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1 **Title:** Red knots (*Calidris canutus islandica*) manage body mass with dieting and activity

2 **Running title:** Dieting and activity in knots

3

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16

17 **Keywords:** mass regulation in birds, mass loss, food quality, diet, activity

18 **Summary Statement:** We show that activity and dieting both contribute to mass regulation in
19 red knots; including predation-related decreases in body mass, and maintenance of body mass
20 under changing food conditions.

21 **Abstract**

22 Mass regulation in birds is well documented. For example, birds can increase body mass in
23 response to lower availability and/or predictability of food and decrease body mass in response
24 to increased predation danger. Birds also demonstrate an ability to maintain body mass across
25 a range of food qualities. Although the adaptive significance of mass regulation has received a
26 great deal of theoretical and empirical attention, the mechanisms by which birds achieve this
27 have not. Several non-exclusive mechanisms could facilitate mass regulation in birds. Birds
28 could regulate body mass by adjusting food intake (dieting), activity, baseline energetic
29 requirements (basal metabolic rate, or BMR), mitochondrial efficiency, or assimilation
30 efficiency. Here, we present the results of two experiments in captive red knots (*Calidris*
31 *canutus islandica*) that assess three of these proposed mechanisms: dieting, activity, and
32 up/down-regulation of metabolic rate. In the first experiment, knots were exposed to cues of
33 predation risk that led them to exhibit presumably adaptive mass loss. In the second
34 experiment, knots maintained constant body mass despite being fed on alternating high- and
35 low-quality diets. In both experiments, regulation of body mass was achieved through a
36 combination of changes in food intake and activity. Both experiments also provide some
37 evidence for a role of metabolic adjustments. Taken together, these two experiments
38 demonstrate that fine-scale management of body mass in knots is achieved through multiple
39 mechanisms acting simultaneously.

40 Introduction

41 The ability to regulate body mass in the face of changing conditions has major functional
42 importance for birds. Both theoretical (Bednekoff et al., 1994; Bednekoff and Houston, 1994;
43 Houston and McNamara, 1993; Lima, 1986) and empirical work (Bednekoff and Krebs, 1995;
44 Cuthill et al., 2000; Ekman and Hake, 1990) have shown that increasing fat stores is an adaptive
45 response to decreased availability or predictability of food. However, carrying fat stores also
46 incurs costs. The metabolic cost of activities increases with increasing body mass (Nagy, 2005;
47 Song and Beissinger, 2020), and flight performance may be especially compromised (Bednekoff,
48 1996; Houston and McNamara, 1993; Kvist et al., 2001; Pennycuick, 1989). All else being equal,
49 carrying more fat should decrease takeoff angle and speed, which can reduce the ability to
50 evade predators (Pennycuick, 1989). However, scenarios of “all else being equal” may not be
51 the norm. For example, many studies show that birds maintain near constant flight
52 performance under changing body mass by invoking compensatory mechanisms such as
53 adjustment in pectoral muscle mass or changes in flight efficiency (Dietz et al., 2007; Kvist et al.,
54 2001; van der Veen and Lindström, 2000; Walters et al., 2017). Nonetheless, as long as these
55 compensatory mechanisms incur costs, it remains that birds must balance the survival benefit
56 of carrying more fat via its effect on the probability of starvation, against the cost of fat on
57 escape flight performance (McNamara and Houston, 1990). Such costs may either be direct
58 survival costs or costs incurred to evoke compensatory mechanisms.

59 Indeed, birds show an exceptional capacity to fine-tune their body mass in response to
60 variation in the availability and/or predictability of food and variation in predation danger. For
61 example, within a single day, birds can increase body mass by up to 10% between dawn and
62 dusk, with fat stores accumulated over the foraging period being subsequently lost during
63 overnight fasting (Lilliendahl, 2002; MacLeod et al., 2005; Moiron et al., 2018; Thomas, 2000).
64 Furthermore, the timing of mass gain during the day depends on the predictability of access to
65 food and the local predator landscape (Bednekoff and Houston, 1994). Under elevated
66 predation danger, birds delay mass gain until later in the foraging period (McNamara et al.,
67 1994).

68 Birds also regulate body mass across longer timescales. For example, across the annual
69 cycle, individual body mass may vary more than two-fold in relation to migration stage
70 (Karagicheva et al., 2016; Piersma et al., 2008; Piersma and Gill, 1998; Piersma and Jukema,
71 2002). Body mass can also vary over longer-time scales, such as across generations. For
72 example, westerns sandpipers (*Calidris mauri*) at stopover sites on migration (Ydenberg et al.,
73 2004) and Eurasian golden plovers (*Pluvialis apricaria*) on autumn staging grounds (Piersma et
74 al., 2003b) have both shown decreases in body mass of approximately 10% over a period of 20
75 years. These multi-generation shifts are thought to be responses to changes in the predator
76 landscape as they coincide with the recovery of populations of a major avian predator,
77 peregrine falcons (*Falco peregrinus*).

78 Even in long-term captive studies, birds continue to exhibit strong body mass regulation
79 that reflects the trade-off between the costs and benefits of carrying extra fat. Captive birds
80 exhibit circadian (Dall and Witter, 1998) and circannual patterns (Karagicheva et al., 2016) of
81 body mass, and adjust their body mass in response to variation in perceived predation risk (van
82 den Hout et al., 2010) and experimental manipulations of food availability (Cuthill et al., 2000;
83 Ekman and Hake, 1990). Even under conditions of unrestricted access to food, unlike mammals,
84 birds rarely become “overweight” (Halsey, 2018). The adaptive significance of mass regulation
85 in birds has received a great deal of attention in both theoretical and empirical studies,
86 however, the mechanisms by which birds regulate their body mass have not (Halsey, 2018; but
87 see Kelly and Weathers, 2002).

88 Several non-exclusive mechanisms could contribute to mass regulation in birds. Birds
89 could regulate their body mass using several non-exclusive mechanisms (reviewed in Halsey,
90 2018). All else being equal, mass loss could be facilitated by decreased food intake, increased
91 activity, higher metabolic rate, lower mitochondrial efficiency or lower digestive efficiency.
92 Here, we present the results of two experiments to evaluate the relative importance of three of
93 these mechanisms for mass regulation in red knots (*Calidris canutus islandica*). In the first
94 experiment, knots exhibited presumably adaptive changes in body mass in response to
95 perceived predation risk (Mathot et al., 2009; van den Hout et al., 2010). We use activity budget

96 observations to evaluate whether predation-related decreases in body mass were driven by
97 decreased food intake, increased activity, or both. In the second experiment, knots maintained
98 their body mass across large experimental manipulations in the quality of their diet (Mathot et
99 al., 2019). We use activity budget observations and respirometry data to evaluate whether
100 variation in diet quality was associated with changes in food intake, activity, BMR or a
101 combination of the three. Taken together, our results provide evidence that both dieting and
102 activity are key mechanisms underlying mass regulation in captive red knots, but also hint at a
103 potential role of metabolic adjustments.

104

105 **Materials and methods**

106 **Study species.** Red knots (*Calidris canutus*) are medium-sized migratory shorebirds, and are
107 ideally suited for studies of the mechanisms of mass regulation (Karagicheva et al., 2016).
108 Previous work in red knots has shown that they exhibit adaptive changes in body mass in
109 response to manipulations of perceived predation danger (Mathot et al., 2009; van den Hout et
110 al., 2010), and that they maintain regular seasonal variation in body mass even after extended
111 periods of time in captivity (Karagicheva et al., 2016).

