# Food insecurity increases energetic efficiency not food consumption

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**Short title:** Food insecurity increases energetic efficiency

**One sentence summary:**

Starlings maintained on food that was both temporally limited and unpredictable gained

body mass despite eating substantially less.

# Abstract

Food insecurity—defined as limited or unpredictable access to nutritionally adequate food—is associated with higher body mass in humans and birds. However, the mechanisms underlying this effect are unknown. Here, we demonstrate that European starlings respond to 1-2 weeks of experimentally imposed food insecurity by increasing their energetic efficiency—calculated as the body mass maintained per unit of food consumed. Overall, food-insecure birds increased their body mass despite eating less. Increased energetic efficiency may be partially explained by increases in energy absorbed from food and decreases in physical activity. These energy-saving responses continued after food security was reinstated. We argue that these findings have implications for research into how food insecurity causes obesity in human populations.

## Introduction

Food insecurity is a concept developed in social science to describe limited or unpredictable access to nutritionally adequate food. The 'food-insecurity-obesity paradox' refers to the robust positive association found in Western developed countries between food insecurity and obesity (*1*). Progress in understanding this effect has been hampered because food insecurity is assessed with general statements on a self-report questionnaire, meaning that we don't know in detail what behavioural changes it causes. Recently we used data from food diaries in the US National Health and Nutrition Examination Survey to show that the clearest behavioural correlate of food insecurity is higher variability in time gaps between meals (*2*). This result licences a link between human food insecurity and a well-developed literature in behavioural ecology exploring the optimal response by animals to temporally variable food (*1*, *3*). A plausible evolutionary explanation for mass gain when food is temporally variable is that increased fat reserves provide insurance against starvation (*1*). However, the proximate mechanisms underlying this response are unknown (*3*, *4*).

It is widely assumed that food-insecure individuals are fatter because they consume more food (*3*, *5*). Experience of unpredictable food could magnify food-seeking motivation, leading to greater food consumption and increased body mass (*3*, *6*). However, the evidence that food-insecure people actually have higher energy intake is weak. While food-insecure participants eat more when given the opportunity in the laboratory (*7*, *8*), there is no evidence that they actually eat more in their home environments (*4*, *9–11*). Furthermore, increases in body mass index in pre-school girls whose households transitioned from food security to food insecurity were not associated with changes in either diet quality or total energy intake (*12*). Thus, it is currently unclear whether the mass gain associated with food

insecurity is caused by increased energy intake. It is equally plausible that food-insecurity-induced weight gain results from decreased energy expenditure, or a combination of consuming more energy and expending less. One approach to resolving this issue is to study the mechanisms underlying the food-insecurity obesity paradox in an animal model.

Here we report the results from a series of experiments in which we tested the effects of food insecurity on body mass and food intake in European starlings (*Sturnus vulgaris*). The starling is an omnivorous passerine bird that has been used as a model in laboratory studies of foraging behaviour and body weight regulation. Starlings thrive in temperate regions characterised by seasonal variation in food availability and respond rapidly to environmental changes that alter optimal fat reserves. Exposure to temporally variable and unpredictable food causes increased fat deposition and body mass (*13–17*), but there are few data on how food insecurity affects foraging or food consumption (*15*). Therefore, our aim was to develop an ecologically-valid model of food insecurity in starlings and use this to test the hypothesis that food-insecurity-induced weight gain is caused by increased foraging motivation leading to increased food consumption.

We conducted four experiments on group-housed birds in large aviaries (Fig. 1, Table S1). In each experiment, birds were exposed to a baseline week of food security (FS1), during which food was available *ad libitum*, followed by one or two weeks of food insecurity (FI, $FI_{low}$, $FI_{high}$), during which food availability was both temporally limited and unpredictable. In experiments 1-3 food insecurity was induced by removing food for 12 out of a possible 20 randomly chosen 20-min periods starting two hours after dawn each day. In experiment 4 food insecurity was induced via an operant schedule, whereby the probability that a key peck was reinforced with 10-s of food access was reduced from 1.0 under food security to 0.4 or 0.2 under food insecurity ($FI_{low}$ and $FI_{high}$ respectively).  In experiments 1

4

and 3, food security was subsequently reinstated for a final period (FS2) of one or two weeks.

In all experiments, a homogeneous complete diet was delivered from custom-built feeding stations (the social foraging system, SFS; Fig. 2) that additionally recorded detailed individual mass data (for details see Fig. S1) via integrated microchip-based identification and an electronic balance. Experiments were conducted in closed economy, with birds receiving the majority of their food from the SFS. To understand energy balance, we recorded the total amount of food consumed per day, and in a subset of experiments we additionally recorded foraging behaviour, inactive roosting behaviour and energy density of guano (faeces plus uric acid). The results presented below focus on meta-analysis of the data, designed to reveal consistent overall effects of exposure to food insecurity.

## Results

### Food insecurity increased body mass

We estimated two measures of body mass for each bird on each day of each experiment: dawn mass, which is the mass before any foraging commenced and reflects changes in body composition including fat reserves, and dusk mass, which is the mass after a day of foraging and additionally reflects gut content (see Fig. S1 or more details). To investigate the effect of food insecurity on body mass we compared dawn and dusk mass on all days during the initial period of food security (FS1) with dawn and dusk mass on all days during the subsequent period of food insecurity (FI in exp. 1-3 and $FI_{high}$ in exp. 4; Fig. 3A-H, Tables S2 and S3). Overall, dawn mass increased by 0.52 g (95% CI -0.12 to 1.17) when birds moved from food security to food insecurity (random effects [RE] meta-analysis: z = 1.59, p = 0.113; Fig. 4A, Table S4) and dusk mass increased by 1.51 g (95% CI 0.78-2.25; RE meta-analysis: z =

4.05, p < 0.001; Fig. 4B, Table S4). These increases correspond to 0.73% and 2.69% of the mean dawn and dusk masses respectively during the initial period of food security.

To address the question of how quickly food insecurity causes changes in body mass, we examined the data from experiment 2, which showed the strongest evidence for food insecurity-induced mass gain. Dawn mass started to show evidence of increasing after three days of exposure to food insecurity and dusk mass was higher after just one day (Fig. S2A,B).

Meta-analysis shows considerable heterogeneity among the effects of food insecurity on dawn and dusk mass (tests for heterogeneity among associations: $\tau^2 \geq 0.95$, Q7 $\geq 29.79$, p < 0.001; Table S4), suggesting possible individual differences in how birds responded to the same (or similar) manipulations. We explored two possible moderators of the effect of food insecurity on mass gain that varied between experiments and aviaries: the baseline mass of the birds in the first food-security period (mean dawn mass) and the degree of competition in the aviary (low, where 2 birds shared one SFS station, or high, where 6 birds shared two SFS stations; see Fig. 1). Addition of these two moderators to the meta-analytic model explained 81.87% of the heterogeneity in the effects of food insecurity on dawn mass (omnibus test of meta-regression: $Q_M2 = 18.52$, p < 0.001) and the test for residual heterogeneity was not significant ($Q_E5 = 5.56$, p = 0.352). The food insecurity-induced increase in dawn mass was greater for birds with lower baseline body mass ($\beta_{baseline\ mass}$ = -0.45 [95% CI -0.67 to -0.23], z = -4.06, p < 0.001; Fig. S3) and for birds in aviaries with higher competition ($\beta_{high\ competition}$ = 1.76 [95% CI 0.55 to 2.96], z = 2.86, p = 0.004; Fig. S3). The results for dusk mass were similar. The moderators explained 76.41% of the heterogeneity in the effects on dusk mass (omnibus test of meta-regression: $Q_M2 = 16.34$, p < 0.001). The effect of food insecurity on dusk mass gain was greater for birds with lower baseline body mass ($\beta_{baseline\ mass}$ = -0.50 [95% CI -0.67 to -0.23], z = -2.90, p = 0.004) and in

6

aviaries with higher competition ($\beta_{\text{high competition}}$ = 3.60 [95% CI 1.76 to 5.44], z = 3.84, p = 0.001). However, the test for residual heterogeneity was still significant in this case ($Q_E5$ = 12.63, p = 0.027).

To investigate the effect of reinstating food security in experiments 1 and 3, we compared dawn and dusk mass in the second period of food security with the preceding periods of food insecurity and food security. Reinstating food security had no effect on dawn mass in either experiment (Fig. 3A,C, Table S2), but dusk mass declined in both experiments relative to the preceding period of food insecurity (Fig. 3E,G, Table S3). Despite this decline, dusk mass in experiment 3 remained marginally non-significantly higher over a two-week period than it had been during the initial period of food security (Fig. 3G, Table S3).

## Food insecurity increased foraging behaviour

We recorded key pecking from the operant schedules in experiment 4 and used these to investigate how birds responded to the reduced probabilities of reinforcement under food insecurity. Birds increased their frequency of key pecking during the periods of food insecurity ($FI_{\text{low}}$ and $FI_{\text{high}}$) compared to food security (LMM: $F_{2,118}$ = 87.16, p < 0.001; Fig. S4A, Table S5). The birds also exploited each 10-s reinforcement more effectively, consuming more food per second under food insecurity (LMM: $F_{2,55}$ = 23.07, p < 0.001; Fig. S4B, Table S5). These responses were graded, with birds pecking and eating more under $FI_{\text{high}}$ than under $FI_{\text{low}}$ (Tale S5). However, this increased foraging effort was insufficient to compensate for the reduced probabilities of reinforcement under food insecurity. The birds earned fewer reinforcements per day (LMM: $F_{2,118}$ = 32.95, p < 0.001; Table S5) and overall ate less food per day under food insecurity (LMM: $F_{2,54}$ = 8.77, p < 0.001; Fig. 3L, Table S6).

## Food insecurity reduced total food consumption

For all four experiments we calculated the mean consumption per bird per day and compared this estimate on all days during the initial period of food security and all days during the subsequent period of food insecurity for each experiment (Fig. 3I-L, Table S6). Overall food consumption dropped by 2.50 g.bird$^{-1}$.day$^{-1}$ (95% CI: -3.13 to -1.87) when birds moved from food security to food insecurity (RE meta-analysis: z = -3.08, p = 0.002; Fig. 4C, Table S4). This corresponds to a 13.21% drop in daily consumption compared to the initial period of food security.

There was heterogeneity among the effects of food insecurity on food consumption (tests for heterogeneity among associations: $\tau^2$ = 3.20, Q7 = 61.76, p < 0.001; Table S3). Addition of baseline body mass and competition to the meta-analytic model as moderators did not explain a significant percentage of this heterogeneity (omnibus test of meta-regression: $Q_M2$ = 5.76, p = 0.056).

