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9 **Flexibility, variability and constraint in energy management patterns across vertebrate taxa**

10 **revealed by long-term heart rate measurements**

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12

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18 metabolic rate

19

20 **Running headline:**

21 Energy management patterns of vertebrates

22 Summary

- 23 1) Animals are expected to be judicious in the use of the energy they gain due to the
24 costs and limits associated with its intake. The management of energy expenditure
25 (EE) exhibited by animals has previously been considered in terms of three patterns:
26 the constrained, independent and performance patterns of energy management.
27 These patterns can be interpreted by regressing daily EE against maintenance EE
28 measured over extended periods. From the multiple studies on this topic, there is
29 equivocal evidence about the existence of universal patterns in certain aspects of
30 energy management.
- 31 2) The implicit assumption that animals exhibit specifically one of three discrete energy
32 management patterns, and without variation, seems simplistic. We suggest that
33 animals can exhibit gradations of different energy management patterns and that the
34 exact pattern will fluctuate as their environmental context changes.
- 35 3) To investigate these ideas, and for possible large-scale patterns in energy
36 management, we analysed long-term heart rate data – a strong proxy for EE – across
37 and within individuals in 16 species of birds, mammals, and fish.
- 38 4) Our analyses of 292 individuals representing 46 539 observation-days suggest that
39 vertebrates typically exhibit predominantly the independent or performance energy
40 patterns at the across-individual level, and that the pattern does not associate with
41 taxonomic group. Within individuals, however, animals generally exhibit some degree
42 of energy constraint. Together, these findings indicate that across diverse species,
43 some individuals supply more energy to all aspects of their life than do others,
44 however all individuals must trade-off deployment of their available energy between
45 competing functions. This demonstrates that within-individual analyses are essential
46 for interpretation of energy management patterns.
- 47 5) We also found that species do not necessarily exhibit a fixed energy management
48 pattern but rather temporal variation in their energy management over the year.
49 Animals' energy management exhibited stronger energy constraint during periods of
50 higher EE, which typically coincided with clear and key life cycle events such as
51 reproduction, suggesting an adaptive plasticity to respond to fluctuating energy
52 demands.

53 Introduction

54 Every biological process of an organism costs energy and animals are therefore limited in
55 their actions by their energy throughput; the amount of energy they consume and use. The
56 limit on their energy throughput may be due to finite food availability in the environment
57 (Stearns 1992; Thomas *et al.* 2001; McNab 2002), or inherent limitations in their capacity to
58 accumulate energy in terms of harvesting, digesting or assimilating it (Drent & Daan 1980;
59 Hammond & Diamond 1997; West, Brown & Enquist 1999; Gearty, McClain & Payne 2018)
60 (fig. 1). Alternatively, animals may have a ceiling on their rate of energy expenditure, perhaps
61 due to limited musculature (Hammond & Diamond 1997), or in order to avoid physiological
62 damage (Piersma 2011) due to, for example, hyperthermia (Speakman & Krol 2010; Nilsson &
63 Nord 2018). Furthermore, energy throughput may be optimised in animals, and any increase
64 in throughput could have fitness consequences such as increased risk of mortality (Daan,
65 Deerenberg & Dijkstra 1996; Santos & Nakagawa 2012), perhaps due to immune suppression
66 (Pontzer 2018) or oxidative stress (Costantini, Dell'Arciccia & Lipp 2008). Although there have
67 been a number of studies about energy management (e.g. Daan, Masman & Groenewold
68 1990; Ricklefs, Kornazewski & Daan 1996; Pontzer 2015; Portugal *et al.* 2016), the resultant
69 observations have not formed a coherent picture and we presently lack an understanding of
70 whether there are governing principles operating across taxa. It seems possible then that the
71 limiter on an animal's energy throughput probably varies between species and may vary
72 within species and individuals, across their life histories and seasonally (Speakman & Krol
73 2010; Careau *et al.* 2013)

74

75 *Patterns of energy management*

76 As previously proposed (e.g. Ricklefs, Kornazewski & Daan 1996), we can consider an animal's
77 management of energy expenditure in terms of two broad sets of processes. The first broad
78 category includes energy spent on 'maintenance' processes required to maintain
79 homeostasis [which can include respiration (Codd *et al.* 2005), immuno-competency
80 (Deerenberg *et al.* 1997), blood circulation, nerve function, thermoregulation (Lewden *et al.*
81 2017), digestion (Secor 2009), reproductive physiology (Perrigo & Bronson 1983; Perrigo
82 1987; Ellison 2003; Wiersma & Verhulst 2005), protein turnover (Yu *et al.* 1999) and somatic

83 repair more broadly (Wiersma & Verhulst 2005)]. The second broad category includes energy
84 spent directly on auxiliary processes, which have typically been termed ‘activity’ and assumed
85 to constitute solely active behaviours such as locomotion, mate competition and parental
86 care (Ricklefs, Kornazewski & Daan 1996; Halsey *et al.* 2015; Careau 2017), but can also
87 include inactive behaviours such as maintaining a posture (Levine, Schleusner & Jensen 2000;
88 Ward, Speakman & Slater 2003) and fidgeting (Levine, Eberhardt & Jensen 1999), (see the
89 Supplementary for more information). Presently, the literature recognises three possible
90 models of energy management patterns that animals could follow (Careau & Garland Jr 2015;
91 Mathot & Dingemanse 2015; Careau 2017). The pattern that is often the default assumption
92 of how energy is managed in animals is that the amount of energy spent on activity is not
93 related to the amount of energy spent on maintenance processes. In this ‘independent’
94 pattern of energy management (Careau & Garland Jr. 2012) overall energy expenditure is not
95 restricted and increases in energy spent on activity do not require a compensatory decrease
96 in energy spent on maintenance. This management pattern is represented by positive,
97 unitary (slope ~ 1) covariation between overall and maintenance energy expenditure (Mathot
98 & Dingemanse 2015) (supplementary fig. 1A). Alternatively, an animal could be constrained
99 to maintain its overall energy expenditure within a narrow range (Pontzer 2015), in which
100 case any increase in activity or other auxiliary processes (resulting in increased energy
101 expenditure) must be countered by a decrease in maintenance energy expenditure
102 (Deerenberg *et al.* 1998; Welcker *et al.* 2014) or, vice-versa, increased maintenance
103 necessitates decreases in auxiliary processes. This energy management pattern is termed
104 the ‘constrained’ pattern (Pontzer 2015) and is defined by a lack of covariation between an
105 animal’s overall energy expenditure (often measured as daily energy expenditure) and its
106 maintenance energy expenditure over time (Careau 2017) (supplementary fig. 1B). The third
107 energy management pattern, which also does not restrain overall energy expenditure, is
108 defined by an intrinsic link between auxiliary and maintenance energy expenditure, such that
109 an increase in one is associated with an increase in the other: the ‘performance’ pattern of
110 energy management (Careau *et al.* 2008). This can arise when sustaining high levels of
111 activity requires subsequent physical and/or physiological recovery. Alternatively, animals
112 becoming more active may require costly digestive organs to assimilate, and/or increased
113 muscularity to expend, the extra energy associated with that activity (Swanson, McKechnie &
114 Vézina 2017; Yap *et al.* 2017). Consequently, this management pattern is represented by

115 positive covariation between overall and maintenance energy expenditure with a slope
116 gradient greater than 1 (Mathot & Dingemanse 2015) (supplementary fig. 1C).

117 Different energy management patterns may be preferable in different scenarios,
118 although studies to date have not formerly investigated such context-dependency. Animals
119 exhibiting high levels of activity during periods of food scarcity might in particular benefit
120 from reducing maintenance energy expenditure - the constrained pattern - because this
121 approach would prevent their overall energy requirements from increasing, which may
122 enhance survivability. For example, mice exposed to a food shortage, and obliged to work for
123 that food, respond by daily torpor (Hut *et al.* 2011). By contrast, energy expenditure
124 represented by the independent pattern in this scenario would cause an increase in overall
125 energy requirements coinciding with periods when starvation risk is highest (Pontzer 2015).
126 The constrained pattern might also prove advantageous when food is abundant but
127 predation risk is high, because limiting energy requirements would reduce the need to
128 forage, in turn limiting exposure to predators (Mathot *et al.* 2016).

129 In some situations, however, an uncoupling of the energy expenditure of different
130 organ systems and thus removing constraints on overall energy expenditure (the
131 independent pattern) might be advantageous, providing the animal with energetic flexibility
132 to respond to their changing ecology or life history. While eider ducks are moulting, their cost
133 of feather production appears to increase their maintenance metabolic rate while their
134 activity energy costs remain unchanged (Guillemette & Butler 2012). During periods when
135 food availability is predictably high and an enhanced physical state is required, such as in king
136 penguins foraging at sea after a fast (Gauthier-Clerc *et al.* 2002), animals may benefit from a
137 pattern of energy expenditure described by the performance pattern of energy management.
138 They could take advantage of the copious energy supplies to augment their physical capacity
139 for foraging and to rebuild their fat stores, during which they are expending increased
140 amounts of energy on activity and other auxiliary processes, and also on maintenance energy
141 expenditure due to their increase in body mass, digestive organs, and muscle volume.

142 The energy management patterns adopted by animals have typically been assessed
143 by looking at the phenotypic correlation between overall and maintenance metabolic rates
144 across individuals (Fyhn *et al.* 2001; Tieleman *et al.* 2008; Careau *et al.* 2013; Portugal *et al.*
145 2016), resulting in varying conclusions. Fyhn *et al.* (2001) reported that a population of

146 kittiwakes *Rissa tridactyla* exhibited no correlation between their maintenance and overall
147 metabolic rates, indicating they followed the independent pattern of energy management,
148 while Tieleman et al. (2008) found that maintenance and overall metabolic rates positively
149 correlated in the house wren *Troglodytes aedon*. Across-individual analyses are complicated
150 by the fact that metabolic rates vary as much within individuals as across individuals, as
151 indicated by only moderate repeatability (White, Schimpf & Matthews 2013). Hence, the
152 phenotypic correlation between overall and maintenance metabolic rates can be shaped by
153 processes occurring at both the across- and within-individual levels (Dingemanse &
154 Dochtermann 2013). Investigating the correlation at both these levels is therefore required
155 to fully interpret the covariation present (Careau & Wilson 2017). The across- and within-
156 individual levels of analysis explore different, though related, biological questions: at the
157 across-individuals level we are asking whether individuals that, on average, have high overall
158 energy expenditure also have, on average, higher maintenance energy expenditure. By
159 contrast, at the within-individual level we are asking whether an individual's changes in
160 overall energy expenditure are correlated with its changes in maintenance energy
161 expenditure.