112 EXPERIMENT 1: ADAPTIVE CHANGES IN BODY MASS IN RESPONSE TO PERCEIVED PREDATION 113 DANGER

114 **Study subjects.** Fifty knots of the *islandica* subspecies were captured using mistnets on the
115 mudflats of Richel (53°16'57"N, 05°23'82"E) and Simonszand (53°29'28"N 06°24'19"E) in the
116 Wadden Sea, The Netherlands, on 8 August and 3 September 2005. Prior to experiments, birds
117 were housed at NIOZ Royal Netherlands Institute for Sea Research in outdoor aviaries and given
118 an *ad libitum* diet of mudsnail, *Peringia ulvae* (formerly *Hydrobia ulvae*).

119 **Experimental procedure.** Experiments were carried out between 21 August and 28 November
120 2005. Birds were randomly assigned to flocks, with 8 flocks of 6 birds being tested (N = 48
121 birds). Experiments were conducted in the indoor experimental shorebird facility at NIOZ (7.0 X

122 7.0 X 2.8m high), under constant photoperiods with light on from 6h00 to 21h00, and
123 'moonlight' mimicking illumination being provided during the dark phase. Flocks were tested
124 sequentially. After being introduced to the mudflat facility, the focal flock was given two days to
125 acclimate to the mudflat before the start of experiments, which consisted of a 5-day control
126 treatment (no disturbance) and a 5-day experimental period (exposure to model predator).
127 Treatment order was randomized, with half of flocks receiving the control treatment first, and
128 half of flocks receiving the experimental treatment first. During the experimental treatment,
129 flocks were subjected to two manipulations of perceived predation each day: one presentation
130 of a gliding sparrowhawk (*Accipiter nisus*), and one presentation of a perching sparrowhawk.
131 The timing and order of events was randomized, and behavioural observations were conducted
132 before and after each predator exposure. The control period consisted of no disturbances, but
133 observation periods were time-matched to the disturbances during the treatment periods to
134 control for temporal variation in activity budgets.

135 **Activity budget observations.** During both the control and experimental phases of the
136 experiment, 5-minute continuous, focal observations were made on each flock member four
137 times each day; before and after each of the two simulated predator encounters. For the
138 control phase, there were no simulated predator encounters, and observations were made at
139 time-matched periods to those of the predator phase. Individual observation order was
140 randomized. Observations were conducted from behind a one-way mirror, dictated into a
141 microcassette recorder, and later transcribed using The Observer 3.0 Event Recorder (Noldus
142 Information Technology, Wageningen, the Netherlands). All observations were made by a single
143 observer (KJM).

144 During focal observations, we noted both feeding and activity. Feeding was defined as
145 the focal bird being present in the food tray and pecking at the food. Although we could not
146 evaluate individual intake rates, we have previously shown that treatment related differences
147 in proportion of time spent foraging coincide with treatment related differences in food intake;
148 when knots spend less time "feeding", less food is consumed (Mathot et al., 2009).

149 We used movement in a familiar environment as our measure of activity (sensu Réale et
150 al., 2007). In this experiment, “activity” comprised both walking with the head oriented
151 upwards, as well as walking with the head oriented downwards, including walking while
152 pecking at the substrate as long as this was not within the food tray (which was scored as
153 “feeding”). Although “flying” would also be considered an active or movement generating
154 behaviour, it was not observed during any of the focal observations included in this analysis,
155 and thus did not contribute overall to our estimated of proportion of time spent active.
156 Additional behaviours were scored including vigilance (standing still with the bill parallel to the
157 horizon or higher with accompanying side to side movement of the head), resting (motionless
158 with the head up), roosting (motionless with bill tucked into a wing), and preening (all
159 behaviours related to plumage maintenance). However, as these behaviours are assumed to be
160 neither indicative of feeding or activity, they are not discussed further.

161 **Data selection and statistical analysis.** We previously showed from this experiment that knots
162 adjusted body mass in response to manipulations of perceived predation danger as expected
163 from theory. At the population-level body mass was lower following the predator treatment
164 compared to the control treatment (van den Hout et al., 2010). We also previously showed that
165 at the population-level, knots showed dramatic short-term behavioural responses to perceived
166 predation danger by decreasing their investment in foraging immediately following
167 experimental presentations of predator models (Mathot et al., 2009). Here we ask how much of
168 the treatment-related changes in body mass can be explained by long-term behavioural
169 adjustments of foraging and activity. We do this in two steps. First, we evaluate long-term
170 responses to the predator treatment relative to control in terms of 1) mass trajectories, 2)
171 proportion of time spent foraging, and 3) proportion of time spent active. To do this, we
172 constructed three separate linear mixed-effect models using the ‘lmer’ function in R with
173 treatment (predator or control) as a fixed effect. We included individual and flock id as random
174 effects to account for non-independence of repeated measures on the same individuals, and on
175 individuals within the same flock, respectively. Because we were explicitly interested in long-
176 term responses, we estimated mass trajectories as the change in body mass across each 5-day
177 treatment period (end body mass minus starting body mass, in grams) such that negative values

178 within a given treatment reflected mass loss, and positive values within a given treatment
179 reflected mass gain. Because the experimental design included measures of behaviour both
180 before and after presentation of sparrowhawk models, repeated over 5 days, we captured both
181 short- and long-term behavioural responses to manipulations of perceived predation danger.
182 For a schematic of the experimental set up and the data included in this study, see ESM Figure
183 S1. As we were explicitly interested in the long-term response to manipulations of perceived
184 predation danger, we chose to use the first daily behavioural observation period from days 2-5
185 of each treatment block because these captured long-term changes in behaviour (i.e., carried
186 over from previous day). We did not include day 1 of each treatment block, as knots had not yet
187 experienced a predator treatment at the start of day 1. Estimates of time spent foraging within
188 each treatment period was done by summing the proportion of time spent feeding across each
189 observation and dividing by the number of observations (N = 4). The same was done for time
190 spent active.

191 Next, we asked whether within-individual changes in mass trajectory across the two
192 treatments was predicted by within-individual changes in time spent foraging and/or time
193 spent active. We calculated the difference between treatments as the average proportion of
194 time feeding during the predator treatment minus the average proportion of time spent
195 feeding during the control treatment, such that negative values reflect relatively lower feeding
196 during the predator compared with the control treatment. The same was done for proportion
197 of time active (i.e. walking when not feeding). We constructed a linear mixed effect model to
198 test whether within-individual changes in mass trajectory (dependent variable) were predicted
199 by within-individual changes in time spent foraging (independent variable) or within-individual
200 changes in time spent active. Each individual only appeared in the data set once, therefore, we
201 did not model individual id. However, we included flock id as a random effect to account for
202 non-independence among-flock members.

203 For all models, we used the “sim” function of the “arm” package to simulate the
204 posterior distribution of the model parameters. Ninety-five percent credible intervals (95% CrI)
205 around the mean (β) were extracted based on 1000 simulations (Gelman and Hill, 2007). Effects

206 were considered significant when the 95% CrI did not overlap 0. Estimates whose credible
207 intervals were biased away from zero, but whose credible intervals overlapped zero by up to
208 15%, were interpreted as showing moderate support for an effect, as these provided more than
209 five times greater support for the interpretation of an effect than they did for the interpretation
210 of no effect (Cumming and Finch, 2005). Bayesian p-values were calculated when estimates
211 were biased away from zero but 95% CrI overlapped zero. Adjusted among-flock repeatability
212 was calculated following Nakagawa and Schielzeth (2010).