Reinstating food security had no effect on consumption in experiment 1, but caused an immediate increase in consumption in experiment 3 (Fig. 3K, Table S6). However, consumption during the second period of food security remained lower than during the initial period of food security in both experiments (Fig. 3I,K, Table S6).

## Food insecurity increased energetic efficiency

An interpretation of the results in Fig. 4A-C is that food insecurity increased energetic efficiency, calculated as the body mass maintained per mass of food consumed per day. To test this hypothesis, we calculated the ratio of the mean dawn mass of the birds in an aviary on a given day to the mean mass of food consumed per bird in the aviary in the previous 24 hours. A higher value of this ratio means that birds maintained a higher dawn mass per gram of food consumed. We compared energetic efficiency on all days during the initial

8

period of food security and all days during the subsequent period of food insecurity (Fig. 3M-P, Table S7). Overall, energetic efficiency increased by 0.85 (95% CI 0.65 to 1.06) when birds moved from food security to food insecurity (random effects meta-analysis: $z = 8.17$, $p < 0.001$; Fig. 4D, Table S4). This corresponds to a 17.96% increase in energetic efficiency compared to the initial period of food security. When expressed in comparable units of standard deviations, the effect of food insecurity on energetic efficiency (1.15 sd) is larger than that on dawn or dusk mass alone (0.17 and 0.42 sd respectively). Furthermore, the effect of food insecurity on energetic efficiency is less heterogeneous between studies than the effects on body mass ($\tau^2 = 0.20$, $Q_7 = 29.35$, $p < 0.001$). Addition of baseline body mass and competition to the meta-analytic model as moderators did not explain a significant percentage of the heterogeneity (omnibus test of meta-regression: $Q_M 2 = 5.26$, $p = 0.072$).

Reinstating food security had no effect on efficiency in experiment 1, but caused an immediate decrease in efficiency in experiment 3 (Fig. 3M,O, Table S7). However, efficiency during the second period of food security remained higher than that during the initial period of food security in both experiments (Fig. 3M,O, Table S7).

## Food insecurity reduced the energy density of guano

In experiments 1 and 3 we used bomb calorimetry to measure the effect of food insecurity on the energy density of the birds' guano. In experiment 1 there was a marginally non-significant effect of treatment (FS1 vs FI vs FS2) on the energy density of guano (ANOVA: $F_{2,19} = 3.48$, $p = 0.051$; Fig. 5A, Table S8) and in experiment 3 the effect was significant (ANOVA: $F_{2,53} = 6.82$, $p = 0.002$; Fig. 5B; Table S8). In experiment 1, in which food insecurity lasted for 14 days, the energy density of guano decreased during food insecurity relative to the initial period of food security ($\beta FI = -0.17$ [95% CI -0.33 to -0.01], t-test, $t_{19} = -2.13$, $p = 0.047$), whereas in experiment 3, in which food insecurity only lasted for only 7 days, there

was no difference between food insecurity and the initial period of food security ($\beta$FI = -0.07 [95% CI -0.22 to 0.09], t-test, t53 = -0.84, p = 0.403). The effect of food insecurity on the energy density of guano observed in experiment 1 corresponds to a 1.31% decrease in energy density compared to the initial period of food security.

Reinstating food security had no effect on energy density of guano in experiment 1 ($\beta$FS2 = -0.06 [95% CI -0.22 to -0.09], t-test, t19 = -0.77, p = 0.452), whereas it was associated with a decrease in energy density of guano in experiment 3 ($\beta$FS2 = -0.17 [95% CI -0.30 to -0.04], t-test, t53 = -2.45, p = 0.018). In both experiments, energy density of guano was lower during the second period of food security than it had been during the initial period of food security (exp. 1: $\beta$FS2 = -0.23 [95% CI -0.41 to -0.05]. t-test, t19 = -2.51, p = 0.022; exp 3.: $\beta$FS2 = -0.24 [95% CI -0.37 to -0.10], t-test, t53 = -3.42, p = 0.001).

## Food insecurity reduced physical activity

In experiments 1-3 we scored the proportion of scans of the aviary in which birds were observed roosting as a measure of physical inactivity. Scans were made during the period between 0900 and 1100 when *ad libitum* food was always available regardless of the food insecurity treatment in place that day. We modelled the effects on roosting of the treatment experienced the previous day (Fig. 6A-C). Overall, the proportion of scans in which the birds were observed roosting increased from 0.62 to 0.67 under food insecurity, but this increase was not significant overall (RE meta-analysis on arcsine square root transformed proportions: estimate = 0.07 [95% CI -0.15 to 0.28], z = 0.60, p = 0.550; heterogeneity: $\tau^2$ = 0.04, Q4 = 33.59, p < 0.001; Fig. 6D). Only in experiment 3 did food insecurity significantly increase roosting ($\beta$FI = 0.17, 95% CI 0.08 to 0.27; t-test, t24 = 3.47, p = 0.002; Fig. 6C, Table S9).

Reinstating food security was associated with an increase in roosting in experiment 1 ($\beta$FS2 = 0.27 [95% CI 0.16 to 0.38], t-test, t76 = 4.87, p < 0.001), but no change in roosting in experiment 3 ($\beta$FS2 = -0.05, 95% CI -0.13 to 0.03; t-test, t23 = -1.19, p = 0.245). In both experiments, roosting was more common during the second period of food security than it had been during the initial period of food security (exp. 1: $\beta$FS2 = 0.21 [95% CI 0.09 to 0.34], t76 = 3.39, p = 0.001; exp 3.: $\beta$FS2 = 0.12 [95% CI 0.04 to 0.20], t-test, t23 = 2.79, p = 0.011).

## Discussion

Starlings responded rapidly to food insecurity—defined here as limited and unpredictable access to food—by increasing their dawn and dusk masses by 0.73 and 2.69%, respectively (Fig. 3A-H, 4AB, S2AB). Moreover, food insecurity induced mass gain even when there were no periods of total food deprivation (experiment 4; Fig. 3H), suggesting a response to a relatively subtle change in the schedule of food availability. Although food-insecure birds increased their appetitive foraging behaviour and ate at a higher rate when they had access to food (Fig. S4), they did not consume more food in total. In direct opposition to the predictions of recent mechanistic models (*3*, *6*), food insecurity was associated with a 13.1% *decrease* in daily food consumption and hence energy intake (Fig. 4C). Our data therefore lead to the novel conclusion that starlings respond to food insecurity by increasing their energetic efficiency—calculated as the body mass maintained per unit of energy intake per day—by 17.96% (Fig. 4D). This response may be partially explained by the birds absorbing more energy from their food (Fig. 5) and in some instances reducing their energy expenditure by increasing inactive roosting behaviour (Fig. 6). The changes caused by food insecurity did not immediately reverse when food security was reinstated: energetic

efficiency, energy absorption and physical inactivity all remained higher than they had been at baseline for 1-2 weeks following reinstatement of food security.

Although increased energetic efficiency was sometimes accompanied by increased body mass, there was considerable heterogeneity in how body mass responded to food insecurity, with some birds maintaining their baseline mass and others gaining mass. In support of previous results from birds, starlings were more likely to gain mass under food insecurity if they were lighter at baseline (*16*, *18*) and if they faced greater competition for food in the aviary (*19*, *20*) (Fig. S3). Both of these findings make sense from the perspective of an adaptive account of food insecurity-induced mass gain. If increased mass provides insurance against starvation, then thinner birds should obtain greater benefits from mass gain than fatter birds, who already have sufficient fat reserves to survive periods without food. Birds facing higher competition for food effectively face harsher food insecurity than birds with lower competition, increasing the risk of starvation and hence the fat reserves it is optimal to carry. The finding that both baseline mass and competition moderate the effect of food insecurity on body mass illustrate the importance of interpreting effects of food insecurity within the ecological context.

While gaining mass was sometimes the response to food insecurity, increasing energetic efficiency was the more general response, characterised by larger effect sizes and less heterogeneity. Increasing energetic efficiency implies either increasing the amount of energy absorbed from food, and/or decreasing the amount of energy expenditure. The energy density of the birds' guano decreased under food insecurity, suggesting that the birds were absorbing more energy from their food. Since energy absorbed is a decelerating function of gut residence time, this result could simply be a passive physical consequence of increased gut passage time resulting from slower food intake. Another (not mutually

exclusive) explanation for the guano data, is that the birds responded to food insecurity by strategically changing their gut anatomy or physiology to increase energy absorption. Starlings increase their gut length when switched to higher fibre diets (*21*), and it is therefore possible that they could respond similarly to food insecurity. Increased energy absorption under reduced food intake has previously been reported in starlings (*22*). Rats and rhesus macaques subject to long-term caloric restriction paradigms do not reduce their total daily energy expenditure by the amount predicted by their energy intake, suggesting that these species too must increase their energy absorption when intake is restricted (*23*). Given that the change in energy density of guano was delayed and did not appear to reverse immediately when food security was reinstated, our data favour a strategic adaptation. It seems unlikely that increased energy absorption could be the only explanation for increased energetic efficiency in the current dataset, due to the relatively small size of the effect (1.31% drop in energy density of guano) in relation to the large decrease in food consumption (13.21% drop in daily food consumption). Therefore, additional mechanisms are required.

There was also some evidence that the birds increased the proportion of time spent roosting under food insecurity. Roosting occurs at night and when the birds are not engaged in other activities such as foraging, eating or bathing, and is likely to be associated with the lowest levels of energy expenditure due to physical activity. We measured roosting during the first two hours of the day when food was always available *ad libitum* in experiments 1-3, meaning that any changes in roosting were not a direct response to the current unavailability of food, but must instead have been caused by the food-insecurity treatment in place previously. The fact that the increase in roosting observed in experiment 3 was simultaneous with body mass gain, suggests that reduced physical activity could have been

causal in mass gain. However, since food insecurity did not induce a significant increase in roosting in either experiments 1 or 2, it seems unlikely that decreased physical activity is sufficient to explain the increases in energetic efficiency observed in all experiments, even in conjunction with increased energy absorption.

We did not measure metabolic rate in the current study, but this could be a third pathway by which food-insecure birds save energy (*22*, *24*). There is relevant evidence from randomised controlled trials in humans showing that the energy spent on digestion (thermic effect of food) is lower when variance in intervals between meals was experimentally increased (*25*, *26*). This effect if sustained would produce body mass increases in participants eating isocaloric diets, suggesting that it would be interesting to measure the thermic effect of food in food-insecure animals.