162

163 *Energy management patterns as a fluctuating continuum*

164 Previous studies considering energy management patterns, including a recent review of
165 those studies by Mathot and Dingemanse (2015), and subsequent single- and multi-species
166 studies (Portugal *et al.* 2016; Careau 2017), have implicitly assumed that species or
167 individuals consistently exhibit one of the patterns discretely. However, there is no reason to
168 suppose that the energy management pattern adopted should be exactly the constraint
169 pattern or exactly the independent pattern, nor that the pattern should be consistent over
170 time. It is more likely that patterns of energy expenditure will typically indicate a blend of
171 patterns. Fig. 2 illustrates how the presence of a threshold constraint on an animal's energy
172 throughput (such as food intake) could drive the pattern of energy expenditure to be that of
173 a degree of energy constraint (slope =0) when the threshold is consistently being reached or
174 alternatively more predominantly the independent pattern (slope =1) when the threshold is
175 consistently not being reached. In turn, animals that reach this threshold sometimes but not

176 always would have an average slope value less than 1, but not 0, indicating partial constraint
177 of their energy expenditure.

178 One of the main limitations to testing whether energy management patterns differ at
179 the across- vs within-individual levels, and over time, is that repeated measures of both
180 overall and maintenance energy expenditure must be obtained in multiple individuals. A
181 viable method for obtaining such data is through the biologging of heart rate (f_H). Heart rate
182 is a robust proxy of metabolic rate, the two positively correlating in every endothermic
183 species and most ectothermic species (cf. Thorarensen, Gallagher & Farrell 1996) examined
184 to date (Green 2011), in accordance with Fick's (1870) principle of convection within the
185 cardiovascular system. Accordingly, Portugal et al. (2016) demonstrated that for multiple bird
186 species, for which metabolic rate- f_H calibrations are available, assessment of energy
187 management patterns does not change when based on metabolic rate estimates compared
188 to f_H measures. Consequently, f_H measures can be analysed to investigate the energy
189 management patterns of those animals, where daily mean f_H represents daily energy
190 expenditure and daily minimum f_H represents (daily) maintenance energy expenditure.
191 Auxiliary energy expenditure is represented by the difference between daily mean f_H and
192 daily minimum f_H .

193 We assembled a dataset that included a total of 46 539 observation-days on 292
194 individuals of 16 species of free-ranging birds and mammals, including humans, and also an
195 ectothermic fish species. Such a dataset allowed us to investigate a number of key questions
196 about energy management patterns in free-ranging vertebrates, including:

- 197 1) Do the patterns of energy management differ between species and taxonomic
198 groups?
- 199 2) Are there systematic differences in energy management patterns between the
200 across- and within-individual levels?
- 201 3) Within species, is there variation in the patterns of energy management over time
202 and can this be explained by their daily energy expenditure or ecology?

203

204 **Methods**

205 The current analysis includes heart rate (f_H) datasets from 9 bird (all water birds), 6 mammal
206 and 1 fish species performing a range of natural behaviours and locomotion modes (Table 1).
207 Some of these datasets have been reported elsewhere; for details of the devices used to
208 measure f_H and the data collection protocols refer to the citations in Table 1. For most of the
209 species included in our analyses, heart rate was obtained from electrocardiography. For
210 alpine ibex and the red deer in dataset 1, however, heart rate was determined from an
211 accelerometer located in the reticulum, which accurately recorded heart rate when the
212 instrumented animal was stationary and during relatively gentle activity (Signer *et al.* 2010).
213 During high levels of activity, heart rate was not discernible in the recorded acceleration data
214 due to signal noise. However, the accelerometer did successfully record the elevated heart
215 rates of the animals immediately after activity. Heart rate measurements for red deer dataset
216 2 were obtained from electrocardiograms and had a range (~ 35 to 85 beats min^{-1}) similar to
217 that of red deer dataset 1 (~ 35 to 75 beats min^{-1}). The dataset for roe deer also included
218 activity count data that we analyse here (see Supplementary). The datasets for human beings
219 *Homo sapiens*, grey seals *Halichoerus grypus*, and sockeye salmon *Oncorhynchus nerka* have
220 not been published previously; see Supplementary for details of the methods of data
221 collection for these species.

222

223 *Calculating variables for analysis*

224 Daily mean f_H was calculated for each 24-h period for each individual of every species.
225 Minimum daily f_H was determined by calculating mean f_H for consecutive short time intervals
226 (2 to 15 min, depending on the study) throughout the 24-h day and selecting the lowest of
227 these values for each day (Portugal *et al.* 2016).

228

229 *Statistical analyses*

230 We assessed the use of alternative energy management patterns by the study species (along
231 the continua between the full constrained and full independent patterns, and the
232 performance patterns) at both the across- and within-individual levels. This was achieved
233 through visual assessment of the slope and 95% confidence intervals of regression between
234 daily mean f_H against minimum daily f_H . These regressions were generated from a single
235 mixed model for each species, including individual identity as a random effect to account for

236 the repeated values representing each individual. Daily mean f_H is very likely to show
237 temporal autocorrelation (Portugal *et al.* 2016), which we accounted for using `lme()` in R
238 (`nlme` package) to fit models that included autocorrelation structure in the residuals.

239 In situations where the within-individual relationship differs from the across-individual
240 relationship, these relationships can be confounded in a standard mixed model (Van de Pol &
241 Wright 2009). We used the within-subject centring approach (Van de Pol & Wright 2009;
242 Dingemanse *et al.* 2010) to distinguish between alternative energy management patterns at
243 the across- and within-individual levels. This involves fitting minimum daily f_H both as
244 individual means (\underline{x}_i) and deviations from individual means ($x_{ij} - \underline{x}_j$), where x_{ij} is a daily
245 observation of minimum f_H i from subject j . In simple terms, the across-individuals slope (β_A)
246 can be obtained by attributing all observations of minimum daily f_H in a given individual the
247 same average value (\underline{x}_i), whereas the within-individual slope (β_W) can be obtained by
248 subtracting the subject's mean value (\underline{x}_i) from each observation value (x_{ij}). Specifically, we
249 analysed i daily observations of average f_H on subject j (y_{ij}) as:

$$250 \quad y_{ij} = (\beta_0 + u_{0j}) + \beta_A \underline{x}_j + (\beta_w + u_{Wj})(x_{ij} - \underline{x}_j) + e_{0ij}$$

251 where;

- 252 • y_{ij} is the response variable (daily mean f_H)
- 253 • β_0 is the fixed effect of the intercept;
- 254 • u_{0j} is a random intercept associated with individual identity;
- 255 • β_A is the across-individual slope fixed effect (β_A) associated with individual means (\underline{x}_i);
- 256 • β_w is the within-individual slope fixed effect (β_w) associated with deviations from
257 individual means ($x_{ij} - \underline{x}_j$);
- 258 • u_{Wj} is the random slope allowing for individual variation in the within-individual slope;
- 259 • and e_{0ij} is a residual error term modelled with an autoregressive function of order 1
260 with day of the year (time covariate) fitted within individual identity (grouping factor).

261 Although we were not specifically interested in u_{Wj} (the individual variance in the slope of
262 the within-individual relationship between mean and minimum daily f_H), allowing individuals
263 to differ in their within-individual slopes is important for properly estimating uncertainty
264 around the population-level within-individual slope (β_w) (Schielzeth & Forstmeier 2008). We
265 did not fit a covariance between u_{0j} and u_{Wj} because the models would not converge in some

266 species where either the random intercepts or slope variance components were close to
267 zero. The energy management patterns were assessed by plotting the slope of the regression
268 line between daily mean f_H and minimum daily f_H , and its 95% confidence interval (CI), on a
269 horizontal, graded box plot (Careau 2017). The fully constrained pattern is represented by
270 slope=0, the fully independent pattern by slope=1 and the performance pattern by slope>1
271 (Ricklefs, Kornazewski & Daan 1996; Mathot & Dingemanse 2015; Careau 2017). A slope
272 value between 0 and 1 would suggest a degree of both the constrained and independent
273 patterns, i.e. partial compensation of high maintenance or high auxiliary energy expenditure.

274 To investigate variation in energy management pattern through the annual cycle and how
275 this relates to daily energy expenditure, we explored changes in the across- and within-
276 individual slopes for each month separately, for red deer dataset 1, alpine ibex, and greylag
277 geese. Each of these datasets included a majority of individuals (14 individuals) with >300 d
278 of heart rate data. Linear regressions formally tested whether variation in the monthly
279 within-individual slopes related to monthly means of daily mean f_H .

280 While there is of course some degree of inaccuracy in estimating metabolic rate from
281 heart rate (Green 2011), we assume this noise is overwhelmed by the signal of heart rate
282 changes at the scale we are observing in our analyses.

283

284 Results

285 In all species except roe deer, there is strong and statistically significant temporal
286 autocorrelation in the residuals at the within-individual level (Supplementary fig.3;
287 Supplementary Table 1). All of the across- and within-individual slope values presented below
288 were extracted from mixed models that accounted for temporal autocorrelation, individual
289 variation in daily mean f_H (random intercepts), and individual variation in the slope of the
290 relationship between mean and minimum daily f_H (random slopes).

