

1 Title: Mating opportunities and energetic constraints drive variation in age-dependent sexual
2 signalling

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25 **Mating opportunities and energetic constraints drive variation in**
26 **age-dependent sexual signalling**

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38 **Summary**

39 1. When males repeatedly produce energetically expensive sexual signals, trade-offs between
40 current and future investment can cause plasticity in age-dependent signalling. Such
41 variation is often interpreted as alternate adaptive strategies: live fast and die young vs.
42 slow and steady.

43 2. An alternative (yet rarely tested) explanation is that condition-dependent constraints on
44 allocation cause variation in signalling with age ('late bloomers' do not have early
45 investment options). Testing this hypothesis is challenging because resource acquisition and
46 allocation are difficult to measure, and energetic reserves both affect and are affected by
47 reproductive effort.

- 48 3. We simultaneously manipulated acquisition (through dietary nutrition) and access to
49 potential mates (as a proxy for manipulating sexual trait allocation) in male decorated
50 crickets (*Gryllodes sigillatus*), while measuring age- and signalling effort-mediated changes in
51 energy storage components.
- 52 4. Increased diet quality caused increased signalling effort and energy storage, while access to
53 females increased both the likelihood of and time spent signalling. Males with lower
54 resource budgets signalled less, but still suffered energetic storage loss and viability costs.
- 55 5. Our results suggest that energetic constraints, rather than strategic resource accumulation,
56 reduced signalling levels in males with lower resource acquisition ability. Our findings imply
57 a non-adaptive explanation for age-dependent variation in sexual signalling, and an
58 important role for energetic constraints in maintaining the honesty of costly behavioural
59 displays.

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63 **KEY WORDS: Condition dependence, life history, phenotypic plasticity, sexual selection, trade offs.**

64 The fitness of an individual depends on its investment in life-history traits (Stearns 1992). The
65 expression of these traits is thought to be affected by trade-offs, caused when a fitness-improving
66 increase in one life history trait is coupled to a fitness-reducing decrease in another (Stearns 1989).
67 One trade-off universal to all organisms occurs because any individual has only a finite pool of
68 resources, for which all of its traits are competing. Most studies on such trade-offs have focused on
69 investment across traits at a single point in the life history, but allocation trade-offs can also occur
70 between investments in the same trait at different ages. Although the concept of age-dependent
71 changes in performance is prevalent in studies of senescence, it is often difficult to disentangle the
72 effects of allocation from other potential causes of decreased performance (Monaghan *et al.* 2008;
73 Nussey *et al.* 2008).

74 An individual's ability to acquire resources, known as its 'condition', is often strongly related to the
75 expression of costly sexual traits in males (Rowe & Houle 1996). Condition is likely determined by a
76 large number of loci because so many genes are involved in acquiring and metabolising resources. If
77 the ability to pay fitness costs associated with increased investment in a sexual trait (e.g. reduced
78 future reproductive effort or survival) is heritable, females can use a male's condition-dependent
79 signals to assess the quality of his genes (in terms of the probable condition of offspring; Nur and
80 Hasson 1984; Andersson 1986; Grafen 1990; Iwasa and Pomiankowski 1994).

81 This relationship between genetic quality and condition depends on trade-offs, with genetic
82 correlations among fitness-related traits affected by relative levels of genetic variation in both the
83 acquisition and allocation of resources (Van Noordwijk & De Jong 1986; Houle 1991; Hunt *et al.*
84 2004b). While theory suggests males should benefit by sacrificing investment in longevity in favour
85 of increased early reproductive success (Vinogradov 1998; Bonduriansky *et al.* 2008), studies often
86 show the opposite pattern, such that males that signal most intensely are also those that survive the
87 longest (Jennions, Møller & Petrie 2001). One possible explanation for this positive covariance is that
88 high-condition individuals have more resources to allocate to all aspects of their life history, masking

89 real life history trade-offs between expensive traits (Van Noordwijk & De Jong 1986; De Jong & Van
90 Noordwijk 1992; Reznick, Nunney & Tessier 2000; Hunt *et al.* 2004b).