Increasing energetic efficiency when food supplies are limited or unpredictable makes adaptive sense, but raises the question of why birds should operate at reduced energetic efficiency when food is plentiful. There must be fitness costs associated with increased energetic efficiency that are only worth bearing in the face of an immediate increased risk of starvation. The costs associated with the reduction in total daily energy expenditure seen under caloric restriction is assumed to be a reduction in reproductive output (*27*). However, it seems unlikely that this would be the case for food insecurity, given that it is associated with mass gain as opposed to mass loss. An alternative hypothesis is that the increased energetic efficiency induced by food insecurity may be bought at a cost of increased oxidative stress resulting in accelerated ageing (*28*). A difficulty with this argument is that caloric restriction, which is effectively a severe form of food insecurity characterised by loss of body mass, is robustly associated with improved health outcomes and decelerated ageing in many species (*29*). A possible resolution to this apparent paradox

14

would be the existence of a J-shaped relationship between degree of caloric restriction and longevity, with the intermediate levels of restriction associated with food insecurity causing a reduction in longevity relative to either *ad libitum* food or more severe restriction. This could occur if food insecure individuals are attempting to defend reproductive potential in the face of limited food.

Our findings have implications for future research on the mechanisms underlying the links between food insecurity and obesity in humans and highlight the dangers of extrapolating from short-term laboratory studies showing increased food consumption in food-insecure humans (*7*, *8*) to food consumption in the home environment. It is clearly possible for food-insecure individuals to show increased foraging motivation when food is currently available, and still consume less overall due to the constraints imposed by food insecurity. The lack of evidence for increased energy intake in food-insecure humans from analysis of food diaries has been dismissed as under-reporting of food intake by the obese (*8*). However, an alternative hypothesis suggested by our results is that mass gain in food-insecure humans is explained by reduced energy expenditure rather than increased intake.

Only women show increased body mass associated with food insecurity (*1*), meaning that much research on human food-insecurity has been restricted to women. However, our results raise the question of whether increased energetic efficiency has been missed in men. A longitudinal study showing that girls responded to becoming food insecure by gaining body mass, despite no change in energy intake, also reported that boys responded by maintaining their body mass, despite reducing their energy intake (*12*). These results support a common effect of food insecurity on energetic efficiency in children of both sexes. Further work is needed to establish whether this result is also found in food-insecure adults.

In the light of the increased morning roosting seen in some food-insecure birds, it is notable that food insecurity is strongly associated with depression in humans (*30*). Given that fatigue is one of the possible diagnostic symptoms of depression, it is worth considering the hypothesis that depression with fatigue (psychomotor-retarded depression) is part of an evolved response to food insecurity, selected to promote energy saving and fat accumulation in the face of unpredictable food supplies. To our knowledge, there have been no studies analysing associations between food insecurity and the different subtypes of depression (e.g. psychomotor-retarded versus agitated).

In summary, we have demonstrated that while starlings gained body mass under food insecurity, they achieved this despite eating less. It is therefore clear that mass gain under food insecurity is not mediated by increased food consumption in this system. Furthermore, our results suggest that a more general effect of food insecurity is to induce increased energetic efficiency. Further work is required to understand the mechanisms underlying this effect and to explore whether the results generalise to other species including humans.

## Materials and Methods

### Subjects and basic husbandry

Subjects were adult hand-reared European starlings (*Sturnus vulgaris*) originally sourced from nest boxes in Northumberland, UK. The numbers, sexes and ages of birds used in each experiment are given in Table S1. During the experiments, the birds were group-housed in indoor aviaries. In experiments 1-3 the aviaries were rooms (215 × 340 × 220 cm;) and in experiment 4, large walk-in cages (90 x 183 x 183 cm) with one cage per room. In all experiments, room temperature and humidity were maintained at ~18°C and ~40% respectively. Each aviary was furnished with rope perches, wood chippings on the floor, a water bath, a drinker providing *ad libitum* clean water supplemented with vitamins and either one or two social foraging system (SFS) stations (Fig. 2). The light cycle, number of birds per aviary and SFS stations per aviary for each experiment are given in Table S1. In all experiments, birds were maintained on a nutritionally complete diet of commercial poultry starter crumb (Special Diets Services Poultry Starter; henceforth 'food'). Each bird was supplemented with 4 live mealworms daily. Daily husbandry took place at 1700 in experiments 1-3 and at 1100 in experiment 4.

The study adhered to ASAB/ABS guidelines for the use of animals in research. Birds were taken from the wild under Natural England permit 20121066 and the research was completed under Home Office licence PPL 70/8089 with approval of the Animal Welfare and Ethical Review Body at Newcastle University. After the completion of the experiments the birds were retained for further studies.

## Social foraging system

In all experiments, food was delivered from custom-built foraging stations (the social foraging system, SFS; Fig. 2). An SFS station comprised a retractable food hopper and an illuminable pecking key, both of which could only be accessed via a perch designed to accommodate a single bird (the pecking key was only used in experiment 4). The perch was mounted on a load cell that functioned as an electronic balance (engineered to a precision of ±2 g). Beneath the perch there was an aerial tuned to read microchips (radio-frequency identification devices, RFIDs), that were mounted on leg rings of the starlings. Each aviary contained either one or two SFS stations depending on the experiment (Table S1). The SFS stations were connected to a computer in an adjacent room running Whisker experimental control software and additional custom-written software. This computer collected continuous data on the identity and masses of birds visiting each station and, in experiment 4, also controlled the operant schedule in place.

## Manipulations of food insecurity

In experiments 1-3 food security was created by maintaining the SFS hopper in the raised position, and thus available for foraging from dawn until dusk. Food insecurity was induced by completely removing food for 12 out of a possible 20 randomly chosen 20-min periods starting two hours after lights-on each day, and ending 1 hour and 20 minutes prior to lights-off.

In experiment 4 the default position of the food hopper was lowered such that food was unavailable. Food security was created via a ratio schedule, whereby a single peck at the illuminated key on the SFS caused the key light to extinguish and the hopper to raise allowing 10-s access to food. At the end of the reinforcement, the hopper lowered and there was a 2-s inter-trial interval before the key re-illuminated signalling the start of the

next available trial. The operant sessions began at 15 minutes after lights-on each day

(0615) and ended 15 minutes before lights-off (2045). This schedule was designed to mimic

a starling foraging by probing for hidden soil invertebrates. Food insecurity was induced by

reducing the probability that a key peck was reinforced on any given trial to 0.4 under $FI_{low}$

or 0.2 under $FI_{high}$. On unreinforced trials, a peck caused the key light to extinguish and there

was a 10-s delay during which the hopper remained lowered followed by a 2-s inter-trial

interval.

## Procedure

All experiments began with birds being caught from their home aviary, manually weighed

and equipped with two plastic leg rings each of which had a unique RFID microchip attached

(birds wore two chips to guard against data loss in the event that one chip fell off, broke or

was not read due to poor alignment with the SFS aerial). Birds were then released into

experimental aviaries. Food was initially provided *ad libitum* by raising the hoppers of the

SFS stations. Birds were initially encouraged to visit the SFS by placing mealworms around

the stations and in the food hopper, but as soon as they were visiting the SFS readily these

extra mealworms were withdrawn. The first experimental treatment of experiments 1-3

began once the birds were maintaining stable body masses on food obtained from the SFS.

Experiment 4 required additional training for the birds to learn that food could only

be accessed by pecking the illuminated key on the SFS. We used an auto-shaping procedure

whereby illumination of the pecking key signalled subsequent unconditional raising of the

food hopper. Birds first learned a Pavlovian association between the lit key and food and

spontaneously started performing appetitive pecks to the lit key. Pecks to the lit key were

reinforced by immediate hopper raising, thus creating an instrumental association between

key pecking and food. As soon as key pecking was established, hopper raising was made

conditional on key pecking and the birds were moved to continuous foraging, whereby they earned all of their daily food by pecking at the lit key on the SFS. The first experimental treatment of experiment 4 began once the birds were maintaining stable body masses on food earned from the SFS.

The sequence and duration of the treatments experienced in each experiment is shown in Fig. 1. In all experiments birds were maintained in closed economy, obtaining all of their daily food intake from the SFS. The diet was supplemented with four mealworms per bird given during daily during husbandry and supplied in spatially separated bowls to prevent one bird from monopolising the worms. The experiments ran seven days a week with no gap between treatments. The birds' body masses were monitored daily using the data obtained from the SFS balances to ensure that no bird became dangerously thin at any point during the experiment. At the end of the final treatment of each experiment the birds were re-caught, manually weighed and returned to their home aviaries.

## Body mass

In all experiments, body masses were recorded by the SFS between lights-on and lights-off each day; each mass was recorded with a bird identity corresponding to the microchip of the bird on the perch. Each balance measured masses at a frequency of 6 Hz. A stable mass was recorded for a bird if the balance measured five consecutive masses of >50 g that were within a range of 5 g. These criteria were chosen to eliminate masses from birds that were perching incorrectly (e.g. by placing one foot on the food hopper), but to maximise the number of stable masses recorded from moving birds. Once a stable mass had been recorded another stable mass could not be recorded until the balance had measured a mass <10 g indicating that the current bird had left the perch. The accuracy of the balances was checked with a 100-g test mass a minimum of twice daily and a balance was calibrated if the

mass was >102 g or <98 g. In order to control for build-up of guano on the perch over the day balances were tared regularly throughout the day.

The SFS recorded a mean of 4.64 stable masses per bird per daylight hour over the four experiments. The raw masses showed a clear trend of mass increase over the day as expected (Fig. S1), but there was a lot of random error due to the imprecision of the balances and movement of the birds whilst on the perch, and masses were not always available at all times of every day. To estimate comparable dawn and dusk masses for each bird on each day we used the following procedure. As long as a minimum of 10 masses were available, the mass data from each bird-day were fitted with a cubic polynomial (Fig. S1A). To remove biologically impossible outliers, any masses >3g from the fitted line were removed and a new cubic polynomial was refitted to the remaining data. This latter fit was used to estimate dawn and dusk masses for that day. To avoid extrapolation beyond the data, a dawn or dusk mass was only estimated if there was a data point within 1 hour of the estimate. Due to differences in daylight hours between experiments, dawn mass was defined as the fitted mass at 0900 for experiments 1-3 and 0615 for experiment 4; dusk mass was defined as the fitted mass at 1800 for experiments 1-3 and 1815 for experiment 4 (Fig. S1B). Thus, the dusk masses for experiments 1-3 and experiment 4 were estimated 9 and 12 hours after lights-on respectively. A later time was not chosen for the dusk masses in experiment 4 due to the fact that birds often stopped foraging hours before lights-off.

