is not to counteract excessive food consumption, however it represents some of
183 the only evidence to date of background metabolic rate increasing in response to feeding in
184 an animal outside of the laboratory. As far as I am aware, no study to date has yet

185 investigated whether any species in the wild adjusts its background metabolic rate to
186 control body weight, despite the plethora of studies documenting many endotherms varying
187 their body temperature considerably [82], sometimes up to sublethal temperatures [79, 83].

188

189 Certain uncoupling proteins in brown adipose tissue function by reducing the amount of
190 usable energy (adenosine triphosphate; ATP) generated per volume of oxygen consumed in
191 the mitochondria, with the rest dissipated as heat [84]. This is termed the P-O (phosphate to
192 oxygen) ratio. Thus the lower the ratio, the less efficiently an animal converts its metabolic
193 substrates into energy; it uses up more endogenous stores for a given amount of energy
194 expended on background metabolic processes such as protein synthesis, or front-line
195 processes associated with active behaviours. Why might some animals exhibit a reduction in
196 their metabolic efficiency during periods of energy acquisition? This reduced efficiency
197 comes with benefits. At lower mitochondrial membrane potentials associated with lower P-
198 O ratios, cell respiration also creates fewer harmful reactive oxygen species (ROS) [85, 86] -
199 molecules which cause cellular and DNA damage. I propose that species which, in contrast
200 to king penguins, do not undergo dramatic fluctuations in body mass nor aspire to large
201 endogenous fat stores may nonetheless gorge when privy to a food glut, accepting a short-
202 term increase in weight in order to reduce production of ROS. The high availability of energy
203 enables them to reduce their rates of ROS production by decreasing their P-O ratio, which
204 will increase their rate of substrate utilisation to maintain their levels of available ATP, their
205 body weight consequently reverting over time to its previous set point.

206

207 While uncoupling proteins are perhaps the most studied mechanism for controlling
208 metabolic efficiency, other mechanisms exist [see 84 and references therein]. For example,

209 specifically mitochondrial efficiency also depends on the fatty acid composition of the
210 mitochondrial membranes because this composition affects both the fluidity of the
211 membranes and the uncoupling activity of the mitochondrial carriers. Moreover, slippage of
212 the proton pumps may influence mitochondrial efficiency. Finally, cellular-level efficiency
213 can be decreased by stimulating futile cycles that generate ATP without any concomitant
214 generation of work. To give an example, sarcolipin is a regulator of the calcium ion-ATPase
215 pump that can uncouple calcium ion transport from ATP hydrolysis, thereby stimulating
216 muscle thermogenesis and, in turn, increasing background metabolic rate [87].

217

218 **Adjusting assimilation efficiency**

219 Bomb calorimetry calculates the energy density of a food by measuring the heat released as
220 a result of incineration [88]. When used to determine the calorie content of meals it returns
221 overestimates [89] because the gut intestinal tract digests food rather than burning it, and
222 thus does not extract all of the available energy. Digestive (assimilation) efficiency is the
223 percentage of energy present in ingested food taken up by the body as that food transitions
224 through the gut. In other words, it is the proportion of ingested food that is digested. In
225 humans, digestive efficiency of protein has been measured at around 86%, and up to nearly
226 100% for available carbohydrates [90]; for energy in meals as a whole typical digestive
227 efficiency is around 90% [91]. Yet surprisingly little research has investigated the variability
228 of digestive efficiency with quantity of food intake. Olefsky [92] found no change in the total
229 amount of fat in the stools of people when overfed by 2000 kcal a day for several weeks,
230 suggesting that there was no malabsorption by the gut resulting from high volumes of food
231 ingestion. Similarly, Levine et al. [45] found no change in stool fat content when people

232 overate by 1000 kcal each day for 8 weeks. Unfortunately, because these studies measured
233 fat proportions in the stool rather than its entire energy content, and did not account for
234 stool volume, they do not provide strong insights into whether the volume of food ingested
235 changed digestive efficiency.

236 In animals, although the research is almost as thin, several investigations relating digestive
237 efficiency to food volume suggest that efficiency can decrease in response to greater energy
238 intake. Lizards exhibit slight decreases in digestive efficiency when given an ad lib diet [93],
239 while both perch *Perca fluviatilis* and midge larvae exhibit a negative correlation between
240 food intake and digestive efficiency [94, 95]. In some animals at least, this raises the
241 possibility that they reduce relative energy assimilation when food intake is higher. A simple
242 way for the body to purposefully reduce digestive efficiency would be to simply move
243 ingested food rapidly through the gut to limit absorption [96]. Importantly then, while
244 energy intake is usually measured as food ingested, ingested calories are only available to
245 the body once they have been absorbed through the gut intestinal tract.