213

214 EXPERIMENT 2: MAINTAINING BODY MASS UNDER CHANGING DIET QUALITY

215 **Study subjects.** Eighty-four red knots were captured using mist nests on the mudflats of Richel
216 (53°16' N, 05°23' E), Griend (53°14' N, 05°15' E) and Schiermonikoog (53°28' N, 06°10' E) in the
217 Wadden Sea, The Netherlands, between August and October 2015 and transported to the
218 experimental shorebird facilities at the NIOZ. Birds were housed in eight outdoor aviaries (4m
219 deep x 1.9m wide x 2.3m high at one end, sloping down to a height of 1.9m at the other end) in
220 flocks of between 14 and 17 individuals (including individuals of the *C.c. islandica* subspecies
221 which were part of another study). Knots were maintained on an *ad libitum* diet of protein-rich
222 trout pellets (Trouvit, Produits Trouw, Vervins, France). Birds were handled each week to assess
223 overall health (Milot et al., 2014) and to allow the aviaries to be cleaned. Further details on
224 husbandry conditions are provided in Mathot et al. (2019).

225 **Experimental procedure.** Experiments were conducted over two years between October 2015
226 and March 2017. Data collection was restricted to between October and March in each year.
227 This is outside the migration period of the *islandica* red knots (Dietz et al., 2007), and thus,
228 knots were expected to exhibit relatively little adaptive seasonal variation in body mass during
229 this time. Birds experienced 4 diet manipulations in each year (8 total). Diets alternated
230 between high digestive quality fish pellets (Trouvit; the same high digestive quality food
231 provided outside the experimental period) and low digestive quality mudsnails (*Peringia ulvae*).
232 Mudsnails are low digestive quality because they must be consumed whole, including the

233 indigestible shell. As a result, Trouvit has a circa 4-fold higher energy density (17.66kJ per gram,
234 value from manufacturer) compared with *Peringia ulvae* (4 kJ/g) (van Gils et al., 2005a). The
235 diet manipulations were used to induce variation in gizzard mass as part of another study (Kok
236 et al., 2019; Mathot et al., 2019). Diet manipulations explained only <1% of the observed
237 variation in overall body mass (Mathot et al., 2019), indicating that knots on average
238 maintained similar body mass across diet manipulations. In this study, we follow up on that
239 finding to ask what are the relative contributions of changes in time spent foraging, activity, and
240 metabolism in allowing for this diet-independence of body mass. Body mass and basal
241 metabolic rate (BMR) was measured for up to 4 birds per night at the end of each staple diet
242 period (see below) in both years (N = 80). However, activity budgets scoring was only
243 implemented during the staple diet periods in blocks 2, 3 and 4 of year two (N = 59 birds).

244 **Activity budget observations.** Behavioural observations were conducted on birds in their home
245 aviary beginning in year 2 of the study, and were carried out in blocks 2, 3 and 4 of that year.
246 Observations were conducted during three time blocks: morning (11:00-12:00), mid-day (13:40-
247 14:40), and afternoon (15:30-16:30). Observers (N= 4) were randomly assigned to an aviary (N=
248 8) on any given observation session, and observations were made through a one-way mirror in
249 the aviary door. All birds present in the aviary were assigned a random observation order. Prior
250 to commencing observations, the observer would record the aviary and the focal bird in
251 JWatcher (<http://www.jwatcher.ucla.edu/index.html>). Next, they would scan the flock until the
252 randomly assigned focal bird was located. Once the bird was located, the observation
253 commenced for 5 minutes. If the randomly assigned bird could not be located within one
254 minute, the observer moved on to the next bird on the list, and the missed bird was attempted
255 again at the end of the observation session. This could occur, for example, if several birds,
256 including the focal bird, were in the roosting posture with one leg tucked under the belly,
257 preventing reading of the full combination of leg bands.

258 During observations, the following behaviours were recorded: walking, flying, resting,
259 roosting, vigilance, preening, stretching, ruffle, eating, drinking, pecking, searching, pooping,
260 bathing, vocalizing, social interactions, miscellaneous and out of sight. The ethogram with

261 description of each behaviour are provided in ESM Table S1. As with experiment 1, we focused
262 on changes in foraging and activity as potential mechanism of body mass regulation. Similar to
263 experiment 1, “activity” was defined as the sum of the proportion of time engaged in
264 movement behaviours. In experiment 2, this included spent walking, flying, and searching. This
265 differs slightly from experiment 1 in that no flying was observed in experiment 1, hence it was
266 not included in the time spent active total in experiment 1. However, in experiment 2,
267 proportion of time spent flying made up a very small amount of the total activity budget (mean:
268 0.06%, range 0.00% to 0.70%). As such, including it neither qualitatively nor quantitatively
269 changed any of the results discussed (analyses not shown). However, as we *a priori* considered
270 flying an active behaviour, we present analyses including it in the main text. Although
271 observations were meant to be 5 minutes each, a number of observations terminated early
272 when the bird was lost from view. Proportion of time spent active and proportion of time spent
273 feeding were calculated based on the total observed duration of the relevant behaviours
274 divided by the total observation duration (i.e., excluding time when bird was out of sight).

275 ***Basal metabolic rate measurements.*** Basal metabolic rate (BMR) was measured using flow-
276 through respirometry to evaluate whether BMR was adjusted in response to changes in diet
277 quality. Knots were allowed three-weeks adjustment to their current diet before BMR
278 measurements were taken, to ensure that birds had sufficient time to physiologically adjust to
279 diet quality. We were able to measure BMR for 3 birds per night in the first year, and 4 birds
280 per night in the second year because we obtained an additional mass flow controller in year 2.
281 The order in which BMR was recorded for each bird was randomly determined. BMR
282 measurements occurred one day after birds were subjected to a 30 minute behavioural
283 observation in a novel environment to score exploration as part of another study (Kok et al.,
284 2019). On the day that an individual was scheduled to have their BMR recorded, individuals
285 were removed from their home aviary at approximately 9h00 and placed in a holding crate
286 without food until BMR measurements commenced later that afternoon. This duration of food
287 deprivation was necessary to ensure that knots had attained a post-absorptive state prior to
288 the start of metabolic rate measurements because red knots have naturally cyclical foraging
289 routines and may require several hours to clear their digestive tracts. In the wild, knots undergo

290 natural fasts that coincide with the tidal cycle; they do not forage during high tides when their
291 foraging grounds are inundated, and forage intensively during low tides (van Gils et al., 2005b;
292 van Gils et al., 2006). At 16h00, birds were weighed to the nearest 0.1g.