## Operant foraging behaviour

In experiment 4, key pecks were recorded by the SFS between 0615 and 2045 each day. The time of each key peck was recorded with a bird identity and whether or not the peck was reinforced with food (probability of 1.0 under food security and either 0.4 or 0.2 under food insecurity for $FI_{low}$ and $FI_{high}$ respectively).

## Food consumption

Total food consumption in each aviary was estimated daily in all experiments by calculating the difference in the mass of the SFS food hoppers at the beginning and end of the day and subtracting any food collected in a spill tray located beneath each hopper. Hence, consumption data were only available at the aviary level.

## Energy density of guano

Energy density of guano was measured by bomb calorimetry in experiments 1 and 3. Guano samples were collected daily from plastic trays positioned beneath perches in each aviary avoiding any feathers or wood chippings. Hence, guano data were only available at the aviary level. Samples were immediately frozen at -80 °C for storage. On completion of the experiment, samples were dried in a flow oven at 55 °C for 48 hours until stable masses were obtained and finely ground to homogenise. In experiment 1, samples from each aviary were pooled over three days, whereas in experiment 3 all days were measured separately. Bomb calorimetry was outsourced to Pemberton Analytical Services, Shropshire, UK and was conducted blind to the treatment group and technical replicates using a PAR 1261 adiabatic bomb calorimeter with a stated precision of ±0.1% on two determinations.

## Physical inactivity

Data on behaviour was collected in experiments 1-3. Video recordings of the aviaries were made for 15 minutes starting at 0900 and 1000 every day before any food insecurity started using a wide-angle surveillance camera mounted in the ceiling of the aviary. The videos were scored manually using BORIS video coding software(31). A scan sampling method was used, whereby the behaviour of each bird in the aviary was scored every 30 seconds for each 15-minute video. Birds were not individually identifiable from the videos, therefore

data were the proportion of birds in an aviary engaged in a behaviour at each scan. For the current analysis we focussed on roosting behaviour—defined as perching motionless on a high rope perch. In all experiments, roosting was negatively correlated with the majority of other behaviour patterns scored (including walking, foraging and bathing), and was therefore used as a measure of physical inactivity.

## Statistical analysis

Data were analysed using R version 3.5.1(*32*). Below we provide an overview of our statistical approach. Further details of statistical models are given in the Tables S2-S9.

For analysis of the effects of food insecurity in individual experiments we used linear mixed models (LMMs) fitted using the R package 'lme4'(*33*). The models contained random effects to account for sources of non-independence in the datasets. In all models we analysed the effect of treatment: FS1 vs FI vs FS2 in experiments 1 and 3; FS1 vs FI in experiment 2; and FS1 vs $FI_{low}$ vs $FI_{high}$ in experiment 4. In cases where a treatment continued for two weeks, the data were pooled from the first and second weeks of a treatment for statistical analysis, but the graphs in Fig. 3 show the data broken down by week. Since roosting data were proportions, they were arcsine square root transformed prior to analysis. Following any necessary transformation, all models gave satisfactory distribution of residuals, hence a Gaussian error structure was assumed throughout. We used restricted maximum likelihood estimation (REML) and conducted overall significances tests of treatment in the LMMs using Satterthwaite's method.

For meta-analysis we used multi-level random effects meta-analysis models fitted using the R package 'metafor'(*34*). The models contained random effects of aviary nested in experiment. The effect sizes used in the meta-analyses were obtained from LMMs fitted to the data from each aviary using the same models for the analysis of individual experiments

23

described above (with the exception that random effects of aviary were no longer required). Effects of food-insecurity were the parameter estimates ($\beta$ values) and associated standard errors corresponding to: the difference between FS1 and FI for experiments 1-3 and the difference between FS1 and FI$_{high}$ for experiment 4. Tests of modifiers were conducted using meta-regression, whereby both baseline mass and competition (number of birds per SFS station) were added to the meta-analytic models. Estimation was by REML in all meta-analytic models. We used aviary-level data as the unit of analysis for the meta-analyses, because in the experiments involving multiple aviaries (1 and 4) there was considerable heterogeneity in results obtained from the different aviaries. Furthermore, increasing the number of replicates available for the meta-analysis increased the power available for the meta-regressions, making it possible to test for effects of baseline mass and competition.

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# Acknowledgements

**Data and materials availability**: The data files and analysis scripts listed below are available at:

Data files:

| File name and type | Description |
| --- | --- |
| Exp 1 food consumption data.csv | Total amount eaten per day per aviary in Exp 1 |
| Exp 1 mass data.csv | SFS mass data in Exp 1 |
| Exp 1 behaviour data.csv | Manual scoring of behaviour from video in Exp 1 |
| Exp 1 bomb calorimeter data.csv | Energy density of guano in Exp 1 |
| Exp 1 data for meta-analysis by aviary.csv | Consumption, mass and efficiency meta-data from Exp 1 |

| | |
|---|---|
| Exp 1 roosting data for meta-analysis.csv | Roosting meta-data from Exp 1 |
| Exp 2 food consumption data.csv | Total amount eaten per day per aviary in Exp 2 |
| Exp 2 mass data.csv | SFS mass data in Exp 2 |
| Exp 2 behaviour data.csv | Manual scoring of behaviour from video in Exp 2 |
| Exp 2 data for meta-analysis.csv | Consumption, mass and efficiency meta-data from Exp 2 |
| Exp 2 roosting data for meta-analysis.csv | Roosting meta-data from Exp 2 |
| Exp 3 food consumption data.csv | Total amount eaten per day per aviary in Exp 3 |
| Exp 3 mass data.csv | SFS mass data in Exp 3 |
| Exp 3 behaviour data.csv | Manual scoring of behaviour from video in Exp 3 |
| Exp 3 bomb calorimeter data.csv | Energy density of guano in Exp 3 |
| Exp 3 data for meta-analysis.csv | Consumption, mass and efficiency meta-data from Exp 3 |
| Exp 3 roosting data for meta-analysis.csv | Roosting meta-data from Exp 3 |
| Exp 4 food consumption data.csv | Total amount eaten per day per aviary in Exp 4 |
| Exp 4 mass data.csv | SFS mass data in Exp 4 |
| Exp 4 peck data.csv | SFS key pecking and reinforcement data from Exp 4 |
| Exp 4 data for meta-analysis by aviary.csv | Consumption, mass and efficiency meta-data from Exp 4 |
| rfids.txt | Look up table for bird IDs from RFID tag numbers (required by multiple analysis scripts) |

R scripts:

| File name and type | Description |
|---|---|
| Exp 1 mass and consumption analysis.R | R script for analysis of consumption and mass in Exp 1 |
| Exp 1 bomb calorimeter analysis.R | R script for analysis of energy density of guano in Exp 1 |
| Exp 1 behaviour analysis.R | R script for analysis of manually coded behaviour in Exp 1 |
| Exp 2 mass and consumption analysis.R | R script for analysis of consumption and mass in Exp 2 |
| Exp 2 behaviour analysis.R | R script for analysis of manually coded behaviour in Exp 2 |
| Exp 3 mass and consumption analysis.R | R script for analysis of consumption and mass in Exp 3 |
| Exp 3 bomb calorimeter analysis.R | R script for analysis of energy density of guano in Exp 3 |
| Exp 3 behaviour analysis.R | R script for analysis of manually coded behaviour in Exp 3 |
| Exp 4 mass and consumption analysis.R | R script for analysis of consumption and mass in Exp 4 |
| Exp 4 foraging analysis.R | R script for analysis of operant peck data from Exp 4 |

| Meta-analysis script.R | R script for meta-analysis of all experiments |

**Supplementary materials:**
Figures S1-S4
Tables S1-S9

## Figures



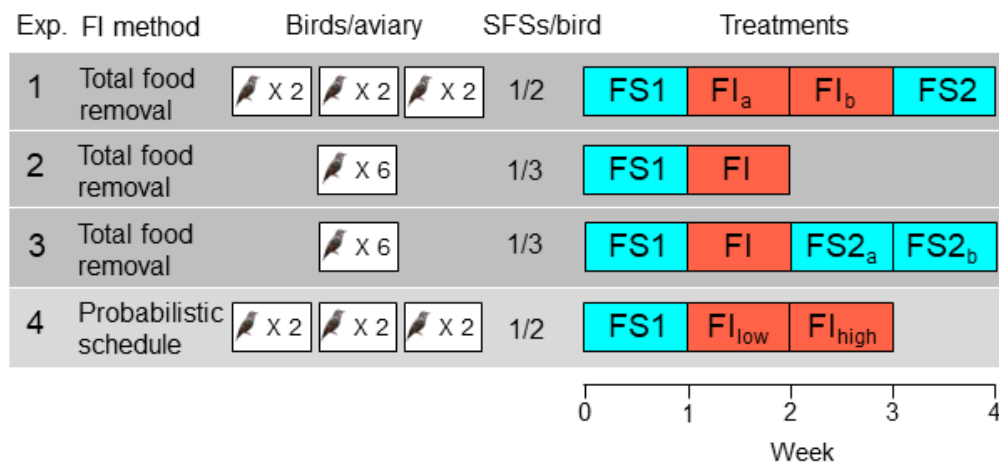**Fig. 1. Experimental designs in experiments 1-4.** Food-secure treatments are shown in blue and food-insecure treatments in red. For treatments that lasted 2 weeks, the first week is designated a, and the second week b, but weeks a and b are pooled in all statistical analyses. In experiment 4, $FI_{low}$ and $FI_{high}$ are treated as two separate treatments in statistical analysis.
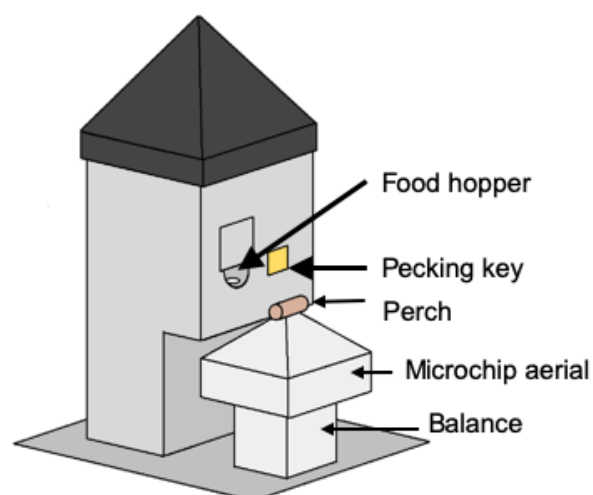