246 I offer the conjecture that in some contexts it might be optimal for an animal to gorge on
247 food when available to guarantee possession of it, and then assess how much of the
248 contents should be assimilated. In a situation where an animal is regulating its body mass
249 after gorging, the animal might respond by accelerating gut transit time such that the
250 energy it assimilates is considerably less than the energy it ingested.

251 **Conclusions**

252 In an environment of abundant nutrition, an animal aspiring to control its weight, for
253 example by keeping it constant, would most obviously achieve this by limiting its food

254 intake. Yet there are numerous reasons why an animal may not choose, or be able, to limit
255 ingestion to exactly match its energy expenditure, and thus over time its weight will
256 increase. In these situations, either energy expenditure must be increased to match food
257 intake or the efficiency with which food is converted to energy must be decreased. Some
258 human individuals increase exercise rates in an attempt to stave off weight gain, but we do
259 not know whether our bodies can also instigate any purely physiological mechanisms that
260 either increase energy expenditure or decrease digestive efficiency. And we know even less
261 about the strategies that animals employ in these regards.

262 This review has synthesised various sources of indirect evidence (Figure 2) to suggest that
263 the process of energy balance could involve a greater array of mechanisms than simply
264 matching energy-in, through the amount of food consumed, to energy-out dictated by
265 involuntary activity. It seems quite possible that an animal can balance its energetics, or
266 indeed force a negative energy balance, through 'exercising', fidgeting or shivering to
267 increase daily metabolic rate, or by decreasing the efficiency with which it extracts energy
268 from ingested food either at the level of the gut or the cell.

269

271 Outstanding questions box

272 We presently know little about the possible mechanisms that animals use to control their
273 energy throughput and thus regulate body mass. Clever experimental designs for the field
274 will be required to uncover the full gamut of strategies that different species employ to
275 control body weight, and how the level of impact of those strategies is moderated between
276 individuals with different nutritional and physiological makeups. It is now possible to
277 measure frequently the locations and body masses of small animals such as passerines in
278 free-living conditions, and track those data within individuals [19, 97, 98]. Furthermore,
279 animal-instrumented devices to measure subtle behaviours such as body posture are
280 becoming progressively more miniaturised [99], as are devices for measuring heart rate as a
281 proxy for energy expenditure [100]. We do not yet have the technology, however, to
282 capture the stools of free-ranging animals consistently, or to measure UCP activity non-
283 invasively.

284 However, there is one fairly simple experiment, not yet undertaken, which requires
285 relatively little technology and could well prove insightful. Sitting ducks ensure they get
286 airborne quickly when hawks and foxes come preying, by maintaining a lean take-off weight
287 [10]. In contrast, humans no longer fear predators, which might explain why they do not
288 regulate their body mass so keenly [101]. Another, and strong, possibility is that people
289 often ingest calorie-dense meals, which overrides their weight-control systems [1], with
290 particularly sugar-dense meals possibly reducing cellular metabolic rate [102], exacerbating
291 weight gain. Are the weight-control systems of flighty, predator-fearing species immune to
292 exceptionally palatable, high-density foods, or will such animals nonetheless succumb to the
293 'Western disease' as our own species has done?

294

295 **Acknowledgements**

296 I am grateful for very helpful email conversations with Tony Williams, Jeff Yap, Maria

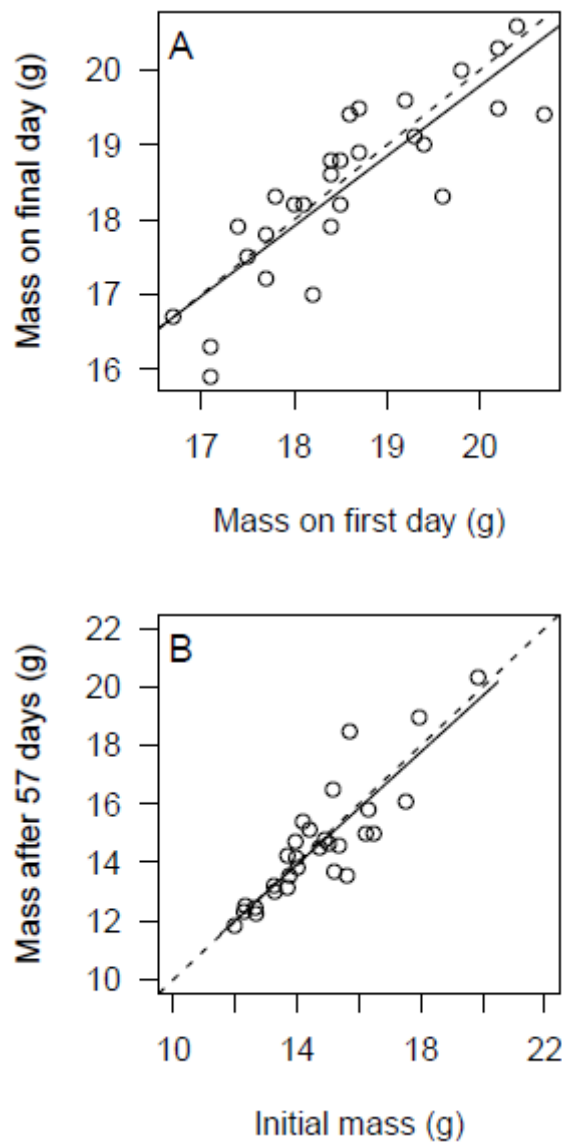
297 Moiron and Stephen Secor.