291 The estimated across-individuals slopes are supportive of the pattern of
292 predominantly energy independence (slope =1) and energy performance (slope >1) (fig. 3A
293 and Supplementary Table 2A). The species most clearly following a pattern of energy
294 performance rather than independence are barnacle geese, European shags, macaroni
295 penguins, eider ducks, and sockeye salmon. While there are differences in the degree of

296 energy performance between species, visual inspection of fig. 3A suggests no differences in
297 pattern between birds in general and mammals in general, or the fish species. By contrast,
298 the within-individual slopes are usually most supportive of an element of energy constraint
299 (Supplementary Table 2B; fig. 3B), with the slope being <1 in 12 out of 16 species, and the
300 95% CI overlapping with slope =1 in only 5 species. Again, there are no apparent differences
301 in the degrees of energy constraint between taxa. Some relationships are similar at the
302 across- and within-individual levels, in particular the Przewalski horse (fig. 4A), and to some
303 degree human beings (fig. 4B). For many of the other species, however, the across- and
304 within-individual slopes are clearly different. For example, eider ducks and sockeye salmon
305 have across-individual slopes that are clearly >1 (indicating a degree of performance pattern)
306 but the within-individual slopes are clearly <1 (energy constraint; fig. 4C-D). In general, there
307 is a decrease in the slope value from the across-individual analysis to the within-individual
308 analysis, summarised by the weighted averages (fig. 3A and B; Supplementary Table 2).

309 Finally, in those species for which year-round data are available for sufficient
310 individuals (red deer, alpine ibex and greylag geese), there is marked variation in the across-
311 and within-individual slopes. This is most notable at the within-individual level for all three
312 species (fig. 5). Linear regression analyses of mean monthly values of daily mean heart rate
313 against monthly within-individual slope values returned statistically significant, negative
314 relationships for all three species (red deer: $r^2=0.53$, $P=0.007$; alpine ibex: $r^2=0.72$, $P=0.000$;
315 greylag geese: $r^2=0.49$, $P=0.011$; fig. 5) indicating that animals were more likely to be under
316 energetic constraint during months where their daily energy expenditure was higher.

317

318 Discussion

319 For most of the 16 species analysed, there is little or no evidence of any constraint on energy
320 expenditure (a slope value <1) across individuals (fig. 3A). The pattern of energy expenditure
321 is either indicative of predominantly the independent pattern of energy management or to
322 some degree the performance pattern of energy management. Moreover, the pattern does
323 not associate with taxonomic group. For those species exhibiting the independent pattern,
324 for example Przewalski horses and humans (fig. 4 A&B), individuals that exhibit a greater
325 maintenance energy expenditure compared to other individuals also show the same increase

326 in daily energy expenditure. For those species exhibiting the performance pattern, for
327 example eider ducks and sockeye salmon (fig. 4 C&D), individuals that expend relatively high
328 amounts of energy daily are doing so due to both a high maintenance energy expenditure
329 and a high auxiliary energy expenditure. By contrast, the within-individual slope value is lower
330 than the across-individual value in nearly all species, and is typically <1 but >0 (fig. 3B). In
331 general, individual animals across a broad range of species exhibit partial constraint of their
332 energy expenditure, whereby daily increases in auxiliary processes are partially compensated
333 for by decreases in maintenance processes and vice-versa. Together, these findings echo the
334 Y-model in life-history theory proposed by van Noordwijk & de Jong (1986), in that in species
335 universally, some individuals have a greater capacity to supply energy to all aspects of their
336 life than do others – they are able to intake, digest and deploy a greater amount of energy
337 than conspecifics. But, nonetheless, for every individual, rate of energy throughput is finite
338 and thus all individuals trade-off deployment of their available energy between competing
339 functions. These findings support the idea that energy management analyses focussed solely
340 at the phenotypic level may miss potentially interesting processes occurring at the among-
341 and within-individual levels (Careau & Garland Jr 2015; Careau & Wilson 2017). Finally, our
342 analyses also demonstrate that the energy management pattern an animal exhibits is not
343 fixed. This variability documents an important aspect of animal plasticity while also providing
344 an opportunity to explore what contexts may influence the pattern employed.

345

346 *Fluctuating energy management patterns*

347 The slope values presented in figs. 4 and 5 are averages over the time of the f_H recordings
348 (Supplementary Table 2), and as such may mask temporal variation in the energy
349 management pattern employed (the fallacy of the average; Denny 2017). A slope value close
350 to 1, indicating predominantly the independent pattern, might in fact reflect that part of the
351 time the performance pattern is being exhibited and the rest of the time some degree of the
352 energy constraint pattern. Animals may exhibit the performance pattern specifically during
353 periods when food availability is high and high energy throughput is advantageous, such as
354 king penguins foraging after a fast and increasing both their muscle and lipid stores
355 (Gauthier-Clerc *et al.* 2002). By contrast, under conditions of food scarcity an increase in
356 activity levels or other auxiliary processes by an individual is more likely to elicit a responsive
357 decrease in maintenance energy expenditure – an element of constrained energy

358 management. The salmon in the current study, which exhibited relatively strong energy
359 constraint within individuals (fig. 3B), were experiencing these energy-stressed conditions
360 during the experiments – they were measured during their reproductive periods and
361 experienced little to no nutritional intake and high levels of locomotor activity. Animals
362 exhibiting independent energy management at a given time might be expected to increase
363 their energy expenditure until they reach a constraint on their energy throughput to
364 maximise their energy use (and hence exhibit a degree of energy constraint); alternatively
365 they might in fact be near the threshold and maintaining flexibility in their energy allocation.

366 These possibilities can be explored most thoroughly by investigating variations in
367 animals' energy management over the annual cycle, where threshold constraints, whether
368 related to food availability or other factors, may fluctuate predictably due to seasonal effects
369 on the environment or the animal's ecology. The proposed analysis was possible for red deer,
370 alpine ibex and greylag geese (fig. 5). Over the yearly cycle, we might expect variation in
371 foraging effort for alpine ibex, with typically less food available in the winter months. By
372 contrast, the red deer (dataset 1) were kept inside an enclosure and periodically given
373 supplemental food in addition to the natural forage available (Turbill *et al.* 2011), and the
374 greylag geese received supplementary food consistently (Wascher, Kotrschal & Arnold 2018).
375 Nonetheless, the red deer exhibited variation through the year in their energy management
376 (fig. 5). At the across-individual level, while overall they exhibited energy independence,
377 through late spring into early summer they exhibited some degree of the performance
378 pattern. At this time of year the females (all the individuals in the study population were
379 female) are finishing gestation and birthing their young. Both daily mean f_H and body mass
380 increase during this period to their yearly peaks; the deer are expending a lot of energy while
381 increasing in size (Clutton-Brock, Guinness & Albon 1982; Turbill *et al.* 2011). The
382 performance pattern exhibited by the deer indicates that at this time some individuals
383 started expending more energy than other individuals both in terms of maintenance
384 processes and auxiliary processes; they were able to achieve a greater energy throughput,
385 supported by supplemental feeding. At the within-individual level, while overall the red deer
386 exhibited a degree of energy constraint, this was strongest around the aforementioned
387 birthing period starting in late spring. Probably, the large energy costs of growth at this time,
388 both of the mother and calf (including pronounced growth of the alimentary organs in the

389 adults; Arnold *et al.* 2015), were supported through a reduction in other energy costs
390 (though not activity; W. Arnould unpublished data).

391 In contrast to the red deer, the alpine ibex exhibit the greatest degree of energy
392 constraint, i.e. the lowest slope values, during the summer months, both across and within
393 individuals (fig. 5). Thus, despite food being relatively abundant at this time of the year, when
394 the ibex expend large amounts of energy on auxiliary processes such as activity their
395 maintenance energy expenditure is low, and vice-versa. Ibex appear to be constrained by
396 their ability to dissipate heat; on hot summer days they move to higher altitudes and reduce
397 their foraging activity, possibly indicating that the heat increment of feeding exacerbates
398 their reduction in auxiliary energy expenditure (Aublet *et al.* 2009).

399 The greylag geese exhibit little clear variability over the yearly cycle in their energy
400 management pattern at the across-individual level, due to large confidence intervals around
401 the slope values. At the within-individual level they exhibit a tendency towards some
402 constraint of their energy expenditure during the summer months, as opposed to
403 uncorrelated auxiliary and maintenance energy expenditure (energy independence) during
404 the rest of the year (fig. 5). Energy expenditure was highest in the geese during the summer;
405 in May for females (coinciding with egg incubation and increased body temperature), and in
406 August for males (coinciding with an increase in agonistic interactions in the newly-formed
407 flock) (Wascher, Kotrschal & Arnold 2018). It appears then that, during the summer months,
408 when energy expenditure is highest, the geese constrain their daily energy expenditure by
409 trading off auxiliary and maintenance energy costs. In January, the start of the courtship
410 season, there is a tendency towards the energy performance pattern within individuals - an
411 increase in both auxiliary and maintenance costs. This pattern may be optimal at this time of
412 the breeding cycle, since it is when males in particular are aggressive, and they attempt to
413 secure a nest site and food access for their females in order to maximise reproductive
414 opportunities. The supplemental feeding they receive surely supports this pattern and may
415 exacerbate it.

416 Studies have usually found that animals obliged to work harder in order to gain a unit
417 of food nonetheless exhibit a limited increase in daily energy expenditure, i.e. they exhibit a
418 degree of energy constraint (Elliott *et al.* 2014; Pontzer 2015). However, data for starlings
419 (Wiersma, Salomons & Verhulst 2005) indicates that maintenance energy expenditure
420 remains constant across experimental conditions resulting in a positive relationship between

421 daily energy expenditure and activity levels. In all of the studies reviewed by Pontzer (2015)
422 that clearly show the maintenance energy expenditure of the subject animals decreasing in
423 response to increases in activity levels, the animals' daily food intake was also decreasing
424 (Perrigo & Bronson 1983; Tiebout 1991; Bautista *et al.* 1998; Vaanholt *et al.* 2007). By
425 contrast, the aforementioned study on starlings is the only one reporting food intake to
426 increase with increasing activity levels (Wiersma, Salomons & Verhulst 2005). This
427 observation supports the idea that food availability could influence the energy management
428 pattern that animals exhibit.

429 Without controlled experiments, of course we cannot be sure what factors are driving
430 changes in the energy management pattern exhibited by this study's red deer, alpine ibex
431 and greylag geese. However, the fact that they all show stronger constrained energy
432 management during months when their energy expenditure is higher (fig. 5C, F and I) is
433 compelling and supports our suggestion that the energy expenditure of animals is
434 constrained as they approach a threshold (fig. 2). Such a threshold could be due to a limit on
435 an animal's ability to assimilate energy, or to expend it (fig. 1), or the result of optimising
436 energy throughput in the long term (Daan, Deerenberg & Dijkstra 1996). Furthermore, those
437 periods of high energy expenditure are associated with clear and costly biological processes,
438 suggesting that key aspects of an animal's ecology and life-cycle drive plasticity in energy
439 management.