**Fig. 2. A social foraging system station.**
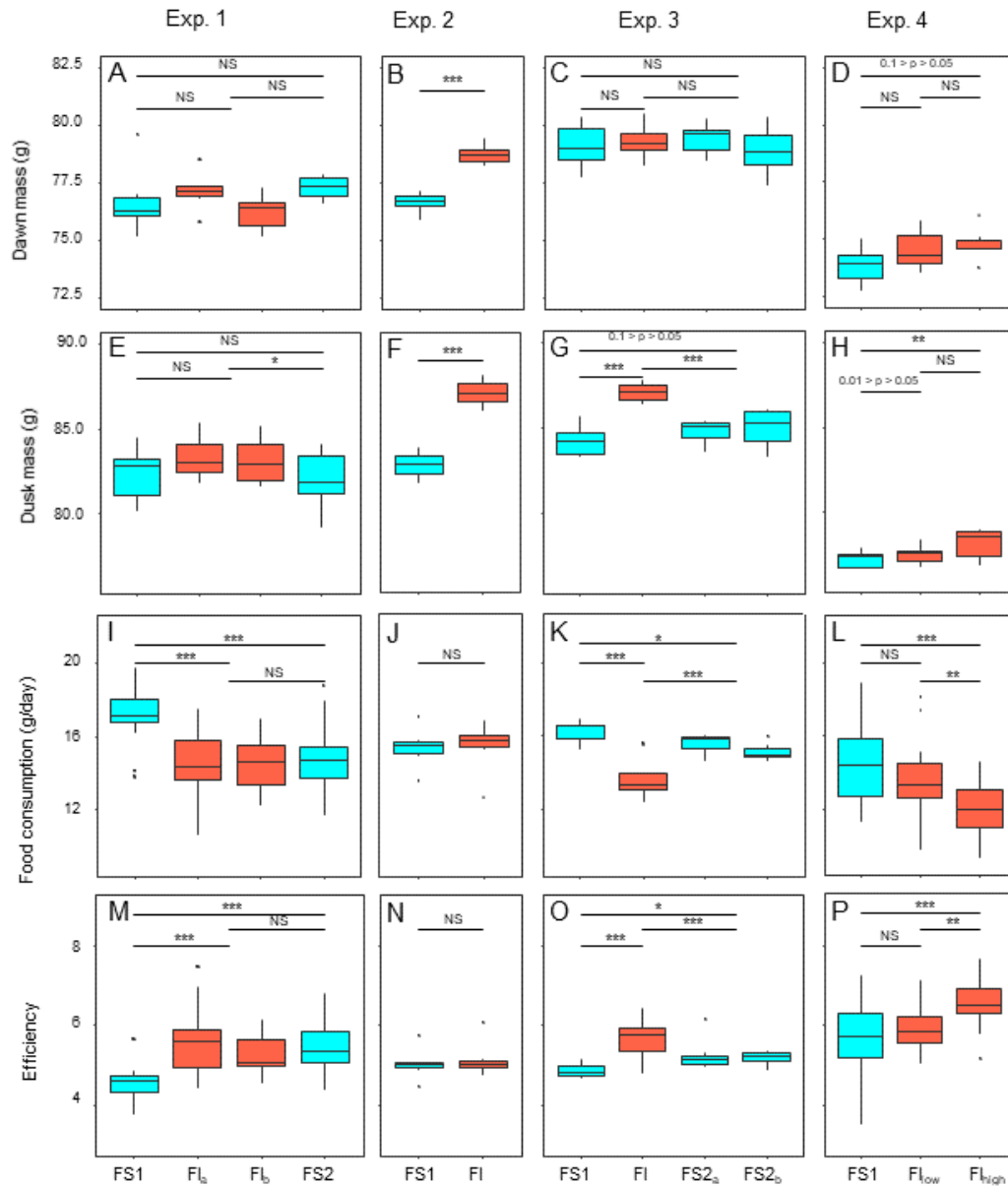
**Fig. 3. The effect of food insecurity on body mass, food consumption and energetic efficiency in experiments 1-4. (A-D)** Dawn mass (g); **(E-H)** dusk mass (g); **(I-L)** total daily food consumption per bird (g); and **(M-P)** energetic efficiency, calculated as the ratio of the mean dawn mass per bird per day to the total mass of food eaten per bird on the previous day. Graphs are box plots with each box corresponding to 7 days of data, but the data from treatments lasting 14 days were pooled for statistical analysis. Mass data were available at the individual bird level, but consumption (and hence also efficiency data) were only available at the aviary level. For this figure, the three separate aviaries are combined for experiments 1 and 4. For display purposes only, data were within-subject centred and shown relative to the grand mean. All experiments involved an n of 6 birds. Significance tests are presented in Tables S2, S3, S6 and S7. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.
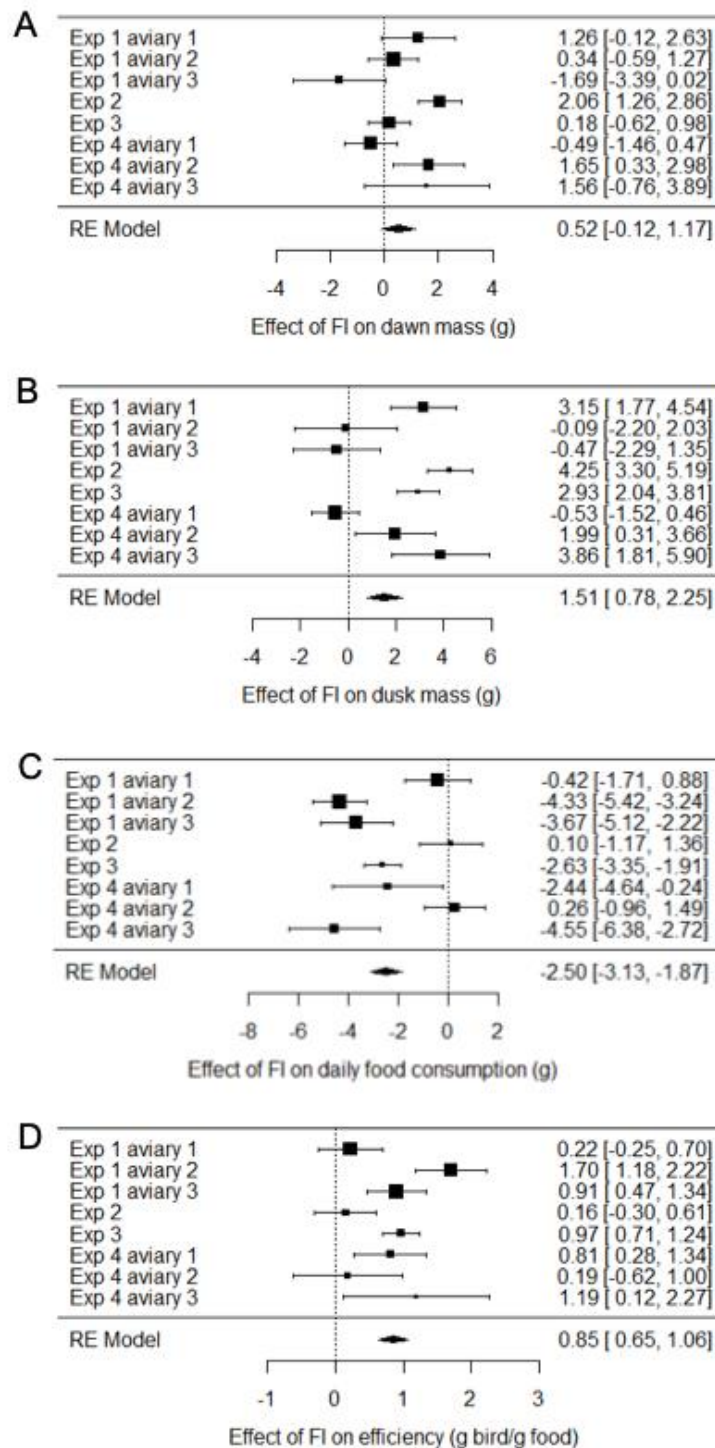
**Fig. 4. Meta-analysis of the effects of food insecurity in experiments 1-4. (A)** Dawn mass
(g); **(B)** dusk mass (g); **(C)** total daily food consumption per bird (g); and **(D)** energetic
efficiency, calculated as the ratio of the mean dawn mass per bird per day to the total mass
of food eaten per bird on the previous day. Graphs are forest plots indicating the size of
effects and 95% CI for the difference between the first period of food security (FS1) and the
period of food insecurity (FI or FI$_{high}$). We treated each aviary in experiments 1 and 4 as
separate replicates due to heterogeneity between aviaries. Meta-analyses used a multi-level
random-effects model with random effects of aviary nested in experiment. All experiments
involved an n of 6 birds. Statistical tests are presented in Table S4.
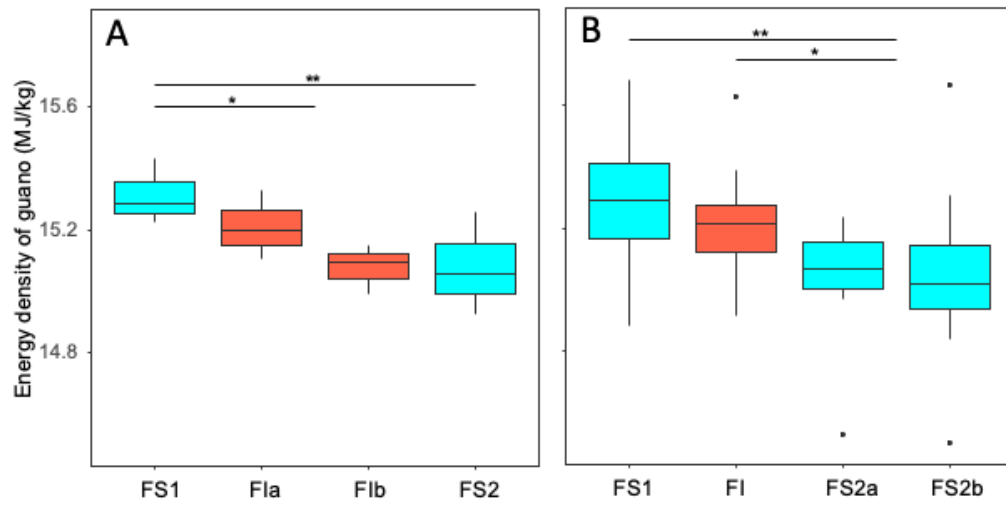
**Fig. 5. The effect of food insecurity on energy density of guano. (A)** Experiment 1; and **(B)** experiment 3. Graphs show boxplots of the energy density of faeces with each box corresponding to 7 days of the experiment. For display purposes, data were within-aviary centred and plotted relative to the grand mean. The n was 6 birds per experiment. Significance tests are presented in Table S8. * $p < 0.05$, ** $p < 0.01$.
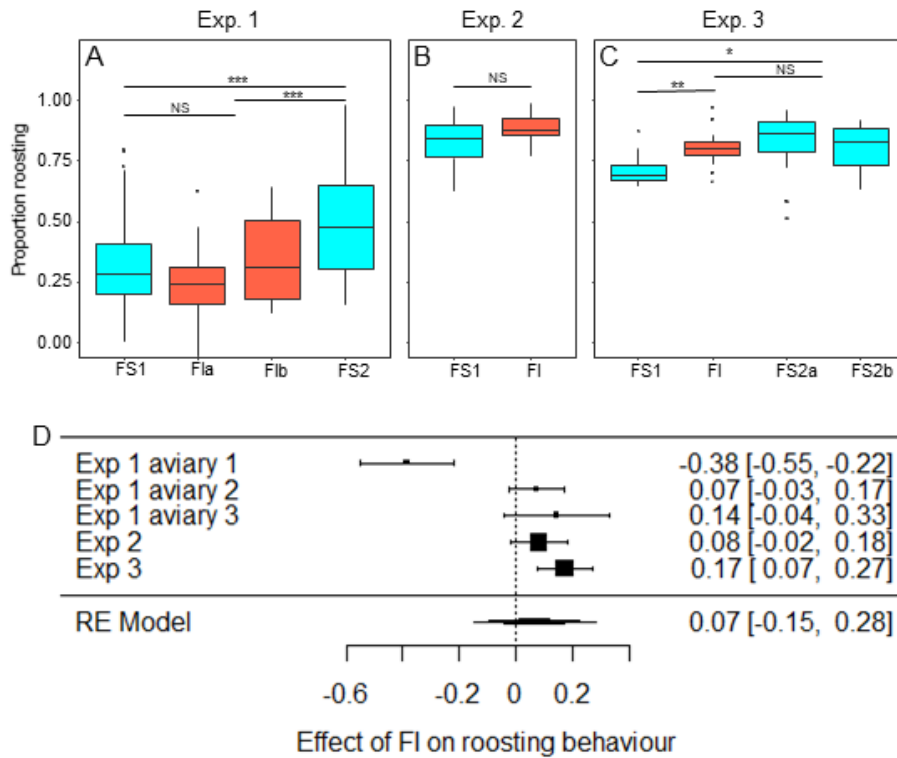
**Fig. 6. The effect of food insecurity on roosting behaviour. (A)** Experiment 1; **(B)** experiment 2; **(C)** experiment 3; and **(D)** forest plot of meta-analysis of the experiments 1-3. Graphs show boxplots of the proportion of scans in which birds were roosting with each box corresponding to 7 days of the experiment. For display purposes, data were within-aviary centred and plotted relative to the grand mean. The n was 6 birds per experiment. Significance tests for panels A-C are presented in Table S9. * p < 0.05, ** p < 0.01, *** p < 0.001.
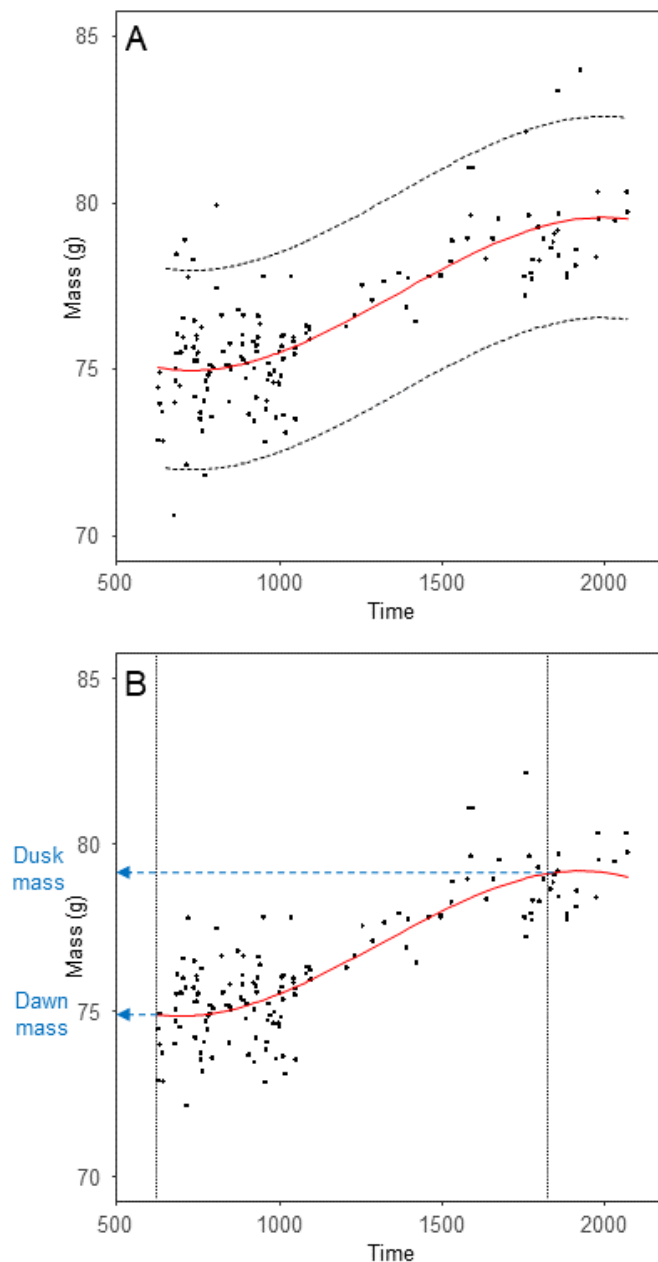