91 Assessing how life history trade-offs affect investment in sexual trait expression is a challenging task.
92 The resource pool itself cannot be measured directly via phenotypic traits: many such traits may
93 covary with an individual's resource budget, but must themselves have been constructed using
94 resources and therefore will necessarily be traded against other life history traits (Hunt *et al.* 2004b;
95 Houslay & Bussière 2012). Residuals of body mass over a fixed measure of body size are commonly
96 used as a proxy for condition (e.g., Peig and Green 2009), yet are unlikely to be consistently
97 adequate (Wilder, Raubenheimer & Simpson 2015; Barnett *et al.* 2015): for example, energetically
98 expensive trait expression (such as sexual display) is fuelled by sugars that are supplied by fat stores
99 (Tomkins *et al.* 2004). Consequently, condition indices can only be used to reliably compare
100 individuals of different sizes if we know how fat content scales with size (Kotiaho 1999). Ideally,
101 direct physiological analyses (rather than genetic or phenotypic approaches) are needed to study the
102 mechanisms mediating energy storage and use, and their consequences for variation in sexual trait
103 expression (Zera & Harshman 2001).

104 The problems inherent in assessing resource trade-offs are compounded when an individual
105 expresses a sexual trait repeatedly over its lifetime. Such individuals face trade-offs not only
106 between the focal trait and other components of life history, but also between current and future
107 expression of the sexual trait: a male that invests many resources when young has fewer resources
108 to spend when old, and vice versa (Badyaev & Qvarnström 2002). To save resources for critical
109 periods, males may elect not to signal at certain ages, or to delay maturation until later in life (Kokko
110 1997). These trade-offs create variation between individuals in patterns of age-dependent
111 expression of sexual traits, and impede females from using signal expression as an index of a male's
112 overall acquisition ability. In other words, investment in sexual signalling at any given age is less

113 likely to be an honest indicator of quality than if this trait remained constant across his lifetime
114 (Kokko 1997).

115 The honesty of sexual traits has long been of interest to students of sexual selection (Zahavi 1975;
116 Andersson 1982; Nur & Hasson 1984; Grafen 1990; Johnstone 1995; Kokko 1997). Strict honesty in
117 sexual trait expression may not always be fulfilled in a population (Candolin 1999; Hunt *et al.* 2004a),
118 but the 'on-average' honesty enforced by life history trade-offs maintains stability in systems where
119 male advertisement is subject to within-individual variation over lifetimes (Kokko 1997). Identifying
120 costs associated with sexual trait expression is therefore crucial to determining variation in age-
121 dependent signalling, and pinpointing mechanisms enforcing honesty in such systems.

122 A primary model for studying investment in age-dependent sexual expression is acoustic signalling
123 (Andersson 1994). In crickets, males produce an advertisement call through stridulation of their
124 forewings, and the amount of time a male spends calling ('calling effort') is a strong predictor of
125 mating success in nature (Hunt *et al.* 2004a; Bentsen *et al.* 2006; Rodriguez-Munoz *et al.* 2010).
126 Calling is highly energetically expensive (e.g., Kavanagh 1987; Hunt *et al.* 2004a; Ophir *et al.* 2010;
127 Mowles 2014), and may increase mortality risk from both intrinsic (calling diverts energy from other
128 functions, such as somatic maintenance, Hunt *et al.* 2004a) and extrinsic sources (male calls attract
129 predators, Walker 1979, or parasitoids, Cade 1975). Among crickets, calling is likely fuelled by
130 aerobic metabolism (Prestwich & Walker 1981; Bailey *et al.* 1993; Prestwich 1994; Hoback & Wagner
131 1997), with variation in calling effort linked to the ability to acquire and mobilise combinations of
132 glycogen, carbohydrates and lipids (*Acheta domesticus*, Bertram *et al.* 2011; *Gryllus assimilis*, *Gryllus*
133 *texensis*, Thomson, Darveau & Bertram 2014). Studies that manipulated resource acquisition have
134 shown that male condition strongly affects the timing and magnitude of calling effort in several
135 different cricket species (*Gryllus pennsylvanicus*, Judge, Ting & Gwynne 2008; *A. domesticus*, Bertram
136 *et al.* 2009; *Teleogryllus commodus*, Maklakov *et al.* 2009; Zajitschek *et al.* 2009, 2012; *Gryllodes*
137 *sigillatus*, Houslay *et al.* 2015), and also that high-condition males sometimes invest so heavily in

138 sexual displays that they suffer heightened mortality compared to lower-condition individuals (*T.*
139 *commodus*, Hunt et al. 2004a).