293 Next, birds were placed in individual air-tight metabolic chambers (6.8 L) which were
294 placed within an environmental cabinet (Weiss Enet Model HETK 3057.S, Wijk bij Duurstede,
295 The Netherlands). The environmental cabinet was kept at 21°C, which is within the
296 thermoneutral zone of red knots (Piersma et al., 1995; Wiersma and Piersma, 1994). Outdoor
297 air was dried (Drypoint membrane dryer model 1201, DPP, Beko, Worcestershire, UK) before
298 being pumped through each chamber at a rate of 50 mL min⁻¹. Flow rates were measured by
299 mass flow controllers (Brooks Instruments, Model 5850Z, Veenendaal, The Netherlands), which
300 were calibrated using a Bubble-O-Meter (Dublin, OH, USA). Effluent air was scrubbed of H₂O
301 using a molecular sieve (2mm granules, Merck, Darmstadt, Germany). The O₂ and CO₂
302 concentrations of influent and effluent airstreams was measured using O₂ (Servomex Model
303 4100, Zoetermeer, The Netherlands) and CO₂ (Servomex Model 1400, Zoetermeer, The
304 Netherlands) analyzers. An automatic valve switched between airstreams so that 10 minutes of
305 baseline was recorded followed by 30 minutes of effluent air from each of two chambers (60
306 minutes total). This sequence was repeated through the 16-hour measurement period for each
307 of two analyzers, allowing up to 4 birds to be measured per night.

308 Analyzers were calibrated daily. Pure nitrogen was used as the low reference for both
309 the O₂ and the CO₂ analyzers. A standard gas of 0.499% CO₂ was used as the high reference for
310 the CO₂ analyzer, and dry air (assumed to contain 20.95% O₂) was used as the high reference
311 for the O₂ analyzer. The following morning at circa 8h00, birds were removed from the
312 chamber, weighed and scored for subcutaneous fat before being returned to their home
313 aviaries with *ad libitum* access to food and water. V_{O₂} and V_{CO₂} were calculated using the
314 equations provided in Piersma et al. (2004). The lowest 10-minute run of V_{O₂} was used as our
315 measure of BMR. Calculations were performed using ExpeData (Sable Systems, Las Vegas, USA).

316 ***Data selection and statistical analysis.*** Using data collected in the same set of experiments, we
317 previously showed that body mass did not vary substantively as a function of diet treatment,

318 but gizzard mass and pectoral muscle mass did (Kok et al., 2019; Mathot et al., 2019). Here, we
319 present analyses on previously unpublished activity budget data and metabolic rate data.

320 To evaluate diet-related differences in body mass (N = 80 individuals), foraging (N = 53
321 individuals), activity (N = 53 individuals), and metabolic rate (N=80 individuals), we constructed
322 four separate linear mixed effect model using the “lme” function of the “lmer” package in the R
323 statistical environment. Sample sizes for behavioural data were lower than for body mass and
324 BMR data because focal observations were only initiated in year 2, and some birds had been
325 removed from the study either due to *Staphylococcus* infections, or to make room for new birds
326 that were brought into the experimental shorebird facility (Kok et al., 2019). For these
327 univariate models, we included diet as a fixed effect, and individual and aviary as random
328 effects. For analyses of metabolic rates, we included the additional random effect of chamber
329 id to account for possible analyzer and/or chamber related effects which would have
330 introduced non-biological noise to the data. Inclusion of this random effect did not alter our
331 interpretation of the effect of diet, but reduced the model residual variance (analyses not
332 shown). We did not include date as a fixed effect in the model because our study design was
333 balanced. During any given observation session, half the birds received the high-quality food
334 treatment and half received the low-quality food treatment. Thus, treatment and seasonal
335 effects (e.g., photoperiod) were not confounded, though we account for potential seasonal
336 variation by including “block” as a random effect. Proportion of time spend foraging and
337 proportion of time active were log (n+0.01) transformed prior to analyses. We used the “sim”
338 function of the “arm” package to simulate the posterior distribution of the model parameters.
339 Ninety-five percent credible intervals (95% CrI) around the mean (β) were extracted based on
340 1000 simulations (Gelman and Hill, 2007). Effects were interpreted in the same way as for
341 experiment 1 based on the effect size and the degree of overlap between the 95% CrI and 0.
342 Adjusted repeatability was calculated following Nakagawa and Schielzeth (2010).

343

344 ***Post-hoc analyses***

345 In both experiments, mass regulation was achieved through changes in the proportion of time
346 spent feeding and changes in the proportion of time spent active (see **Results**). Coincident
347 increases in activity with decreases in feeding could be due to the fact that proportions are
348 bounded between 0 and 1, and that increases in one force a concomitant decrease in the other.
349 If that was the case, then shifts in feeding should be directly offset by shifts in activity (i.e., the
350 within-individual correlation should be $r = -1$). Within-individual correlations of $0 > r > -1$ would
351 indicate that there was scope for partial independence in the investment towards these two
352 components of the total activity budget, while a correlation of $r = 0$ would be indicative of
353 complete independence.

354 To evaluate the scope for independent regulation of activity and feeding, we constructed
355 bivariate mixed effects models using the MCMCglmm function in the R statistical environment.
356 The proportion of time spent active and the proportion of time spent feeding (both natural log
357 + 0.01 transformed) were fitted as the response variables, and we modelled a random intercept
358 for individual identity. We did not include additional random effects because none of the
359 effects that were found to be important varied within-individuals (Tables 1 and 3), and
360 therefore, would not influence our ability to estimate the within-individual correlation.

361 Results presented use an inverse gamma prior. However, we confirmed that the prior
362 specification did not unduly influence the results. Results were quantitatively similar when
363 using an inverse wishart prior, and were not sensitive to ν (degrees of belief in the prior). We
364 present estimates obtained when $\nu = 2$. Models were run for 103,000 iterations (i.e., nitt), a
365 burn-in period of 3000, and a thinning interval of 100 to produce a total of 1000 estimates. The
366 estimates were used to calculate the posterior mode of the distribution (i.e. the most likely
367 value), as well as the 95% credible interval.

368

369 **Results**

370 **EXPERIMENT 1**

371 Knots had significantly lower mass trajectories during the predator treatment compared to the
372 control treatment, and spent significantly less time foraging and less time active (Table 1, Figure
373 1). At the within-individual level, increased investment in feeding was associated with
374 significantly more mass gain ($\beta = 19.98$, 95% CrI = 7.20, 43.60). That is, for every 0.1 increase in
375 the proportion of time spent feeding during the predator treatment, knots gained an average of
376 2.00 g (Figure 1A). In contrast, increased investment in activity was associated with lower rates
377 of mass gain ($\beta = -22.93$, 95% CrI = -56.05, 20.53, Bayesian p-value = 0.15). That is, for every 0.1
378 increase in the proportion of time active during the predator treatment, knots gained on
379 average 2.29 g less than the mean weight gain (Figure 1B). Further, our multivariate analyses
380 revealed that increasing activity did not force a concomitant decrease in feeding, or vice versa,
381 as the estimated within individual correlation from the bivariate model was 0.48 (95%CrI 0.27,
382 0.66). However, even for knots that showed no net change in proportion of time feeding or
383 proportion of time active, there was moderate support that exposure to predators resulted in a
384 decrease in body mass trajectory (intercept estimate: $\beta = -3.81$ g, 95% CrI = -11.40, 1.00,
385 Bayesian p-value = 0.04, Table 1).

386

387 EXPERIMENT 2

388 There was moderate support for body mass varying with diet when analyzing the subset of
389 birds (N = 59 individuals) for which we had BMR data available (Table 2, $\beta = 1.09$, 95% CrI = -
390 0.27, 2.33, Bayesian p-value = 0.06). We interpret this small estimated effect size, together with
391 the fact that diet explained a negligible proportion of the overall variance in body mass in this
392 sample of individuals (marginal $r^2 = 0.001$, estimated using the `r.squaredGLMM` function from
393 the `MuMIn` package in R), as support for diet-independent body mass.

