1 Opinion piece

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

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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.

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

Birds and other animals staying slim

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

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

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

Adjusting activity and posture

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

period of time before they would reach emaciation. This has also been observed, albeit subtly, in humans [61, 62].

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

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

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

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

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

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

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

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

Adjusting assimilation efficiency

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

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

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

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

Conclusions

In an environment of abundant nutrition, an animal aspiring to control its weight, for 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.

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Outstanding questions box

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

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

294

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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

Figure 2. Possible mechanisms in humans and other animals to regulate energy throughput in order to maintain or even decrease body mass when food availability is high. Most obviously, foraging time could be reduced (open arrow) to reduce energy intake. Beyond this, increases in metabolism would serve to increase energy expenditure (black arrows), while the efficiency with which food is converted to energy could be reduced both in terms of digestion efficiency and the efficiency with which metabolic substrates are converted into energy (grey arrow).

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