440

441 *Conclusions and future work*

442 Understanding what drives constraint in individual animals is the natural next
443 research step. The month-by-month data presented in this study offers some evidence that
444 periods of high energy expenditure are related to increased energy constraint, and that
445 ecological factors can be important influences on energy constraint, and influence the degree
446 of constraint exhibited over time. Variation in levels of constraint between individuals might
447 be explained by sex, age, status in a hierarchy or personality type. However, while the seven
448 Przewalski horses analysed exhibit very similar slopes (fig. 4A), they represent animals of both
449 sexes and a variety of ages. Alternatively, the degree of variation between individuals may be
450 driven predominantly by the degree of similarity in their behaviours and lifestyles (Biro *et al.*
451 2018). For example, it could be that individual Przewalski horses are more similar to each

452 other behaviourally than are, for instance, eider ducks (fig. 4C), possibly exacerbated by the
453 fact that the horses were maintained in a large but confined area (Kuntz *et al.* 2006).

454 Comprehensive information on the environment (food availability, temperature,
455 predation pressure), the physiology (age, body condition) and life-stage of free-living animals
456 (moulting, reproducing, lactating, preparing for migration) will be necessary to better
457 understand the variation in energy patterns they exhibit, and to design meaningful
458 experiments to elucidate the underlying mechanisms.

459

460

461 **Authors' contributions**

462 Concept development: LGH, VC and JAG. Data collation: LGH helped by VC. Analysis and
463 interpretation: VC, LGH. Unpublished data: SDT, TSP and SJC, KM and LGH. Manuscript
464 writing: LGH and VC led on writing the manuscript, with support on later drafts especially
465 from JAG and SDT, and input from all authors; all authors gave final approval. No funding was
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467

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470

471 **Data accessibility**

472 Data deposited in the Dryad Digital Repository: [http:// doi:10.5061/dryad.cj4733b](http://doi:10.5061/dryad.cj4733b), (Halsey *et*
473 *al.* 2019).

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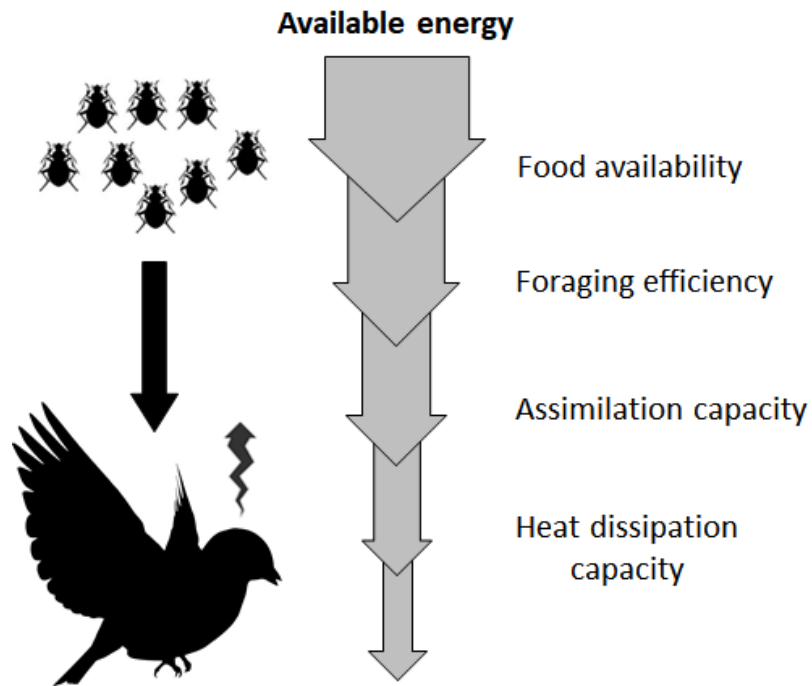
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650

651 **Table 1.** Heart rate datasets included in this study, collected on free-ranging vertebrates, including 15 endotherms species (9 birds, 6 mammals)
 652 and one ectotherm species (salmon). Shown are the number of individuals (N_{ID}), the range of total daily observations per individual (range n_{OBS}),
 653 the average number of daily observations per individual ($n_{OBS/ID}$), the principal mode(s) of locomotion, and the ecological context of the period of
 654 data collection.

Species	N_{ID}	Range		Main locomotion mode(s)	Key ecological factors	Reference
		n_{OBS}	$n_{OBS/ID}$			
Barnacle geese	6	272-361	331.8	Walking, swimming, flying	Year-round	Portugal et al submitted
Greylag geese	22	44-527	315.6	Walking, flying	Year-round*	Wascher et al 2018
Great cormorants	7	46-122	99.6	Diving, flying	Over-wintering	Grémillet et al 2005
European shags	8	5-35	16.5	Diving, flying	Breeding, foraging	Hicks et al 2017
Australasian gannets	6	28-237	154.3	Flying	Breeding, foraging	Green et al 2013
Little penguins	5	9-200	135.2	Swimming, diving	Non-breeding season	Portugal et al 2016
King penguins	6	6-30	23.8	Swimming, diving	Foraging, breeding	Halsey et al 2010
Macaroni penguins	63	18-450	204.1	Swimming, diving	Year-round	Green et al 2005
Eider ducks	13	131-219	203.4	Swimming, diving, flying	Moulting	Guillemette et al 2007
Przewalski horses	7	37-264	149.9	Walking	Large enclosure	Arnold et al 2006
Alpine ibex	20	6-647	347.9	Walking	Year-round*	Signer et al 2011
Red deer (dataset 1)	15	278-549	441.1	Walking	Year-round, large enclosure*	Turbill et al 2011
Red deer (dataset 2)	9	11-607	203.6	Walking	Year-round, large enclosure	Arnold et al 2004
Roe deer	15	8-372	152.7	Walking	Year-round, large enclosure	Reimoser 2012
Human beings	7	12-20	14.4	Walking	Daily modern life	This study: KJM and LGH
Grey seals	29	6-20	10.4	Body undulation	On land, resting, nursing	This study: SDT
Sockeye salmon	54	1-17	7.0	Swimming	Competitive terminal reproduction	This study: TSP and SJC

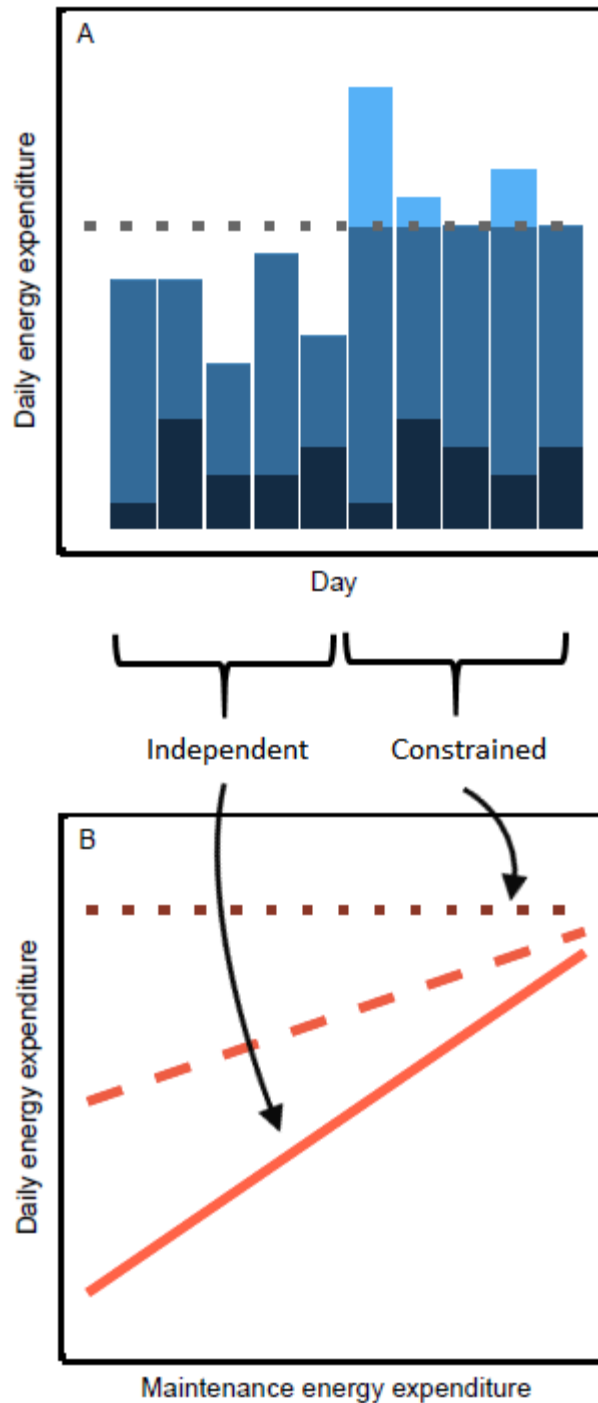
655 *These datasets contain yearlong data for sufficient individuals in order for month-by-month analyses over the annual cycle to be conducted
 656 robustly (see main text for further details).



657

658 **Figure 1.** Animals have a maximum possible throughput of energy, because they inevitably
 659 experience energy constraints. These can arise from a number of exogenous or endogenous
 660 factors: limited food availability in the environment; limited capacity to harvest available
 661 food; limited capacity to assimilate the food harvested; limited capacity to release heat
 662 generated by the expenditure of energy. Thus the theoretically available energy to an animal
 663 (widest grey arrow, top) is in reality a much smaller energy availability once all potential
 664 constraints are factored in (thinnest grey arrow, bottom).