394 Knots exhibited large and significant changes in their activity budgets in response to
395 experimental manipulations in diet. Knots spent significantly more time feeding ($\beta = 3.21$, 95%
396 CrI = 2.98, 3.38) and significantly less time active ($\beta = -0.50$, 95% CrI = -0.73, -0.40) when
397 provided with low quality diets. Again, bivariate analyses indicate that there was scope for
398 activity and feeding to be adjusted partially independently of one another. The estimated

399 within-individual correlation was $r = -0.32$ (95% CrI = -0.44, -0.18). Finally, there was no support
400 for an effect of diet quality on BMR ($\beta = 0.02$, 95% CrI = -0.02, 0.06) (Table 2 and Figure 2).

401

402 **Discussion**

403 Here, we report the results of two studies that address the mechanisms of mass regulation
404 birds. We show that decreases in body mass in knots exposed to cues of predation coincide
405 with decreased foraging effort and increased activity, and further, that within-individual
406 changes in mass trajectories can be predicted by individual differences in the extent of foraging
407 restraint and activity upregulation. We also provide evidence that both dieting and activity play
408 a role in maintaining body mass under changing diet quality. When provided with low quality
409 diets, knots increased their time spent foraging, and decreased their time spent active.
410 Although we found no support for diet-related differences in metabolic rate, we discuss the
411 potential for metabolic adjustments to contribute to mass regulation in knots in light of our
412 results (see below).

413 When exposed to model sparrowhawks over 5 consecutive days, red knot mass
414 trajectories shifted significantly downwards. Reduction in body mass in response to increased
415 perceived predation has been documented in several other studies (e.g., Abbey-Lee et al., 2016;
416 Lilliendahl, 1997; MacLeod et al., 2005; Witter et al., 1994). However, such reductions are often
417 assumed to come about because increased investment in vigilance or other anti-predator
418 behaviours limits opportunities to search for food (Brown, 1999; Houston et al., 1993; Lima,
419 1998). While this may be the case in free-living birds, we show here that reductions in foraging
420 effort also occur in captive birds, with *ad libitum* access to food. We previously showed that the
421 long-term upregulation of vigilance in response to manipulated perceived predation danger
422 meant that knots shifted the percent of time spent vigilant from circa 55% during the control
423 treatment to 75% during the predator treatment (Mathot et al., 2009). Given that the mean
424 proportion of time spent feeding and active during the control was < 10% each, neither of these
425 necessarily had to be downregulated to accommodate the increased vigilance. For example,

426 time allocated to other behaviour (e.g., resting, roosting), could have decreased instead. We
427 suggest that the predation-related decrease in mass trajectory appears to be brought about in
428 part via reduced intake (i.e., dieting), and appears similar to the restraint in eating shown in a
429 captive knot undergoing seasonal mass loss even while provided with *ad libitum* access to food
430 (Piersma and Poot, 1993).

431 Importantly, time allocation tradeoffs did not force a negative correlation between time
432 spent active and time spent foraging. In red knots, walking and probing the substrate increases
433 energy expenditure by approximately 35% compared to resting (Piersma et al., 2003a). As such,
434 we predicted that upregulation in activity in response to the predator treatment might also
435 contribute to mass loss. In contrast, we found that at the population-level, activity decreased
436 significantly during the predator treatment, though the magnitude of the decrease was small
437 (Figure 1C). This small decrease in percent of time spent active was coincident with a large
438 decrease in the percent of time spent foraging. Post-hoc analyses corroborate this result; at the
439 within-individual level, there was a positive correlation between proportion of time spent
440 active and proportion of time spent feeding ($r = 0.48$, 95% CrI = 0.27, 0.66). Importantly
441 however, when considering within-individual changes in mass trajectories, time spent foraging
442 and time spent active, there was strong support that both restraint in foraging and increased
443 activity contributed to mass regulation (Figure 2). Knots that showed the greatest decrease in
444 the proportion of time foraging between predator and control treatments also showed the
445 greatest decrease in mass trajectory. At the same time, knots that showed the greatest increase
446 in time spent active between these treatments showed the greatest decrease in mass
447 trajectories. Interestingly, these two mechanisms had very comparable effects on mass
448 trajectories in terms of the magnitude of change in mass trajectory brought about per unit
449 change in effort spent foraging or active (Table 1), suggesting that they are equally effective
450 means of managing body mass in knots.

451 Our within-individual analyses also revealed moderate support for the interpretation
452 that there was a downward shift in mass trajectory in knots between the predator and control
453 treatment, even when there was no net change in foraging or activity (Table 2; intercept

454 estimate). This could be due to the additional effects of the acute, short-term responses to
455 predator exposure during which time steeper reductions in food intake occurred (i.e., indicating
456 that the long-term response was an underestimate of the overall average effect of predator
457 treatment on knots) (Mathot et al., 2009). It may also indicate that additional, unmeasured,
458 mechanisms, also contributed to the shift in mass trajectory, such as changes in digestive
459 efficiency, or changes in metabolism (Halsey, 2018; Zanette et al., 2014). Although digestive
460 efficiency is often stable across different food intakes and food qualities (Karasov, 1996;
461 McWilliams and Karasov, 1998), we are not aware of any study investigating digestive efficiency
462 as a function of predation risk. However, many birds defecate immediately prior to anti-predator
463 escape flights (van der Veen and Sivars, 2000). While this may result in an immediate, small,
464 decrease in body mass (van der Veen and Sivars, 2000), it also implies that birds can plastically
465 adjust gut transit time. All else being equal, decreasing gut transit time would provide a means
466 of reducing the amount of energy extracted per unit of food consumed (i.e., reduce digestive
467 efficiency; see Levey and Karasov, 1992; McWilliams and Karasov, 1998). Similarly, fecal energy
468 loss has recently been proposed as may be an important mechanism contributing to energy
469 homeostasis in humans (Lund et al., 2020). However, the role of changes in gut transit time as a
470 mechanism of mass management in birds requires investigation.

471 Predator-related decreases in mass trajectories may also have resulted from metabolic
472 adjustment. Indeed, when exposed to predators over short-time scales, many organisms have
473 been shown to exhibit increases in metabolic rate (Beckerman et al., 2007; Okuyama, 2015;
474 Steiner and Van Buskirk, 2009). Though this is often interpreted as an unavoidable consequence
475 of predator-induced stress, upregulation of metabolic rates in response to increased perceived
476 predation danger may also facilitate adaptive decreases in body mass over intermediate time
477 scales. Studies tracking changes in metabolic rate across different time scales are needed to
478 address this possibility.