**Fig. S1. Raw body mass data and method for estimating dawn and dusk masses. (A)** Scatterplot of body mass against time of day for a single bird on a single day in experiment 4. The red line shows the polynomial fit to the raw data. The dashed black lines show the 3 g band either side of the fitted line; masses lying outside this band were deleted. **(B)** Scatter plot of the cleaned body mass data. The red line shows the slightly modified polynomial fit after removing the outliers. The vertical dotted lines show the times designated as dawn and dusk in experiment 4 (0615 and 1815 respectively) and the blue arrows show the estimates of dawn and dusk mass for this bird on this day.
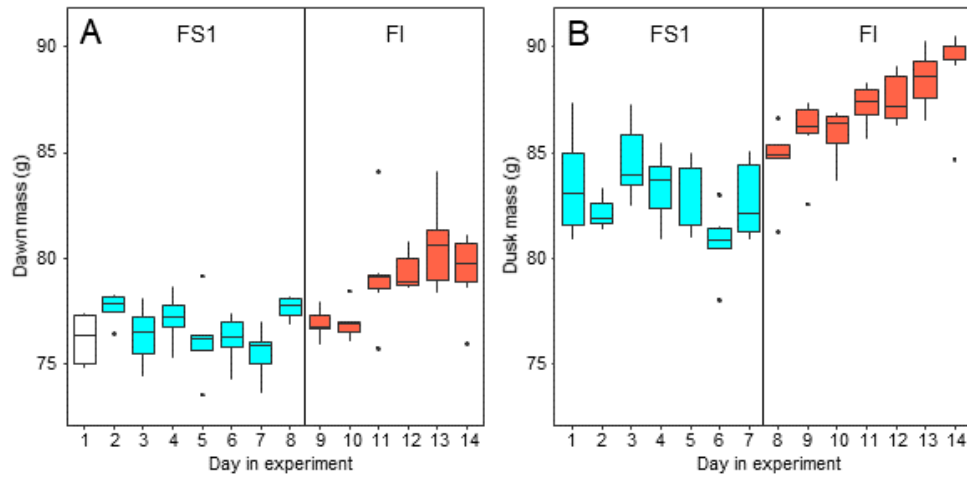
**Fig. S2. The rapidity of the effect of food insecurity on body mass. (A)** Dawn mass (g) and **(B)** dusk mass (g). Graphs are box plots of the mass data from experiment 2, with each box corresponding to a single day of data. For dawn mass the treatment is that in place the previous day, whereas for dusk mass the treatment is that in place the same day (the first box of panel A is white because there was no treatment in place the previous day). The vertical lines indicate when treatment changed from FS1 to FI. For display purposes, data were within-subject centred and plotted relative to the grand mean. The n was 6 birds.
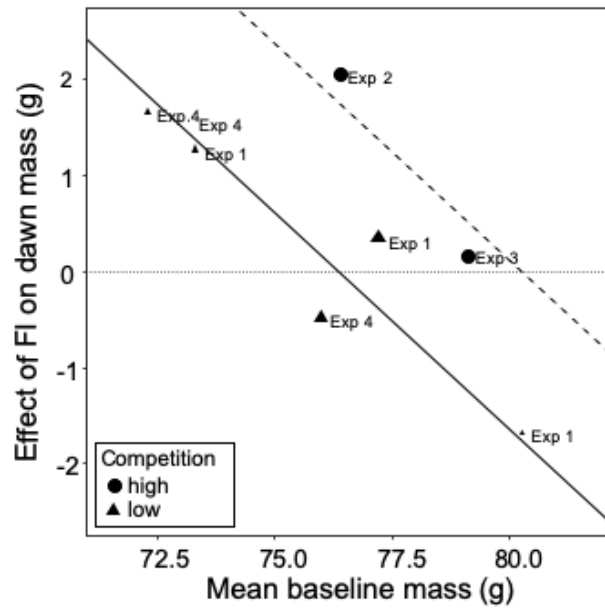
**Fig. S3. The moderating effect of baseline mass on the effect of food insecurity on body mass.** Baseline mass is the mean dawn mass (g) in the first period of food security (FS1). The effect of FI is the parameter estimate ($\beta$) representing the difference in dawn mass between the first period of food security (FS1) and the period of food insecurity (FI or $FI_{high}$) taken from mixed linear model for each aviary of each experiment. Points are plotted with size inversely proportional to the precision of the estimates. The horizontal dotted line shows no effect of food insecurity on dawn mass. The fitted lines come from a multi-level meta-regression model with baseline mass and degree of competition as moderators and random effects of aviary nested in experiment; the solid line is the fit for low competition and the dashed line the fit for high competition.
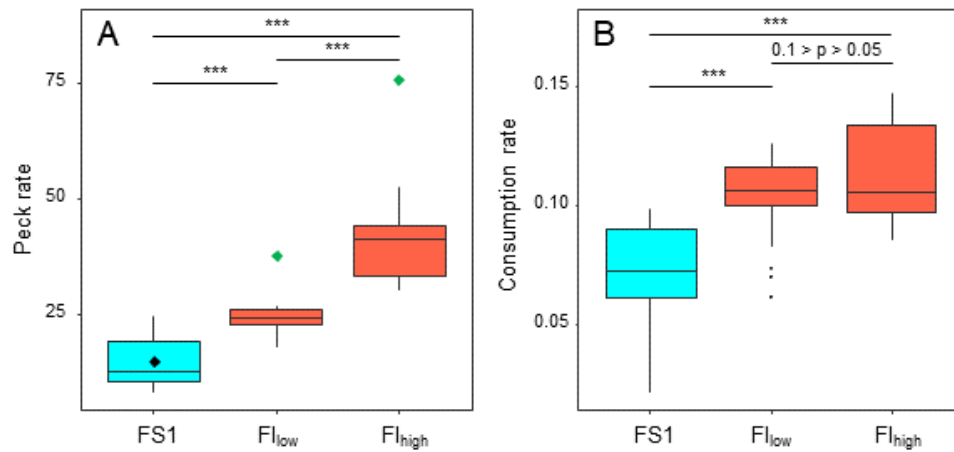
**Fig. S4. The effect of food insecurity on foraging behaviour in experiment 4.** (**A**) Peck rate (pecks.hr$^{-1}$); and (**B**) consumption rate (g food eaten.reinforcement$^{-1}$). Graphs are box plots of data from experiment 4, with each box corresponding to 7 days of data. The green diamonds in A indicate the peck rate that would have been required to fully compensate for the reduced probability of reinforcement in the food-insecure treatments and hence receive the same rate of reinforcement obtained under food security (black diamond). For display purposes, data were within-subject centred and plotted relative to the grand mean. The n was 6 birds. Significance tests are presented in Table S5. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