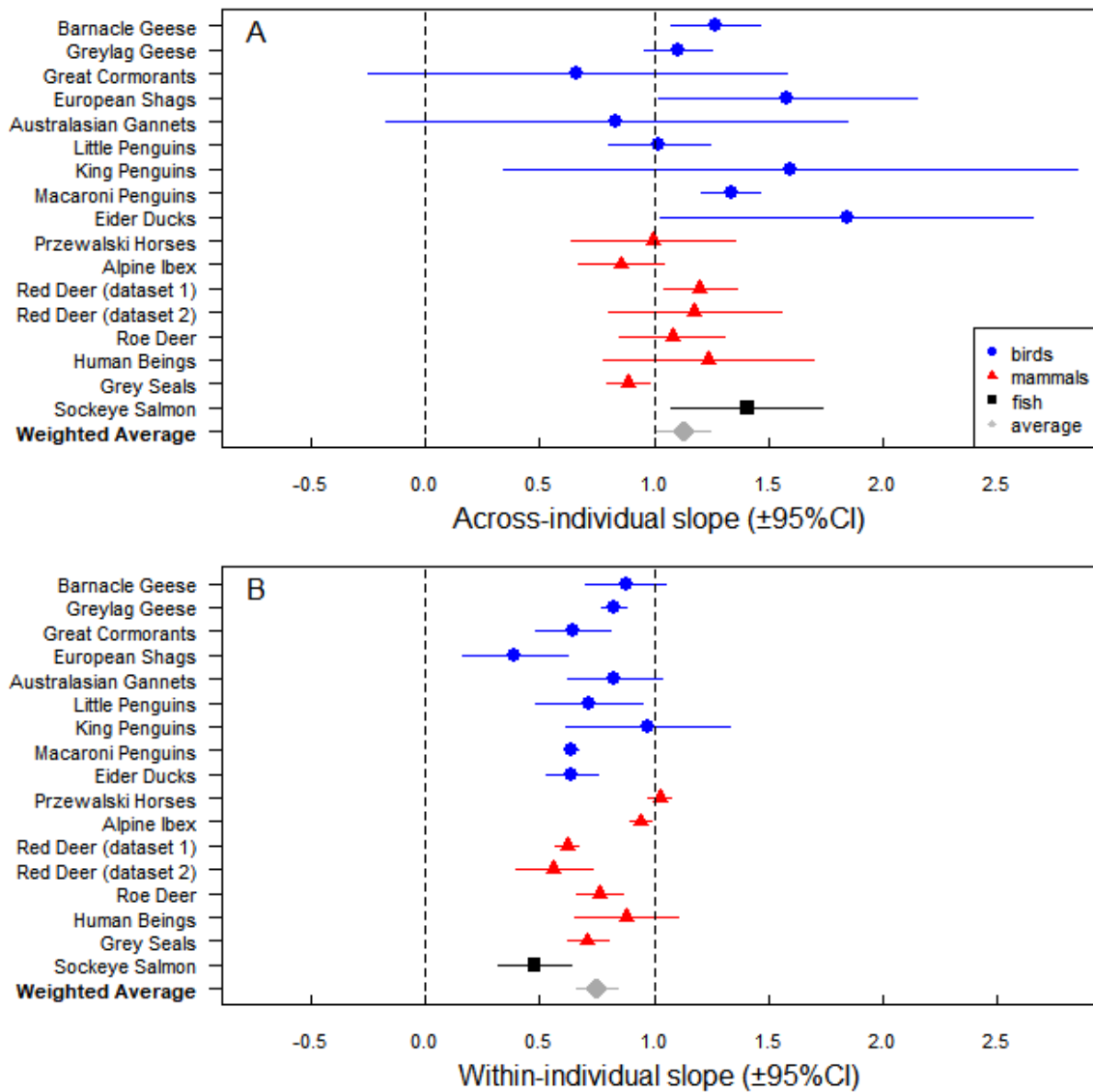
665



666

667 **Figure 2.** Illustration of a hypothesis to explain intra-individual variation in patterns in energy
 668 expenditure. During periods when daily energy expenditure is below a threshold (panel A, the
 669 first five days), the energy expended on maintenance processes (darkest blue) is
 670 unconstrained by the energy expended on auxiliary processes such as activity (medium blue).
 671 In a regression of daily energy expenditure against maintenance energy expenditure (panel
 672 B), this manifests as a slope value of 1 (light, full red line). By contrast, during periods when
 673 auxiliary energy expenditure is high and daily energy expenditure is reaching the threshold

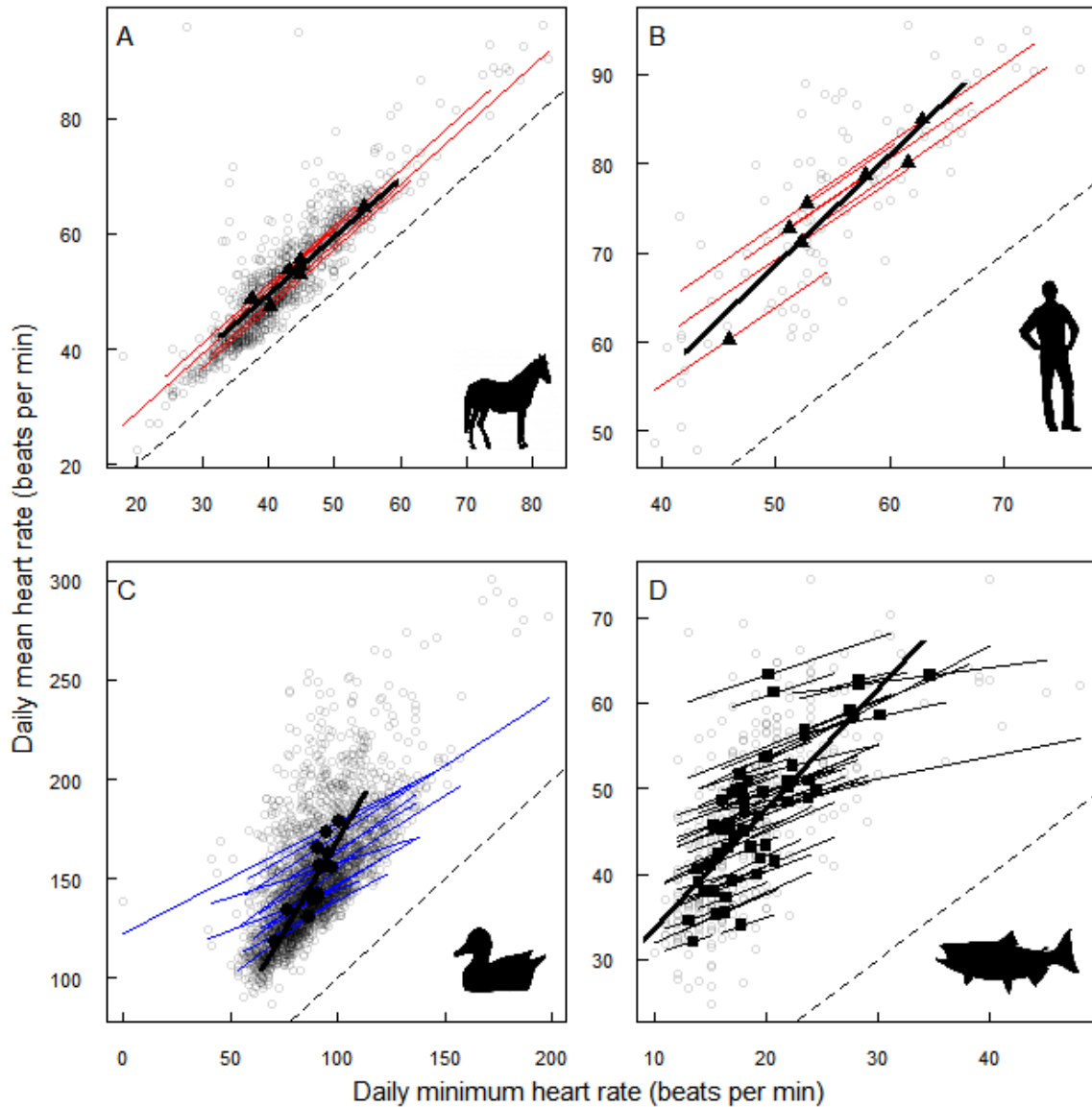
674 (panel A, the second five days), daily energy expenditure is constrained by a reduction in
675 auxiliary energy expenditure (the light blue bars indicate what auxiliary and daily energy
676 expenditure would be without constraint), which manifests as a slope value of zero (dark,
677 dotted red line). Consequently, the slope of the relationship between daily energy
678 expenditure and maintenance energy for the entire 10 d lies between the slope values of the
679 relationships for the first and last five days (medium, dashed red line), and thus has a slope
680 value $0 < 1$, indicating partial energy constraint.



682

683 **Figure 3.** Slope ($\pm 95\%$ confidence intervals; CI) of the relationship between daily mean heart
 684 rate (f_H , a proxy of daily energy expenditure) and daily minimum f_H (a proxy of daily
 685 maintenance energy expenditure) estimated at the A) across- and B) within-individual levels
 686 in 9, 6, and 1 species of free-ranging birds (blue dots), mammals (red triangles), and fish
 687 (green squares). The slope and 95% CI can be used to identify the energy management
 688 pattern adopted in each species. While complete energetic constraint is represented by a
 689 slope of 0, complete energetic independence is predicted by a slope of 1 because of the
 690 whole-part correlation (i.e., daily minimum f_H is included within daily mean f_H). By contrast,