479 In a second experiment, we manipulated diet quality provided to knots. We previously
480 showed that large changes in the quality of the diets had no appreciable effect on overall body
481 mass (Mathot et al., 2019). In the subset of birds included in the present study (n=59), we again

482 find that the diet manipulations used here had no biologically important effect on body mass
483 when birds are given sufficient time to acclimate to the diet. The maintenance of body mass
484 under decreasing energetic quality of food was achieved through significant upregulation in
485 foraging effort (from circa 1% of time spent foraging to circa 45% of time spent foraging), and a
486 concomitant decrease in the proportion of time spent active (from circa 25% to 15%). Several
487 studies have shown that the increased foraging intake necessitated by low quality diets results
488 in substantive increases in the gizzard (i.e., muscular stomach used for food processing) (e.g.,
489 Bijleveld et al., 2014; Dekinga et al., 2001; Mathot et al., 2017). This was also true in this cohort
490 of birds; changes in diet quality were associated with a 2-fold difference in gizzard mass (Kok et
491 al., 2019; Mathot et al., 2019). Importantly, the magnitude of the shift in the percentage of time
492 spent foraging observed in this study (from 1.5% to 47.5%) was not sufficient to force a
493 coincident change in activity. The percent of time active during the high-quality diet treatment
494 (27%) could have been maintained on the low-quality diet while still allowing nearly 25% of the
495 overall activity budget for other behaviours such as preening or roosting. Post-hoc analyses
496 confirm this interpretation. Although there was a negative within-individual correlation
497 between proportion of time spent active and proportion of time spent feeding ($r = -0.32$, 95%
498 CrI = -0.44, -0.18), the correlation was moderate. This suggests that there was at least partial
499 independence in how time was allocated to these two categories of behaviour, as complete
500 dependence would have resulted in a correlation of -1. Taken together, we suggest that the
501 changes in activity patterns may have been adopted as a means of conserving energy under
502 conditions of low diet quality.

503 We also investigated whether diet induced changes in metabolic rate could have
504 contributed to the observed mass regulation. All else being equal, lower BMR under conditions
505 of low food quality would facilitate mass regulation. We found no support for diet-induced
506 changes in BMR. However, changes in diet are known to induce changes in body composition,
507 which may complicate interpretation of this null result. For example, in knots, low quality diets
508 result in increases in gizzard mass (Bijleveld et al., 2014; Dekinga et al., 2001; Mathot et al.,
509 2019), and decreases in pectoral muscle mass (Mathot et al., 2019). These muscles each have
510 high metabolic activity, though gizzard is more metabolically active compared with pectoral

511 muscle (i.e., contributes more to basal metabolic rate per gram of tissue) (Daan et al., 1990;
512 Kersten and Piersma, 1987; Piersma et al., 1996). In a previous analysis with the same set of
513 birds, we showed that diet induced changes in the mass of gizzard and pectoral muscle were
514 roughly equal, but in opposite directions; for each 1 g increase in gizzard mass within-
515 individuals, there was on average a 1.26 g decrease in pectoral muscle mass (Mathot et al.,
516 2019). Thus, any diet-induced changes in BMR due to increased gizzard mass may have been
517 offset by the concomitant changes in pectoral muscle mass.

518 In contrast with our results, an earlier study found that knots switched from Trouvit (the
519 same high quality food as used in the current study) to blue mussels (*Mytilus edulis*) exhibited
520 increases in total body mass, gizzard mass, and decreases in BMR after 3 weeks on the low
521 quality diet (Piersma et al., 2004). However, there are key differences between our study and
522 the study by Piersma et al. (2004) that may account for the contrasting results. The knots used
523 in the current study were recently wild-caught, and repeatedly shifted between high and low
524 digestive quality diets. In contrast, the knots used in the study by Piersma et al. (2004) had been
525 in captivity for five to six years prior to the experiments and maintained on *ad libitum* Trouvit
526 since capture. Given that knots generally exhibit a reluctance to switch from high quality to low
527 quality food (Piersma et al., 1993), in the earlier study by Piersma et al. (2004), three weeks on
528 a diet of blue mussels may not have been sufficiently long for knots to fully acclimate to the
529 change in diet. Studies tracking changes in gizzard mass and metabolic rate in response to diet
530 quality manipulations over different time scales would help clarify whether metabolic
531 responses to diet quality [in knots and other birds] are indeed time-dependent.

532 Taken together, these two experiments both provide evidence that adjustments in
533 foraging effort and activity in red knots contribute to patterns of mass regulation. Foraging
534 decreased under increased predation danger, which facilitated mass loss relative to the low
535 danger treatment. Foraging also decreased when knots were provided higher quality food.
536 However, the absolute investment in foraging on the low-quality diet was markedly different
537 across the two experiments; proportion of time spent foraging was 0.10 in experiment 1 versus
538 0.40 in experiment 2 (see Figures 1 and 2). Although some of this might reflect variation in the

539 quality of *Peringia* provided, differences the housing densities of knots across the two
540 experiments (experiment 1: 0.16 knots/m²; experiment 2: 1.75 knots/m²) likely also resulted in
541 differences in perceived competition and the degree of interference competition, which has
542 previously been shown to result in increased time spent searching in a food patch (Bijleveld et
543 al., 2012).

544 Interestingly, voluntary flight did not appear to play an important role in mass
545 regulation in either experiment. In the first experiment, no voluntary flight was observed, and
546 in the second experiment, voluntary flight made up a very small percentage of the total activity
547 budgets (<1%). Voluntary flight can result in energy expenditure of 9 -10 times basal metabolic
548 rate (Piersma and van Gils, 2011), and would therefore be a very effective means of increasing
549 energy expenditure. Our failure to detect voluntary flight as a mechanisms of mass
550 management may be because our focal observations were too short to capture this relatively
551 rare behaviour, or because voluntary flight is not used to manage body mass in captive knots.
552 The latter might be the case because the experimental arena and aviaries used in the present
553 study are too small to allow for unencumbered flight. Alternatively, flight may impose
554 additional, non-energetic costs. For example, voluntary flight for mass loss may increase an
555 individual's vulnerability to predation by reducing flock cohesion (Mathot et al., 2009).
556 Ultimately, longer observation sessions are needed to assess the potential for small shifts in
557 voluntary flight as a mechanism of body mass management.

558 **Conclusion**

559 We show that both adaptive changes in body mass, and maintenance of body mass under
560 changing conditions, coincide with changes in foraging effort and activity. Loss of body mass is
561 often seen as a consequence of missed foraging opportunities when mitigating predation
562 danger (e.g., due to increase of vigilance, or avoiding risky activities). However, our results
563 suggest that birds are able to exhibit restraint in foraging, analogous to "dieting". Under
564 conditions of *ad libitum* access to food, knots spent less time feeding when weight reduction
565 was adaptive (Experiment 1), and when the food provided was of higher energetic quality
566 (Experiment 2). Although, the second experiment provides no evidence that mass regulation

567 was achieved through metabolic adjustment, the regulation of body mass was studied over a
568 long-time period, once body mass had the opportunity to stabilize (i.e. > 3 weeks' adjustment
569 to the new diet). Thus, we cannot rule out the possibility that metabolic adjustments
570 contributed to mass regulation over shorter time scales (e.g., the first few days adjusting to a
571 new diet). Indeed, Experiment 1 provides some evidence that additional mechanisms, such as
572 metabolic adjustment, could have contributed to mass regulation, and other studies have also
573 suggested that metabolic adjustments have time-dependent effects. Understanding whether,
574 and under what circumstances, metabolic adjustments plays a role in mass regulation in birds
575 requires further investigation.

576

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589

590 **Competing interests**

591 No competing interests declared.

592

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599

600 **Data availability**

601 All data and r-scripts required to reproduce the analyses presented in this manuscript are
602 available in an Open Science Framework digital repository (<https://osf.io/uswk7/>). Link for peer
603 review: https://osf.io/uswk7/?view_only=686b5d2c38a24a769fc3fa307fa2c5b0. Data and
604 scripts will be deposited on Dryad upon final acceptance.