140 However, manipulating acquisition alone may not necessarily reveal differential costs of sexual trait
141 expression, as males in good condition have more resources to allocate to all traits (Kotiaho 2001).
142 Testing for differential costs requires manipulating both acquisition and trait investment, then
143 studying their effects on other life history traits (e.g., future reproductive effort or survival).
144 Moreover, behavioural signals are highly phenotypically plastic, which may allow males to react
145 quickly to changes in the local environment so as to maximise fitness (Komers 1997; Bretman, Gage
146 & Chapman 2011). We do not know the importance of resource trade-offs relative to other factors in
147 causing distinct age-specific investment strategies (live fast and die young vs. slow and steady). Male
148 crickets respond plastically to the social environment: juveniles reared in environments indicating
149 high competition for females invest more in reproductive tissues (*T. oceanicus*, Bailey et al. 2010)
150 and age-specific calling effort (*T. commodus*, Kasumovic et al. 2012a). During adulthood, rival male
151 presence can cause plastic shifts towards increased calling effort (*T. commodus*, Callander et al.
152 2013), while the introduction of females can affect call frequency (*Gryllus bimaculatus*, Simmons
153 1986) and timing (*G. sigillatus*, *Gryllus veletis*, Burpee & Sakaluk 1993). The simultaneous
154 manipulation of diet and the socio-sexual environment can therefore be used to evaluate both the
155 energetic and life history consequences of trait investment, and reveal whether plasticity in the male
156 signal is due to the strategic saving of resources or resource constraints.

157 In this study, we measure changes in allocation to sexual signalling and resource storage as a
158 function of both acquisition and the demands of prior signalling in male decorated crickets (*G.*
159 *sigillatus*). We measure calling effort, and use biochemical assays to estimate the energetic resource
160 budgets of separate subsets of males before and after manipulating resource acquisition and access
161 to potential mates. Furthermore, we assess the consequences of our experimental manipulations on
162 longevity. Our measurements of male daily calling behaviour reflect two processes: a male's decision

163 as to whether or not he calls, and – given a positive decision – his calling effort. The presence of
164 females should present universal incentive in the decision to call, enabling us to separate this choice
165 from the more resource-dependent component (the non-zero amount of calling effort). By isolating
166 components of male investment decisions in this way, we can disentangle variation due to
167 constraints from variation due to adaptive planning. If future planning is the primary force shaping
168 an individual's response to social conditions, low levels of calling early in life among males with
169 reduced resource acquisition ability should also be associated with increased energy reserves and
170 greater calling later in life (Kokko 1997; Hunt *et al.* 2004a). If, however, there is no evidence of
171 greater energy reserves for allocation at a later point, it is likely that low calling levels are due simply
172 to a lack of energy for current allocation to reproductive effort. In the latter case, we would also
173 expect all males to respond to the availability of potential mates by investing their resources more
174 heavily in calling effort, rather than saving for the future.

175

176 *Materials and Methods*

177 **CRICKET HUSBANDRY**

178 We used *G. sigillatus* (Figure 1) descended from a 2001 collection of 500 adult crickets in Las Cruces,
179 New Mexico, which had been used to initiate a laboratory culture maintained at a population size of
180 approximately 5000 crickets and allowed to breed panmictically (Ivy & Sakaluk 2005). Crickets were
181 housed in 15-litre plastic containers in an environmental chamber maintained at $32\pm 1^\circ\text{C}$ on a
182 reversed 14:10 hours light/dark cycle. We provided juvenile crickets with egg cartons for shelter, *ad*
183 *libitum* water in cotton wool-plugged test tubes, and a standard diet of ground cat food (Friskies Go-
184 Cat Senior®, Purina, London, UK). We provided moistened cotton wool pads to adults as an
185 oviposition substrate. We maintained crickets at a density of approximately 300 individuals per
186 container.