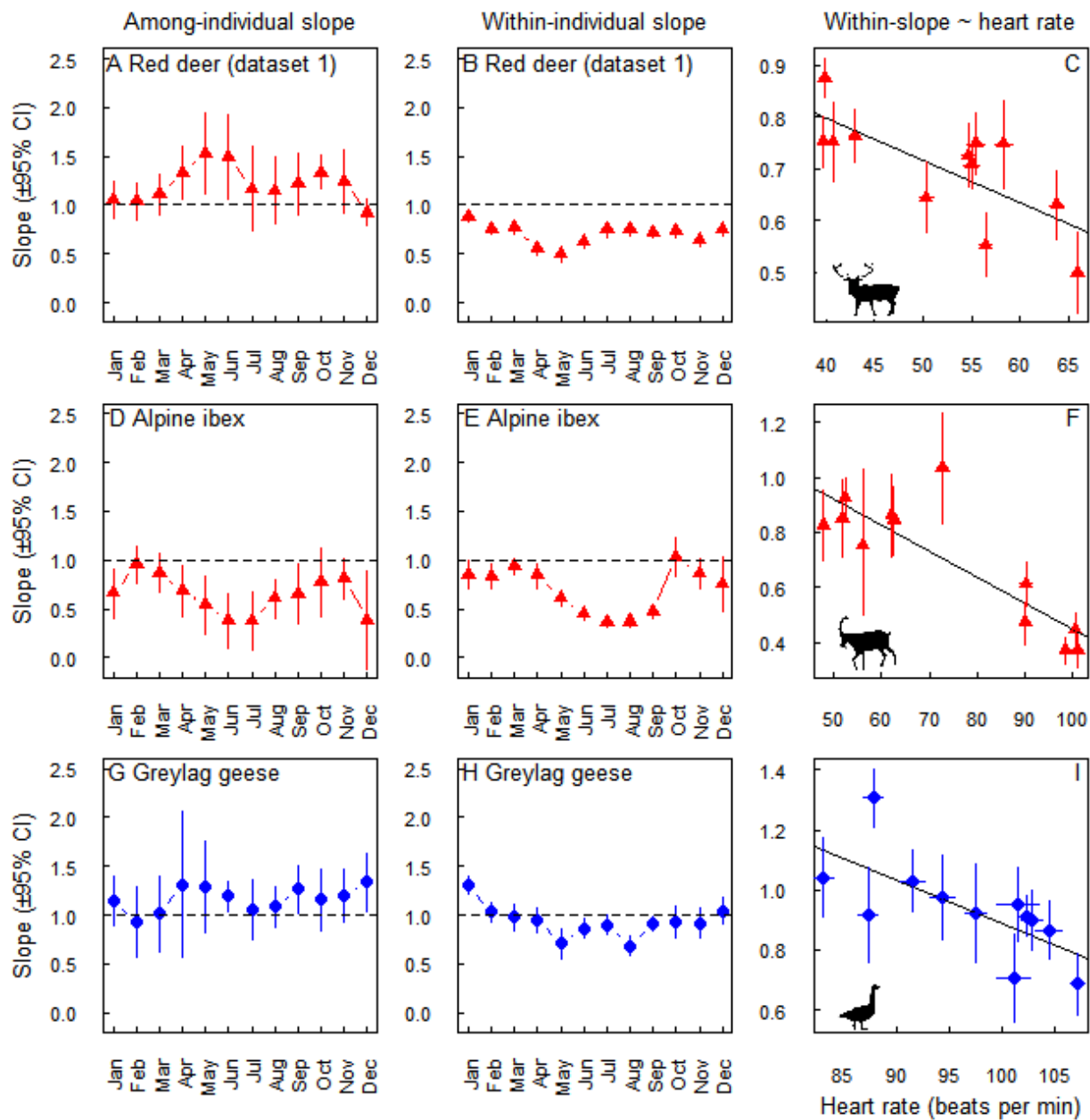
691 the performance energy pattern is represented by a slope >1 because maintenance energy
692 expenditure increases with auxiliary energy expenditure.



694

695

696 **Figure 4.** Relationship between daily mean heart rate (f_H) (a proxy of daily energy
 697 expenditure) and minimum daily f_H (a proxy of daily maintenance energy expenditure) in
 698 representative species where both the across- and within-individual slopes are close to 1 (A
 699 and B), and the across- and within-individual slopes are clearly >1 and <1 (C and D,
 700 respectively). In all panels, filled data points represent individual means and unfilled grey
 701 circles represent all observations (one data point per individual per day). The across-
 702 individual slope is represented by the thick black line and the within-individual slopes are
 703 shown by the thinner, coloured lines. The dashed line represents the line of unity.



705 **Figure 5.** Across- and within-individual best-fit slope values for the regression of daily mean heart rate (f_H) against mean minimum f_H in A-B) red
706 deer dataset 1, D-E) alpine ibex, and G-H) greylag geese, plotted month-by-month. Vertical lines represent the 95% confidence interval (CI).
707 Within-individual slope values linearly regressed against mean monthly daily mean heart for these three species are also presented (C, F and I).
708

709

710 SUPPLEMENTARY

711 *Methods for data collection of new datasets*

712 The dataset on human beings *Homo sapiens* was collected in 2016 and 2017 by K.J.M. and
713 L.G.H. Seven participants wore a Bioharness (v.3; Zephyr Technology) for around a fortnight.
714 This device measured their f_H at 1 Hz continuously. Occasional periods where f_H was clearly
715 spuriously low (presumably due to a temporary loss of contact between the electrodes and
716 the skin) were replaced with daily mean values using an automated procedure in Microsoft
717 Excel. Ethical approval was provided by the Department of Life Sciences at the University of
718 Roehampton.

719 The dataset on lactating (and fasting) adult female grey seals *Halichoerus grypus* was
720 obtained by S.D.T. during the 2015, 2016, and 2017 breeding seasons at the Isle of May
721 (56.1856° N, 2.5575° W), using modified Firstbeat(TM) f_H belts ([https://international-
722 shop.firstbeat.com/product/team-pack/](https://international-shop.firstbeat.com/product/team-pack/)). The transmitter portion of the belt was mounted
723 dorsally between the scapulae, and the belt was replaced with protected cables leading to
724 silver chloride electrodes located immediately posterior of the fore flippers. Inter-beat
725 interval data (in milliseconds) were transmitted to a Firstbeat(TM) Team receiver located
726 between 50 and 100 m away from instrumented seals. Raw data were corrected for artefacts
727 (von Borell *et al.* 2007; Brannan 2017) using Firstbeat(TM) Sports software (v.4.5.0.2) and
728 RHRV (Martínez *et al.* 2017). Heart rate was summarised over discrete 15-minute periods,
729 and traces with >50% of flats and stairs (calculated using bespoke R scripts) were excluded
730 from analyses (Brannan 2017, unpublished data). Heart rate data were collected during
731 daylight hours only. Before further analysis, the dataset was restricted to days with five or
732 more measurement periods and then those animals for which there were data on six or more
733 such days. These procedures conformed to the UK Animals (Scientific Procedures) Act, 1986
734 and were performed in collaboration with the Sea Mammal Research Unit (University of St.
735 Andrews), operating under UK Home Office project licence #60/4009. All research was
736 approved ethically by the Durham University Animal Welfare Ethical Review Board as well as
737 by the University of St. Andrews Animal Welfare and Ethics Committee.

738 During the summer of 2016, data were collected on mature sockeye salmon *Oncorhynchus*
739 *nerka* by T.S.P. and S.J.C. They were dip-netted from the mouth of the Gates Spawning
740 Channel in British Columbia (50.5481°N, 122.4832°W). Fish were electro-sedated using fish
741 handling gloves (Smith-Root, Inc., Washington, USA, <http://www.smith-root.com>; 10-25mA).
742 They were then instrumented with heart rate and temperature biologgers (DST milli HRT,
743 13mm x 39.5mm, Star-Oddi, Iceland; <http://www.star-oddi.com/>) programmed to record
744 heart rate at 100 Hz, and raw electrocardiogram (ECG) every 1.5 hours. Instrumentation
745 involved surgical implantation next to the pericardial membrane via a 3 to 5 cm incision
746 (surgical methods described in (Prystay *et al.* 2017)). The fish were then released into the
747 spawning channel. Sockeye salmon die after spawning, therefore corpses were collected
748 after natural death, at which point the heart rate biologgers were retrieved. This research
749 was conducted in accordance with the Canadian Council on Animal Care Guidelines for Use of
750 Fishes in Research under protocol 102935 issued by Carleton University.

751

752

753 **Supplementary Table 1.** Variance components extracted from univariate mixed models of daily mean heart rate (a proxy of daily energy
 754 expenditure) in 16 endotherm species, including variance attributed to random intercepts ($V_{\text{intercept}}$), random slopes (V_{slope}), and residual variance
 755 (V_{residual}). Significance of random intercepts and slopes was tested using a log-likelihood ratio test of a full model vs. a reduced model that excluded
 756 the variance component of interest. Also shown are total raw variance (V_{total}), and autocorrelation structure of order 1, fitted Julian day as a
 757 continuous time covariate.

Species	Variance components									Autocorrelation		
	Random intercepts			Random slopes			V_{residual}	V_{total}	estimate	χ^2	P	
	$V_{\text{intercept}}$	χ^2	P	V_{slope}	χ^2	P						
Barnacle geese	4.45	1.17	0.28	0.04	49.76	<0.001	439.44	1885.72	0.65	700.12	<0.001	
Greylag geese	6.41	198.06	<0.001	0.02	122.39	<0.001	43.17	243.80	0.52	1911.06	<0.001	
Great cormorants	18.65	16.54	<0.001	0.03	1.73	0.19	114.41	160.70	0.70	179.58	<0.001	
European shags	15.99	0.28	0.60	<0.001	<0.001	1.00	231.43	576.98	0.51	10.70	0.001	
Australasian gannets	81.49	55.37	<0.001	0.06	25.91	<0.001	483.87	948.38	0.08	6.17	0.01	
Little penguins	0.00	0.00	1.00	0.06	15.85	<0.001	290.87	1229.27	0.71	245.09	<0.001	
King penguins	156.00	3.51	0.06	0.11	6.79	0.01	132.90	732.93	0.74	85.61	<0.001	
Macaroni penguins	88.28	210.21	<0.001	0.01	198.21	<0.001	310.75	1706.17	0.69	5076.61	<0.001	
Eider ducks	90.18	31.02	<0.001	0.03	23.44	<0.001	350.18	833.81	0.80	2177.42	<0.001	
Przewalski horses	2.60	25.23	<0.001	<0.001	0.001	0.98	18.54	100.99	0.41	106.20	<0.001	
Alpine ibex	14.18	176.02	<0.001	0.01	115.80	<0.001	61.69	504.14	0.46	1187.43	<0.001	
Red deer (dataset 1)	<0.001	<0.001	0.98	0.01	177.74	<0.001	27.85	147.33	0.92	1560.95	<0.001	
Red deer (dataset 2)	<0.001	<0.001	1.00	0.05	160.20	<0.001	81.46	208.05	0.95	1732.36	<0.001	
Roe deer	11.37	37.63	<0.001	0.03	77.88	<0.001	33.13	221.20	0.63	925.98	<0.001	
Human beings	4.05	1.47	0.23	<0.001	0.00	1.00	37.64	117.13	0.15	1.58	0.21	
Grey seals	4.05	7.61	0.01	0.03	13.86	<0.001	19.73	162.98	0.23	5.52	0.02	
Sockeye salmon	<0.001	<0.001	1.00	0.06	2.43	0.12	53.61	95.92	0.71	94.78	<0.001	

758

759 **Supplementary Table 2.** Relationships between daily mean heart rate (f_H ; a proxy of daily
760 energy expenditure) and daily minimum f_H (a proxy of daily maintenance energy expenditure)
761 estimated at the A) across- and B) within-individual levels in 16 free-ranging endotherms
762 species (9 bird, 6 mammal and a fish species). r^2 GLMM(m) means marginal r^2 estimated for
763 general linear mixed models.