605

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773

774 **Table 1:** Experiment 1. Treatment related differences in body mass trajectories, proportion of
 775 time spent feeding, and proportion of time spent active in knots exposed to experimental
 776 manipulations of perceived predation risk. Foraging and activity data were ln transformed prior
 777 to analyses to meet assumptions of normality for model residuals. The intercept estimate is for
 778 the control treatment.

| | Mass trajectory | Ln (proportion of time feeding) | Ln (proportion of time active) |
|-----------------------|--|--|--|
| Fixed effects | β (95% CrI) | β (95% CrI) | β (95% CrI) |
| Intercept | 4.66 (2.55, 6.15) | -2.32 (-2.75, -2.02) | -2.20 (-2.28, -1.75) |
| Predator treatment | -6.26 (-7.67, -3.52) | -0.44 (-0.70, -0.08) | -0.48 (-0.74, 0.22) |
| Random effects | σ^2 (95% CrI) | σ^2 (95% CrI) | σ^2 (95% CrI) |
| Bird ID | 1.18 e-14 (7.11 e -15, 1.88 e-14) | 0.023 (0.016, 0.041) | 0.07 (0.04, 0.10) |
| Flock ID | 1.94 (0.33, 6.76) | 0.16 (0.06, 0.49) | 0.63 (0.18, 1.23) |
| Residual | 31.46 (21.55, 38.45) | 0.60 (0.49, 0.85) | 0.41 (0.31, 0.55) |

779

780 **Table 2: Experiment 1.** Sources of variation in relative mass trajectory and relative activity
 781 trajectory in red knots exposed to manipulation of perceived predation danger. Relative mass
 782 trajectory refers to the mass trajectory during the 5-day predator treatment minus the mass
 783 trajectory during the control treatment, such that negative values indicate a relative decrease
 784 in mass during the predator treatment.

| Fixed effect | Delta mass trajectory β (95% CrI) |
|--|--|
| Intercept ¹ | -7.75 (-11.95, 0.34) |
| Change in proportion of time spent foraging ² | 25.97 (7.71, 45.96) |
| Change in proportion of time spent active ² | -22.49 (-56.83, 17.27) |
| Random effects | σ^2 (95% CrI) |
| Flock ID (N = 8 levels) | 73.31 (46.14, 96.39) |
| Residual (N = 48 levels) | 27.00 (17.37, 41.25) |

785 1. Intercept estimates the average change in body mass trajectory in perceived predation
 786 periods relative to control periods for individuals that show no adjustment in the proportion of
 787 time spend feeding.

788 2. Change in proportion of time spent feeding/active in predator treatment relative to control,
 789 where zero equals no net change, positive values indicate increase in time allocation during
 790 predator treatment, and negative values indicate decrease in time allocation in predator
 791 treatment.

Table 3: Experiment 2. Sources of variation in foraging, activity and metabolic rate.

| | Body mass (g) | Ln (proportion of time foraging) | Ln (proportion of time active) | Metabolic rate (Watts) |
|------------------------|--|---|--|--|
| Fixed effects | β (95% CrI) | β (95% CrI) | β (95% CrI) | β (95% CrI) |
| Intercept ¹ | 132.29 (126.26, 137.78) | -4.08 (-4.19, -3.91) | -1.40 (-1.59, -1.26) | 1.17 (0.87, 1.45) |
| Diet (Low quality) | 1.09 (-0.28, 2.32) | 3.21 (2.98, 3.38) | -0.50 (-0.73, -0.40) | 0.01 (-0.03, 0.06) |
| Random effects | σ^2 (95% CrI) | σ^2 (95% CrI) | σ^2 (95% CrI) | σ^2 (95% CrI) |
| Individual | 188.02 (165.78, 214.55) | 0 ³ | 0.010(0.006, 0.014) | 0.021 (0.017, 0.028) |
| Aviary | 4.83 (0.82, 14.40) | 0.0030 (0.0006, 0.0077) | 0.0015 (0.0004, 0.0044) | 0.0005 (0.0001, 0.0019) |
| Treatment Block | 24.19 (18.61, 31.22) | 0 ³ | 0.0015 (0.0004, 0.0044) | 0 ³ |
| Respirometry Chamber | NA | NA | NA | 0.061 (0.047, 0.073) |

| | | | | |
|----------------------------------|----------------------|--------------------|----------------------|----------------------|
| Year | 0 ³ | NA | NA | 0.013 (0.006, 0.020) |
| Residual | 49.99 (44.90, 57.45) | 0.45 (0.35, 0.53) | 0.35 (0.29, 0.44) | 0.062 (0.05, 0.068) |
| Repeatability² | r (95% CrI) | r (95% CrI) | r (95% CrI) | r (95% CrI) |
| Individual | 0.79 (0.76, 0.82) | 0 ³ | 0.025 (0.018, 0.037) | 0.27 (0.22, 0.32) |

-
1. Intercept estimates are for high quality diet. Diet estimate is the change in response variable for knots on low quality diet relative to the high quality diet.
 2. Adjusted repeatability calculated after correcting for fixed effects.
 3. Variance components non-estimable.

Figure legends

Figure 1: Experiment 1. Treatment related differences in (A) mass trajectory, (B) proportion of time spent feeding, and (C) proportion of time spent active. The same individuals (N= 48) were included in both “control” and “predator” treatments.

Figure 2: Experiment 1. Within-individual changes in (A) the proportion of time spent feeding and (B) the proportion of time spent active predict within-individual changes in mass trajectory in response to manipulations of perceived predation danger in red knots. Each point represents an individual (N = 64 total). The lines fitted to the data are derived from the intercept and slope estimates from the mixed effects model presented in Table 1.

Figure 3: Experiment 2. Treatment related differences in (A) body mass (N = 80), (B) the proportion of time spent feeding (N= 59), (C) the proportion of time spent active (N = 59), and (D) basal metabolic rate (BMR) in Watts as a function of diet quality (N= 80).