**Table S1**: Details of the four experiments.

| Exp. | No. birds | Sex | Age | Lights on | Light: Dark hours | Birds/aviary | SFS/aviary | Duration of FI (weeks) | Reinstatement of FS? |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 6 | M | ~6 years | 0900-1800 | 9:15 | 2 | 1 | 2 | Yes (1 week) |
| 2 | 6 | M | ~6 years | 0900-1800 | 9:15 | 6 | 2 | 1 | no |
| 3 | 6 | M | ~6 years | 0900-1800 | 9:15 | 6 | 2 | 1 | Yes (2 weeks) |
| 4 | 6 | F | ~4 years | 0600-2100 | 15:9 | 2 | 1 | 1 $FI_{low}$ and 1 $FI_{high}$ | no |

Notes:
- The birds used in experiments 1-3 were in reproductive condition at the time of the experiments.
- The birds used in experiment 4 had been permanently maintained on long days since hand-rearing and were thus non-reproductive and non-photosensitive.

**Table S2**. Summary of linear mixed models of effects of food insecurity on dawn[1] mass (g).

| Expt. | Random effects | Treatment effect[2] | Parameter estimate (g)[3] | 95% CI (g) | Test statistic | | p-value |
|---|---|---|---|---|---|---|---|
| | | | | | Type df | Value | |
| 1 | Aviary/bird | Overall[4] | | | $F_{2,142}$ | 0.91 | 0.404 |
| | | FI v. FS1 | $\beta FI = -0.06$ | -0.89 to 0.76 | $t_{142}$ | -0.15 | 0.878 |
| | | FS2 v. FS1 | $\beta FS2 = 0.53$ | -0.45 to 1.52 | $t_{142}$ | 1.05 | 0.294 |
| | | FI v. FS2 | $\beta FI = -0.59$ | -1.48 to 0.29 | $t_{142}$ | -1.32 | 0.291 |
| 2 | Bird | Overall | $\beta FI = 2.06$ | 1.25 to 2.87 | $F_{1,70}$ | 25.37 | <0.001*** |
| 3 | Bird | Overall | | | $F_{2,152}$ | 0.10 | 0.909 |
| | | FI v. FS1 | $\beta FI = 0.18$ | -0.62 to 0.98 | $t_{152}$ | 0.44 | 0.664 |
| | | FS2 v. FS1 | $\beta FS2 = 0.10$ | -0.61 to 0.80 | $t_{152}$ | 0.27 | 0.791 |
| | | FI v. FS2 | $\beta FI = 0.08$ | -0.62 to 0.79 | $t_{152}$ | 0.23 | 0.819 |
| 4 | Aviary/bird | Overall | | | $F_{2,115}$ | 2.14 | 0.123 |
| | | $FI_{low}$ v. FS1 | $\beta FI_{low} = 0.70$ | -0.16 to 1.57 | $t_{115}$ | 1.59 | 0.115 |
| | | $FS_{high}$ v. FS1 | $\beta FI_{high} = 0.93$ | -0.02 to 1.87 | $t_{115}$ | 1.91 | 0.059 |
| | | $FI_{high}$ v. $FI_{low}$ | $\beta FI_{high} = 0.22$ | -0.72 to 1.16 | $t_{115}$ | 0.46 | 0.646 |

Notes:
1. The mass before birds start foraging for the day when their gut is still empty. Unit of analysis is bird-day.
2. The reference category is always given second.
3. For comparisons involving food insecurity the parameter estimates are always expressed such that a positive number means that birds gained weight under greater FI.
4. Overall tests: type III ANOVA with Satterthwaite's method.
5. * p < 0.05, ** p < 0.01, *** p < 0.001.

**Table S3.** Summary of linear mixed models of effects of food insecurity on dusk[1] mass (g).

| Expt. | Random effects | Treatment effect[2] | Parameter estimate[3] | 95% CI | Test statistic and df | value | p-value |
|---|---|---|---|---|---|---|---|
| 1 | Aviary/bird | Overall[4] | | | $F_{2,138}$ | 2.86 | 0.061 |
| | | FI v. FS1 | $\beta FI = 0.82$ | -0.29 to 1.93 | $t_{138}$ | 1.45 | 0.150 |
| | | FS2 v. FS1 | $\beta FS2 = -0.50$ | -1.76 to 0.75 | $t_{138}$ | -0.79 | 0.432 |
| | | FI v. FS2 | $\beta FI = 1.32$ | 0.20 to 2.45 | $t_{138}$ | 2.30 | 0.023* |
| 2 | Bird | Overall | $\beta FI = 4.25$ | 3.33 to 5.18 | $F_{1,76}$ | 82.01 | <0.001*** |
| 3 | | Overall | | | $F_{2,151}$ | 23.90 | <0.001*** |
| | | FI v. FS1 | $\beta FI = 2.93$ | 2.04 to 3.81 | $t_{151}$ | 6.50 | <0.001*** |
| | | FS2 v. FS1 | $\beta FS2 = 0.72$ | -0.05 to 1.49 | $t_{151}$ | 1.83 | 0.069 |
| | | FI v. FS2 | $\beta FI = 2.21$ | 1.44 to 2.97 | $t_{151}$ | 5.64 | <0.001*** |
| 4 | | Overall | | | $F_{2,94}$ | 4.01 | 0.021* |
| | | $FI_{low}$ v. FS1 | $\beta FI_{low} = 0.79$ | -0.12 to 1.71 | $t_{94}$ | 1.69 | 0.094 |
| | | $FS_{high}$ v. FS1 | $\beta FI_{high} = 1.33$ | 0.41 to 2.27 | $t_{94}$ | 2.82 | 0.006** |
| | | $FI_{high}$ v. $FI_{low}$ | $\beta FI_{high} = 0.55$ | -0.36 to 1.45 | $t_{94}$ | 1.19 | 0.239 |

Notes:
1. Mass estimated at 1800 hours for exp. 1-3. and 1815 for exp. 4. These times equate to 9 hours after dawn and 12 hours after dawn respectively. Unit of analysis is bird-day.
2. The reference category is always given second.
3. For comparisons involving food insecurity, the parameter estimates are always expressed such that a positive number means that birds gained weight under greater FI.
4. Overall tests: type III ANOVA with Satterthwaite's method.
5. * p < 0.05, ** p < 0.01, *** p < 0.001.

**Table S4.** Summary of statistics from meta-analysis[1] of experiments 1-4.

| Dependent variable | Test of random-effects model | | | | Heterogeneity statistics[2,3] | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Estimate | 95% CI | z | p-value | $\rho$ | $\tau^2$ | Test for heterogeneity | | |
| | | | | | | | Q | df | p-value |
| Dawn mass (g) | 0.52 | -0.12 to 1.17 | 1.59 | 0.113 | -0.35 | 0.95 | 29.79 | 7 | <0.001*** |
| Dusk mass (g) | 1.51 | 0.78 to 2.25 | 4.05 | <0.001*** | -0.47 | 3.14 | 67.07 | 7 | <0.001*** |
| Daily food consumption (g) | -2.50 | -3.13 to -1.87 | -7.77 | <0.001*** | -0.49 | 3.20 | 61.76 | 7 | <0.001*** |
| Energetic efficiency | 0.85 | 0.65 to 1.06 | 8.17 | <0.001*** | -0.53 | 0.20 | 29.35 | 7 | <0.001*** |

Notes:
1. As the dataset includes multiple associations from the same experiment, we used multilevel models containing nested random effects of association and experiment. Unit of analysis is aviary.
2. $\tau^2$ estimates the heterogeneity between associations.
3. $\rho$ estimates the intra-class correlation coefficient between the associations from the same experiment.
4. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