Species	A) Among-individual slope			B) Within-individual slope			r^2 GLMM(m)
	estimate	95%CI		estimate	95%CI		
		lower	upper		lower	upper	
Barnacle geese	1.27	1.08	1.46	0.88	0.70	1.05	0.71
Greylag geese	1.11	0.96	1.26	0.83	0.77	0.88	0.76
Great cormorants	0.66	-0.25	1.58	0.64	0.48	0.81	0.24
European shags	1.58	1.02	2.15	0.39	0.16	0.62	0.61
Australasian gannets	0.84	-0.17	1.84	0.83	0.62	1.04	0.40
Little penguins	1.02	0.80	1.25	0.72	0.48	0.95	0.71
King penguins	1.60	0.34	2.85	0.98	0.62	1.34	0.61
Macaroni penguins	1.34	1.21	1.46	0.64	0.61	0.67	0.72
Eider ducks	1.84	1.03	2.66	0.64	0.53	0.75	0.40
Przewalski horses	1.00	0.64	1.35	1.03	0.98	1.08	0.77
Alpine ibex	0.86	0.67	1.05	0.94	0.89	0.99	0.83
Red deer (dataset 1)	1.20	1.04	1.36	0.62	0.57	0.67	0.69
Red deer (dataset 2)	1.18	0.80	1.56	0.56	0.39	0.73	0.45
Roe deer	1.08	0.85	1.31	0.76	0.66	0.87	0.74
Human beings	1.24	0.78	1.70	0.88	0.65	1.11	0.64
Grey seals	0.89	0.79	0.98	0.71	0.62	0.80	0.83
Sockeye salmon	1.41	1.08	1.74	0.48	0.32	0.64	0.39
Weighted average	1.13	1.01	1.25	0.75	0.66	0.84	0.62

764

765 Coefficient of determination (r^2) values were calculated for each model using
766 `sem.model.fits()` in the `piecewiseSEM` package (Nakagawa & Schielzeth 2013). We checked
767 the validation of the models by visually assessing plots of the residuals against the fitted
768 values, and against minimum f_H (Zuur, Hilbe & Ieno 2013).

769

770 *Investigating auxiliary energy expenditure*

771 The constrained pattern of energy expenditure is associated with lower maintenance energy
772 expenditure during periods when ‘energetically costly behaviours’ are higher, or vice-versa
773 (Mathot & Dingemanse 2015). For roe deer the slope of the relationship between daily mean
774 heart rate (f_H ; a proxy for daily energy expenditure) and daily minimum f_H (a proxy for daily

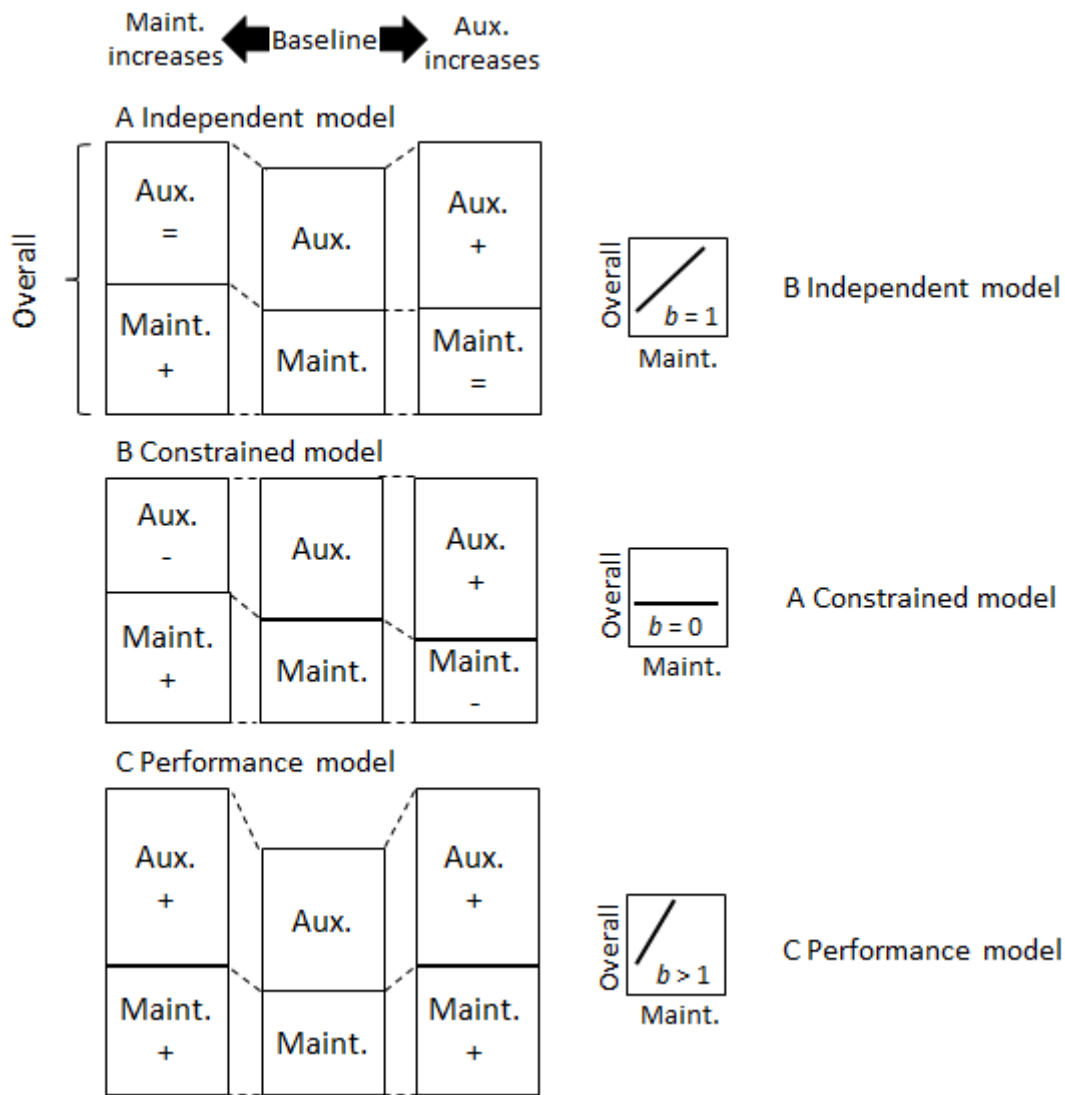
775 maintenance energy expenditure) within individuals is substantially less than 1 (fig. 2B),
776 which is assumed to indicate that during periods when energetically costly behaviours are
777 performed, maintenance energy expenditure attenuates, or vice-versa. This relationship can
778 be illustrated by a scatterplot of the negative relationship between daily minimum f_H and
779 daily activity f_H , where the latter is calculated as the difference between daily mean and
780 minimum f_H (Portugal *et al.* 2016) (Supplementary fig. 2A; $p < 0.001$ for the within-subject
781 effect slope).

782

783 The roe deer dataset analysed in the present study also includes activity measures, enabling
784 further interrogation of this aspect of the constrained energy pattern. A tilt switch implanted
785 in the neck measured whether the animal's head was up or down, while changes in signal
786 strength recorded by the antenna that received information from the collar transmitter on
787 each animal indicated locomotion (Arnold *et al.* 2004; Reimoser 2012). Combining these two
788 measures, along with heart rate, enabled classification of each minute of measurement as
789 either 'active' or 'not active'. Activity per day was then calculated as the percentage of
790 minutes active. While there is a positive relationship between daily mean f_H and activity levels
791 (Supplementary fig. 2B; $p < 0.001$ for the within subject effect slope), the regression
792 relationship between daily minimum f_H and activity levels within each individual does not
793 follow the prediction of the constrained pattern since there is no evidence that daily
794 minimum f_H covaries negatively with activity level (Supplementary fig. 2C; $p=0.26$ for the
795 within-subject effect slope). The explanation for this is that daily activity f_H is not represented
796 exclusively by the energy costs of activity. This is evidenced by the lack of a relationship
797 between daily activity f_H and activity levels (Supplementary fig. 2D; $p=0.33$ for the within-
798 subject effect slope). Rather, daily activity f_H also includes important other energy costs; we
799 suggest it is better termed daily auxiliary f_H . At least some of these auxiliary energy costs,
800 which are not activity per se, are low when activity levels are high. These non-activity
801 auxiliary energy costs, reduced in compensation for activity energy costs, could be associated
802 with low intensity behaviours such as reductions in levels of fidgeting (Levine, Eberhardt &
803 Jensen 1999) or changes in body posture (Levine, Schleusner & Jensen 2000; Ward,
804 Speakman & Slater 2003). Evidence for this possibility comes from studies including an
805 across-school investigation of children, in which the amount of physical activity the children
806 undertook at school did not relate to their levels of physical activity over the entire day

807 (Mallam *et al.* 2003), and an investigation of elderly participants who exhibited no increase in
808 daily activity levels during periods of physical training (Meijer, Westerterp & Verstappen
809 1999). Garland *et al.* (2011) report data showing that in young adults, daily energy
810 expenditure is not as high as expected on days when physical activity is high. Furthermore, a
811 meta-analysis by Wing *et al.* (1999) found that only 2 out of 13 studies reported statistically
812 significant differences in weight loss for participants both dieting and undertaking exercise
813 versus participants who were dieting only. Finally, Westerners have similar daily energy
814 expenditures to the more physically active Hadza people of Tanzania (Pontzer *et al.* 2012).
815 Thus for roe deer at least, rather than maintenance energy expenditure decreasing in
816 response to high levels of energy spent on activity, maintenance energy expenditure does
817 not systematically change; specific auxiliary costs decrease instead (resulting in the lack of
818 relationship between daily auxiliary daily activity f_H and activity levels (Supplementary fig.2D).
819 These specific auxiliary costs decrease sufficiently so that the relationship between daily
820 mean activity f_H and daily minimum daily activity f_H is less than 1 indicating an element of the
821 energy constrained pattern (fig. 2B).