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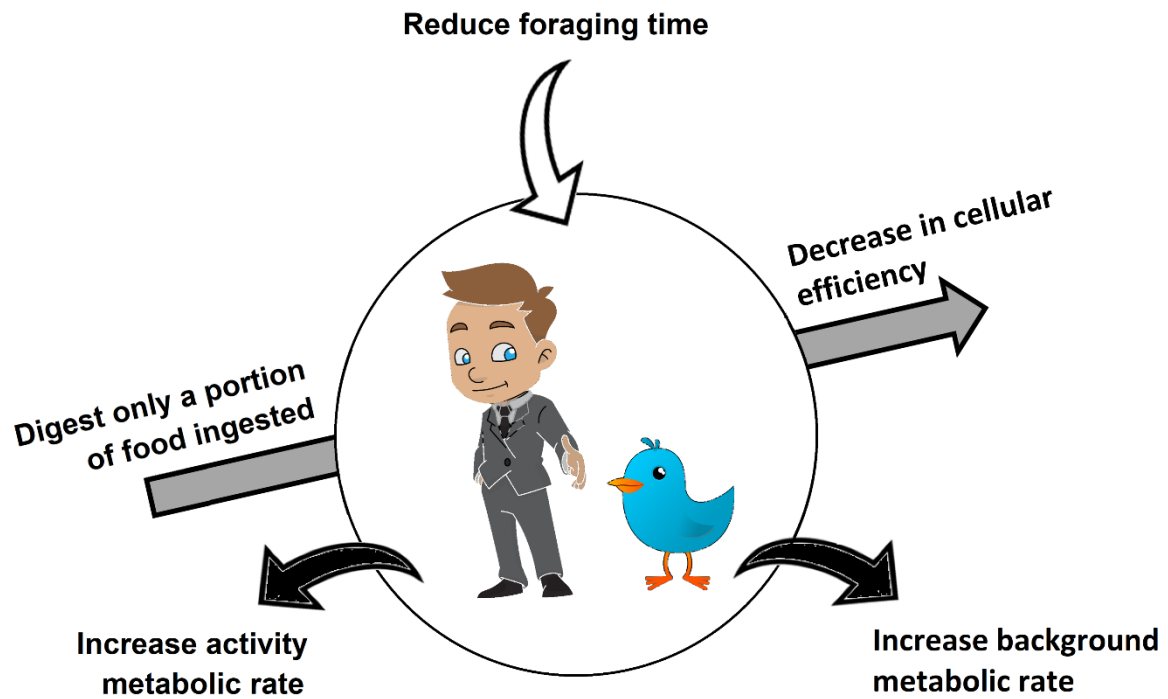


302

303 Figure 1. (A) The body masses of great tits *Parus major* were automatically measured when
304 they foraged ad libitum at feeders placed in their natural habitat. Differences in their body
305 mass between the first measurement obtained and the final measurement (spanning up to
306 40 days) were negligible - the line of best fit (full line) is very close to the line of unity.

307 Analysis undertaken on data published in [19] and made available in a Dryad data package
308 [103]. (B) Similar body mass consistency is displayed by passerines in a laboratory context.
309 Zebra finches *Taeniopygia guttata* living in cages with ad libitum access to food for 57 days
310 exhibited no systematic change in body mass. Again, the line of best fit is very close to the
311 line of unity. Data reported in [104].

312



313

314

315 Figure 2. Possible mechanisms in humans and other animals to regulate energy throughput

316 in order to maintain or even decrease body mass when food availability is high. Most

317 obviously, foraging time could be reduced (open arrow) to reduce energy intake. Beyond

318 this, increases in metabolism would serve to increase energy expenditure (black arrows),

319 while the efficiency with which food is converted to energy could be reduced both in terms

320 of digestion efficiency and the efficiency with which metabolic substrates are converted into

321 energy (grey arrow).

322

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