**Table S5.** Summary of linear mixed models of effects of food insecurity on foraging variables in experiment 4.

| Dependent variable | Treatment effect[3] | Parameter estimate | 95% CI | Test statistic | | p-value |
|---|---|---|---|---|---|---|
| | | | | Type, df | Value | |
| Peck rate[1] (pecks.hr$^{-1}$) | Overall[4] | | | $F_{2,118}$ | 87.16 | <0.001*** |
| | $FI_{low}$ v. FS1 | $\beta FI_{low} =$ 8.81 | 5.01 to 12.62 | $t_{118}$ | 4.54 | <0.001*** |
| | $FS_{high}$ v. FS1 | $\beta FI_{high} =$ 25.27 | 21.46 to 29.07 | $t_{118}$ | 13.01 | <0.001*** |
| | $FI_{high}$ v. $FI_{low}$ | $\beta FI_{high} =$ 16.46 | 12.65 to 20.26 | $t_{118}$ | 8.47 | <0.001*** |
| Reinforcement rate[1] (reinforcements.hr$^{-1}$) | Overall | | | $F_{2,118}$ | 32.95 | <0.001*** |
| | $FI_{low}$ v. FS1 | $\beta FI_{low} = -$5.51 | -7.32 to -3.71 | $t_{118}$ | -5.97 | <0.001*** |
| | $FS_{high}$ v. FS1 | $\beta FI_{high} = -$7.16 | -8.97 to -5.35 | $t_{118}$ | -7.75 | <0.001*** |
| | $FI_{high}$ v. $FI_{low}$ | $\beta FI_{high} = -$1.65 | -3.46 to 0.16 | $t_{118}$ | -1.79 | 0.077 |
| Consumption rate[2] (g.reinforcement$^{-1}$) | Overall | | | $F_{2,55}$ | 23.07 | <0.001*** |
| | $FI_{low}$ v. FS1 | $\beta FI_{low} =$ 0.032 | 0.019 to 0.045 | $t_{55}$ | 4.89 | <0.001*** |
| | $FS_{high}$ v. FS1 | $\beta FI_{high} =$ 0.043 | 0.030 to 0.056 | $t_{55}$ | 6.57 | <0.001*** |
| | $FI_{high}$ v. $FI_{low}$ | $\beta FI_{high} =$ 0.011 | -0.001 to 0.024 | $t_{55}$ | 1.77 | 0.082 |

Notes:
1. Models include random effects of aviary/bird. Unit of analysis is bird-day.
2. Model includes random effect of aviary. Unit of analysis is aviary-day.
3. The reference category is always given second.
4. Overall tests: type III ANOVA with Satterthwaite's method.
5. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

**Table S6.** Summary of statistical analyses of effects of food insecurity on total food consumption (g/bird/day)[1].

| Expt. | Random effect(s) | Treatment effect[2] | Parameter estimate[3] | 95% CI | Test statistic and df | value | p-value |
|---|---|---|---|---|---|---|---|
| 1 | Aviary | Overall[4] | | | $F_{2,79}$ | 21.73 | <0.001*** |
| | | FI v. FS1 | $\beta FI = -2.81$ | -3.66 to -1.96 | $t_{79}$ | -6.47 | <0.001*** |
| | | FS2 v. FS1 | $\beta FS2 = -2.39$ | -3.37 to -1.41 | $t_{79}$ | -4.78 | <0.001*** |
| | | FI v. FS2 | $\beta FI = -0.41$ | -1.26 to 0.44 | $t_{79}$ | -0.96 | 0.343 |
| 2 | None | Overall | $\beta FI = 0.10$ | -1.31- to 1.50 | $F_{1,12}$ | 0.02 | 0.885 |
| 3 | None | Overall | | | $F_{2,25}$ | 26.62 | <0.001*** |
| | | FI v. FS1 | $\beta FI = -2.63$ | -3.39 to -1.87 | $t_{25}$ | -7.12 | <0.001*** |
| | | FS2 v. FS1 | $\beta FS2 = -0.89$ | -1.55 to -0.23 | $t_{25}$ | -2.79 | 0.010* |
| | | FI v. FS2 | $\beta FI = -1.74$ | -2.40 to -1.08 | $t_{25}$ | -5.43 | <0.001*** |
| 4 | Aviary | Overall | | | $F_{2,54}$ | 8.77 | 0.001*** |
| | | $FI_{low}$ v. FS1 | $\beta FI_{low} = -0.71$ | -1.88 to 0.46 | $t_{54}$ | -1.19 | 0.239 |
| | | $FS_{high}$ v. FS1 | $\beta FI_{high} = -2.44$ | -3.62 to -1.26 | $t_{54}$ | -4.05 | 0.001*** |
| | | $FI_{high}$ v. $FI_{low}$ | $\beta FI_{high} = -1.73$ | -2.88 to -0.58 | $t_{54}$ | -2.94 | 0.005** |

Notes:
1. Unit of analysis is aviary-day.
2. The reference category is always given second.
3. For comparisons involving food insecurity the parameter estimates are always expressed such that a negative number means that birds ate less under greater FI.
4. Overall tests: type III ANOVA with Satterthwaite's method.
5. * p < 0.05, ** p < 0.01, *** p < 0.001.

**Table S7.** Summary of linear mixed models of effects of food insecurity on energetic efficiency[1].

| Expt. | Random effect(s) | Treatment effect[2] | Parameter estimate[3] | 95% CI | Test statistic and df | value | p-value |
|---|---|---|---|---|---|---|---|
| 1 | Aviary | Overall[4] | | | $F_{2,74}$ | 17.5 | <0.001*** |
| | | FI v. FS1 | $\beta FI = 0.93$ | 0.61 to 1.25 | $t_{74}$ | 5.72 | <0.001*** |
| | | FS1 v. FS2 | $\beta FSI = 0.86$ | 0.48 to 1.24 | $t_{73}$ | 4.42 | <0.001*** |
| | | FI v. FS2 | $\beta FI = 0.07$ | -0.26 to 0.41 | $t_{74}$ | 0.43 | 0.668 |
| 2 | None | Overall | $\beta FI = 0.16$ | -0.36 to 0.67 | $F_{1,11}$ | 0.45 | 0.515 |
| 3 | None | Overall | | | $F_{2,24}$ | 27.70 | <0.001*** |
| | | FS1 v. FI | $\beta FI = 0.97$ | 0.69 to 1.26 | $t_{24}$ | 7.13 | <0.001*** |
| | | FS1 v. FS2 | $\beta FS2 = 0.28$ | 0.03 to 0.53 | $t_{24}$ | 2.32 | 0.029* |
| | | FI v. FS2 | $\beta FI = 0.70$ | 0.45 to 0.94 | $t_{24}$ | 5.81 | <0.001*** |
| 4 | Aviary | Overall | | | $F_{2,55}$ | 7.99 | <0.001*** |
| | | $FI_{low}$ v. FS1 | $\beta FI_{low} = 0.38$ | -0.14 to 0.91 | $t_{55}$ | 1.43 | 0.160 |
| | | $FS_{high}$ v. FS1 | $\beta FI_{high} = 1.14$ | 0.58 to 1.72 | $t_{55}$ | 3.95 | 0.001*** |
| | | $FI_{high}$ v. $FI_{low}$ | $\beta FI_{high} = 0.76$ | 0.21 to 1.31 | $t_{55}$ | 2.71 | 0.009** |

Notes:
1. Defined as the ratio of the mean dawn mass of the starlings in a room on a given day to the mean mass of food consumed per bird in the room in the previous 24 hours. The higher this ratio, the greater the body mass maintained per gram of food consumed. Unit of analysis is aviary-day.
2. The reference category is always given second.
3. For comparisons involving food insecurity the parameter estimates are always expressed such that a positive number means greater efficiency under greater FI.
4. Overall tests: type III ANOVA with Satterthwaite's method.
5. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

**Table S8.** Summary of linear mixed models of effects of food insecurity on energy density of guano (MJ/kg).

| Expt. | Random effect(s) | Treatment effect[1] | Parameter estimate[2] | 95% CI | Test statistic and df | value | p-value |
|---|---|---|---|---|---|---|---|
| 1 | Aviary | Overall[3] | | | $F_{2,43}$ | 4.43 | 0.018* |
| | | FI v. FS1 | $\beta FI = -0.17$ | -0.31 to -0.03 | $t_{43}$ | -2.40 | 0.021* |
| | | FS2 v. FS1 | $\beta FS2 = -0.23$ | -0.39 to -0.07 | $t_{43}$ | -2.82 | 0.007** |
| | | FI v. FS2 | $\beta FI = 0.06$ | -0.08 to 0.20 | $t_{43}$ | 0.87 | 0.392 |
| 3 | None | Overall | | | $F_{2,53}$ | 6.82 | 0.002** |
| | | FI v. FS1 | $\beta FI = -0.07$ | -1.76 to 0.09 | $t_{53}$ | -0.84 | 0.403 |
| | | FS2 v. FS1 | $\beta FS2 = -0.24$ | -0.37 to -0.10 | $t_{53}$ | -3.42 | 0.001** |
| | | FI v. FS2 | $\beta FI = 0.17$ | 0.03 to 0.31 | $t_{53}$ | 2.45 | 0.018* |

Notes:
1. The reference category is always given second.
2. For comparisons involving FI the parameter estimates are always expressed such that a negative number means the guano contained less energy under FI.
3. Overall tests: type III ANOVA with Satterthwaite's method.
4. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

**Table S9.** Summary of linear mixed models of effects of food insecurity on the proportion of scans in which a bird was roosting[1].

| Expt. | Random effect(s) | Treatment effect[2] | Parameter estimate[3] | 95% CI | Test statistic and df | value | p-value |
|---|---|---|---|---|---|---|---|
| 1 | Aviary/day | Overall[4] | | | $F_{2,76}$ | 11.98 | <0.001*** |
| | | FI v. FS1 | $\beta FI = -0.06$ | -0.16 to 0.047 | $t_{76}$ | -1.06 | 0.293 |
| | | FS2 vs FS1 | $\beta FS2 = 0.21$ | 0.09 to 0.34 | $t_{76}$ | 3.39 | 0.001** |
| | | FI v. FS2 | $\beta FI = -0.27$ | -0.38 to -0.16 | $t_{76}$ | -4.87 | <0.001*** |
| 2 | Day | Overall | $\beta FI = 0.08$ | -0.02 to 0.18 | $F_{1,24}$ | 2.50 | 0.127 |
| 3 | Day | Overall | | | $F_{2,23}$ | 6.49 | 0.006** |
| | | FI vs FS1 | $\beta FI = 0.17$ | 0.08 to 0.27 | $t_{24}$ | 3.47 | 0.002** |
| | | FS2 vs FS1 | $\beta FS2 = 0.12$ | 0.04 to 0.20 | $t_{23}$ | 2.79 | 0.011* |
| | | FI vs FS2 | $\beta FI = 0.05$ | -0.03 to 0.13 | $t_{23}$ | 1.19 | 0.245 |

Notes:
1. The dependent variable (proportion of scans in which birds were roosting) was arcsine square root transformed prior to analysis.
2. Given that behaviour was measured between 0900-1100, and thus before any treatment effect has been experienced on the current day, the predictor variable used in the models is the treatment to which the birds were exposed on the previous day. The reference category is always given second.
3. For comparisons involving food insecurity the parameter estimates are expressed such that a positive number means that birds roost more under FI.
4. Overall tests: type III ANOVA with Satterthwaite's method.
5. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.