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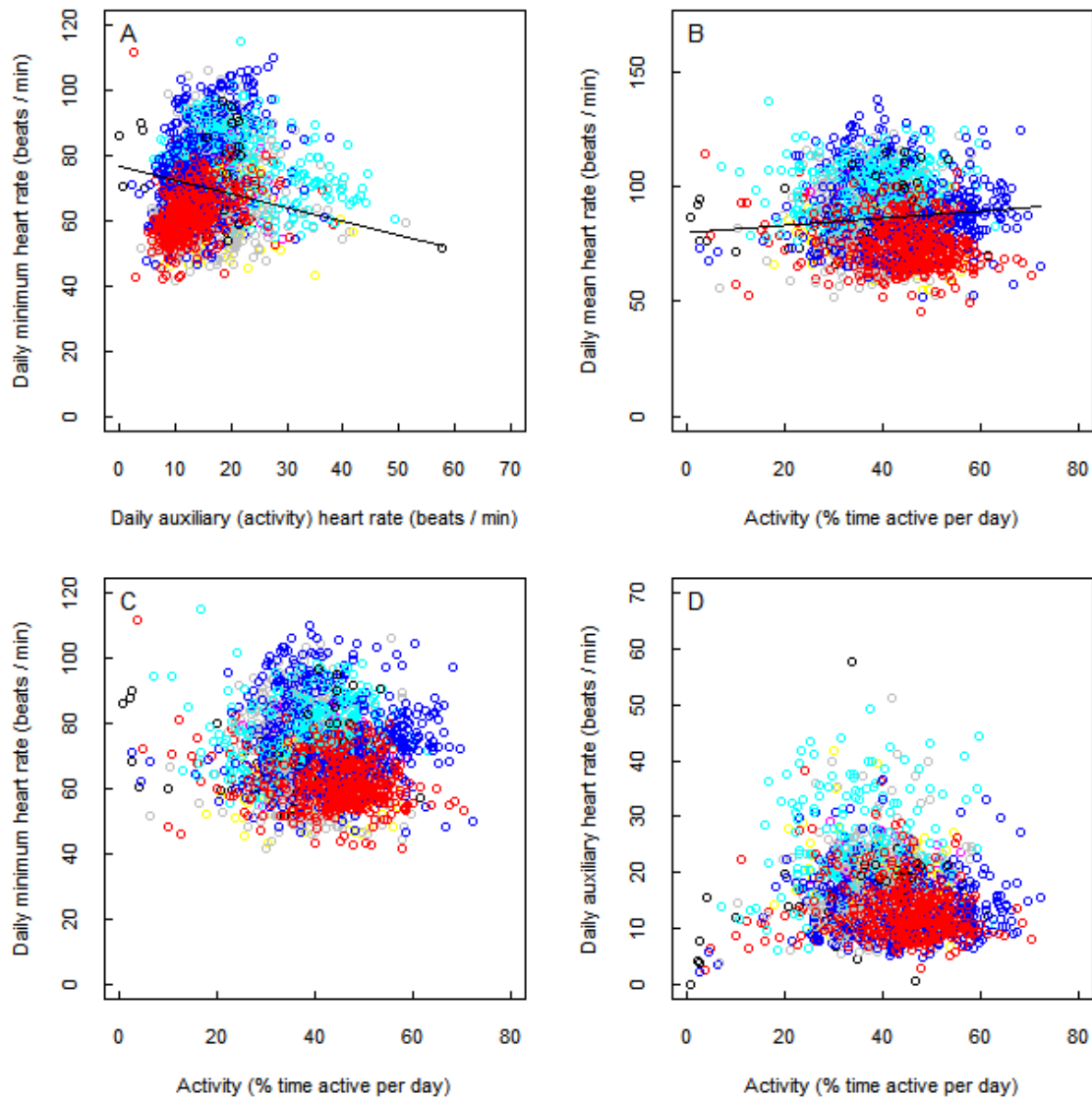


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825 **Supplementary Figure 1.** Hypothetical representations of three energy management patterns
 826 (modified from Careau 2017; refer to that paper for a full explanation). Comparing the middle
 827 versus right stacks shows the effect of an increase in auxiliary energy expenditure on daily
 828 energy expenditure and maintenance energy expenditure. Comparing the middle versus left
 829 stacks shows the effect of an increase in maintenance energy expenditure on daily energy
 830 expenditure and auxiliary energy expenditure. The right-hand panel shows the predicted
 831 relationship between daily energy expenditure and maintenance energy expenditure, along
 832 with the predicted slope (b) of the relationship, as suggested by Mathot and Dingemans
 833 (2015). A) The independent pattern, where maintenance and auxiliary energy expenditure
 834 are independent of each other. B) The constrained pattern, where increases in maintenance
 835 energy expenditure are associated with decreases in auxiliary energy expenditure and vice-

836 versa. C) The performance pattern is defined by increases in maintenance energy
837 expenditure in response to increases in auxiliary energy expenditure, and vice-versa.
838



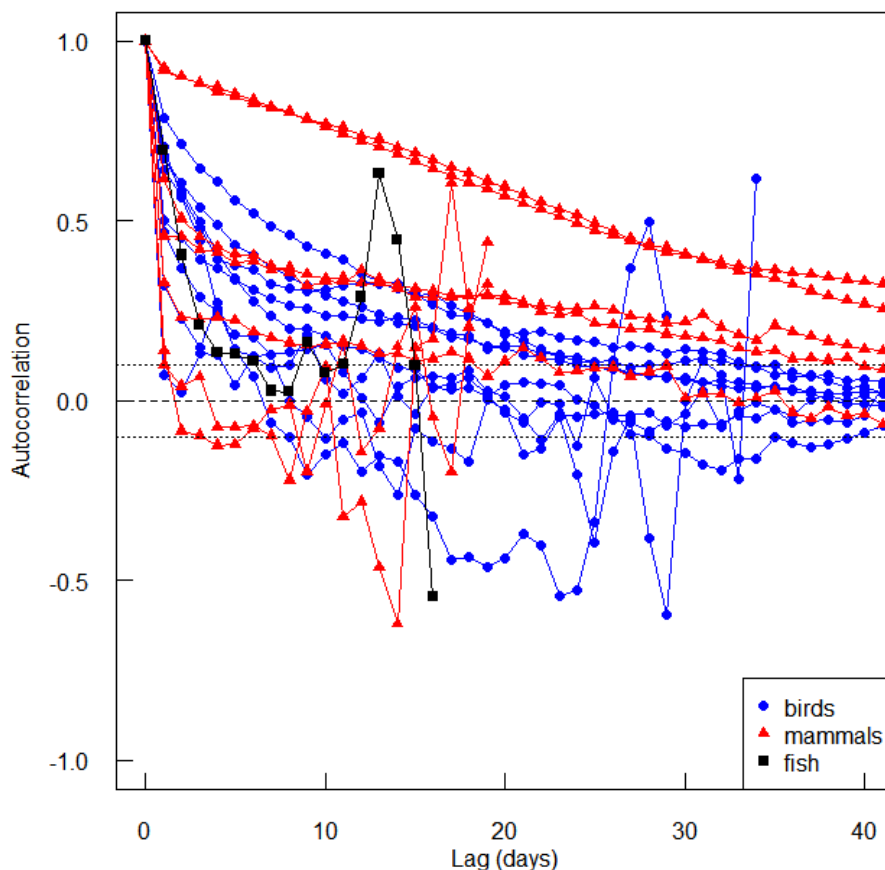
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841 **Supplementary Figure 2.** Relationships within individual roe deer between (A) minimum daily
842 heart rate (f_H ; a proxy for daily maintenance energy expenditure) and daily auxiliary (activity)
843 f_H (a proxy for activity energy expenditure). The relationship is negative, indicating some
844 degree of energy constraint is exhibited by this species. (B) daily mean f_H (a proxy for daily
845 mean energy expenditure) and daily activity levels. The relationship is positive. (C) minimum
846 daily f_H and daily activity levels. There is no evidence for a relationship. (D) daily auxiliary
847 (activity) f_H and daily activity levels. There is no evidence for a relationship. Individual animals

848 are represented by different colours. All observations included in this study's analysis are
849 presented in these panels but a large number are obscured due to data points overlapping.
850 The presented lines of best-fit represent the overall within-individual relationships. They
851 were calculated from mixed models that were input within-subject centred values of
852 minimum daily f_H , and also accounted for temporal autocorrelation. To calculate the
853 intercept of these particular best-fit lines correctly, the data had to be centred on $x=0$ for the
854 mixed model, and then the resultant intercept adjusted to account for the true x values.
855

856 *Autocorrelation functions in the data*

857 In all species except roe deer, there was strong and statistically significant temporal
858 autocorrelation across successive daily measurements at the within-individual level
859 (Supplementary fig.2; Table 2).



860

861 **Supplementary Figure 3.** Autocorrelation functions fitted in the residual structure of
862 univariate mixed models of daily mean heart rate (a proxy of daily energy expenditure) in 9
863 species of free-ranging birds (blue dots), 6 species of free-ranging mammals (red triangles)

864 and an ectothermic species of fish. The autocorrelation values are calculated using pairs of
865 residuals at the within-individual level within each species. The strong significance of the
866 autocorrelation term in most models indicates that some important explanatory variables
867 determining daily mean heart rate (f_H) are missing, particularly those operating at scales of
868 approximately 2-20 d. Presumably, if the relevant variables were available (e.g. temperature,
869 food availability, breeding status etc.), their inclusion in the model would reduce the amount
870 of autocorrelation in the residuals.

871

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