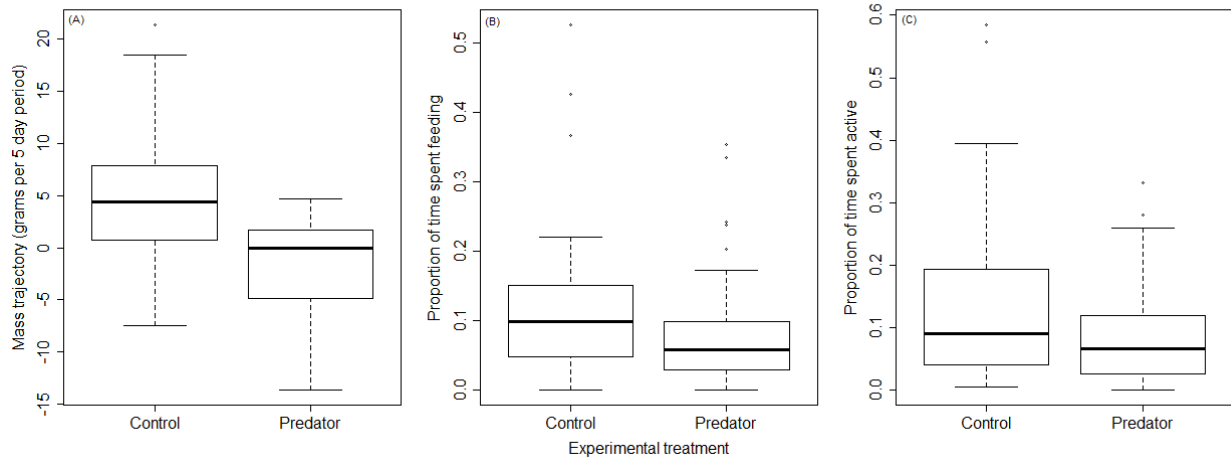


Figure 1

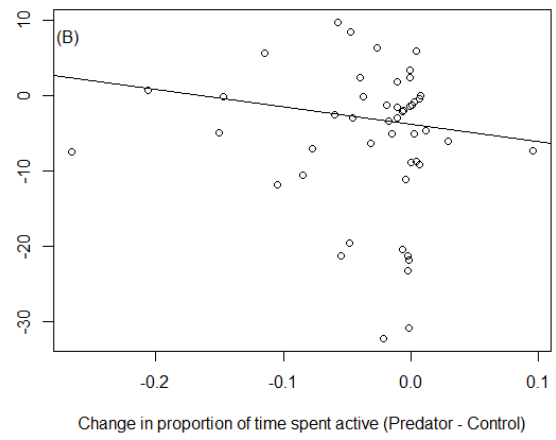
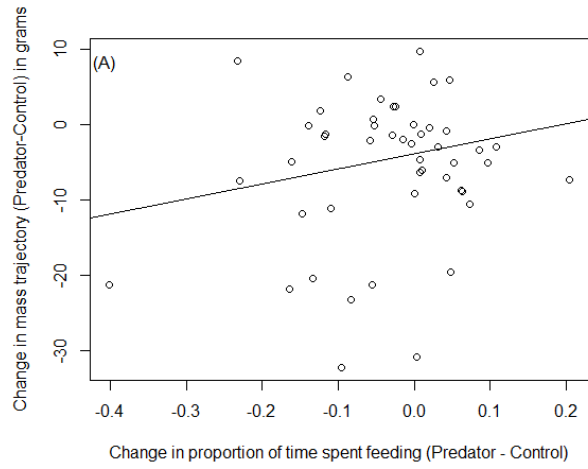


Figure 2

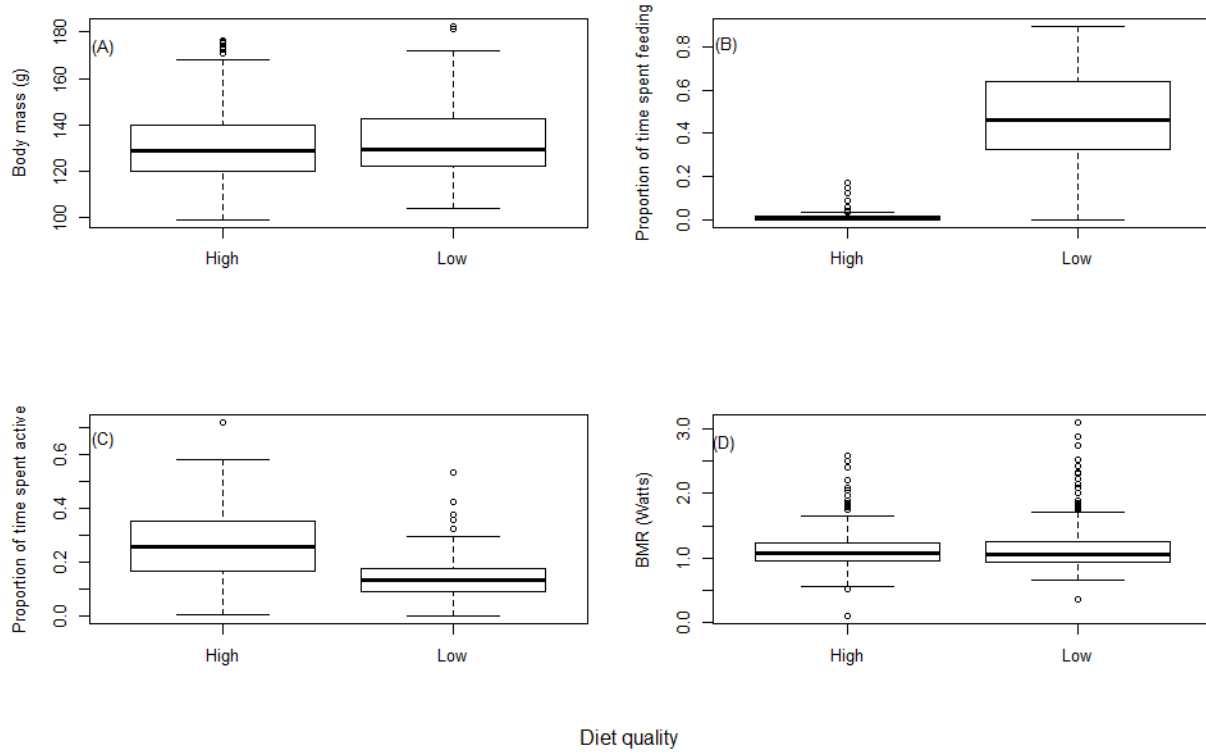


Figure 3

Electronic supplementary material

Table S1: Ethogram used for behavioural observations in Experiment 2. Type refers to whether the behaviour was scored as a state or point event. State events are scored for their whole duration; any given state event continues until a new state event is registered. Point events are scored for their number of occurrences. These were generally behaviours that were too short in duration to allow for accurate duration estimates. Activity was estimated as the sum of time spent walking, flying and searching (see main text).

| Behaviour | Description | Type |
|-----------------------|---|-------|
| Walking | Stepping forward, backward, or on one side in order to move to another location | State |
| Flying | Taking off by flapping, and move to another location | State |
| Resting | Standing still without any visible action | State |
| Roosting | Standing with its bill between the feathers, often on one leg | State |
| Vigilance | Looking around with a horizontal bill and/or looking up by tilting the head | State |
| Preening | Cleaning or rearranging its feathers with the bill or by flapping, scratching with one of its feet | State |
| Stretching | Stretching wings and/or legs | Point |
| Ruffle | Shaking all its feathers | Point |
| Eating | Pecking some food of the feeder and swallowing it | State |
| Drinking | Putting its bill in the water, then turning its head up to send the water to the back of his throat | State |
| Pecking | Pecking solid objects with the bill (often repeatedly) | State |
| Searching | Looking at the ground in order to find food with the bill forming a 45° angle with the horizontal, or probing in the sand | State |
| Pooping | The bird releases excrement from the body | Point |
| Bathing | Cleaning its feathers using water, often shaking the body | State |
| Vocalizing | Producing vocalisations | Point |
| Interaction initiator | The bird attacks one of the other bird | Point |
| Interaction victim | The bird is being attacked by one of the other birds | Point |
| Miscellaneous | Behaviour that does not fit the descriptions above | Point |
| Out of sight | The bird cannot be seen by the observer | State |

Figure S1. Schematic representation of an experimental block in experiment 1. Black rectangles represent each day of the block (1 through 5). On each day, two predator events occurred (purple = presentation of a perching sparrowhawk, green = presentation of a gliding sparrowhawk), with behavioural observations conducted immediately before and after each presentation (small grey and yellow rectangles). Only the observation periods shown in yellow were used to calculate long-term behavioural responses, as they reflected carry-over responses from presentations on the previous day. Mass of all individuals was calculated at the beginning and end of each block. For the control (i.e., non-predator) block of the experiment, the same sampling design was used except that no predators were presented (blank controls).