187 **EXPERIMENTAL PROTOCOL**

188 We manipulated male resource acquisition through diet treatment, and also manipulated access to
189 females (as a proxy for manipulating resource allocation). We investigated variation in allocation to
190 four different energy storage components (carbohydrates, glycogen, lipids and proteins; details
191 given below) by sacrificing subsets of the experimental population (by placing individuals in a -80°C
192 freezer) at three different ages: immediately at eclosion (baseline variation); one week post-
193 eclosion (effect of resource acquisition manipulation); and two weeks post- eclosion (effects of both
194 resource acquisition and female-access manipulations). A fourth group of males were allowed to die
195 naturally, to estimate how acquisition and prior signalling investment affected lifespan.

196 We separated 630 male cricket nymphs from laboratory stock cultures during the final instar. Upon
197 eclosion, we photographed individuals (Motic SMZ-168 with Moticam 2000) and measured
198 pronotum length using NIH ImageJ v1.48 (Schneider, Rasband & Eliceiri 2012). We measured body
199 weight using a high-precision electronic balance (Denver Instrument, model PI-225DA) at eclosion
200 and weekly intervals thereafter. At eclosion, we assigned males randomly to one of four groups:
201 those to be sacrificed immediately ($n = 58$), after one week ($n = 56$), after two weeks ($n = 256$), or
202 allowed natural lifespan ($n = 260$). We transferred male crickets that were not immediately sacrificed
203 to individual clear plastic containers (5×5×5cm), each containing plastic mesh as substrate, a cotton
204 wool-plugged water bottle, and the food treatment. We cleaned containers and provided fresh food
205 and water weekly.

206 We quantified allocation to the male sexual trait as ‘calling effort’, the duration (in seconds) that
207 each individual spent broadcasting his sexual advertisement call. We measured each male overnight
208 from 2pm-9am (dusk until afternoon of the following day on the reversed light cycle; lights off
209 2.30pm-12.30am, with 30 min rampdown) every day from the day after eclosion up to a maximum
210 of 35 days. We mounted a microphone (C1163, Dick Smith Electronics) in the lid of each individual
211 container, placing that container into a hollowed-out cube of soundproofing foam (15×15×15cm) to

212 minimise outside disturbance and prevent crosstalk between containers during recording. We
213 removed a corner of the foam lid to maintain crickets on the set light cycle. An electronic acoustic
214 recording system (Bertram and Johnson 1998) sampled from each microphone of each 10 times per
215 second to determine whether or not a male was calling (see Hunt et al. 2004a).

216 **CREATION OF ARTIFICIAL DIETS**

217 We manipulated resource acquisition by creating seven artificial, dry, granular diets that varied in
218 the amount of total nutritional content (see Appendix S1). All diets had a protein:carbohydrate ratio
219 of 1:8, based on the effect of a high-carbohydrate diet in maximising calling effort and longevity in
220 this species (J. Hunt, unpublished data). Diets ranged from 12-84% (in 12% increments) in total
221 protein and carbohydrate content (referred to throughout as nutritional content).

222 **FEMALE-ACCESS TREATMENT**

223 During the second week post-eclosion, we allowed male crickets access to a single different adult
224 female cricket during the recording period each night for between 0 and 7 consecutive nights
225 (always beginning on the first day of the second week post-eclosion; i.e., eight distinct treatment
226 groups). As logistical constraints prevented us from providing virgin females of similar age each day,
227 we instead controlled female 'experience' to be similar to the male with which she would be placed:
228 on the first day virgin males had access to virgin females, on the second day a male would gain
229 access to a female that had had a single night's access to males, and so forth. When not housed with
230 an experimental male in his container, females were maintained in single-sex groups according to
231 experience, and provided with water, shelter, and stock diet. Female experience was manipulated to
232 the necessary level by housing them overnight with random stock males. Before being placed with
233 an experimental male, females were also given at least a day without access to a male (considered
234 sufficient as female *G. sigillatus* have a high remating rate, averaging 22 times over a 20-day period;
235 Sakaluk 1987). During the week that access to females was manipulated, the food was removed

236 from each male's container during the call recording period (regardless of female presence). Males
237 were given access to food whenever calling effort was not being recorded (9am – 2pm).

238 During the female-access treatment period, we allowed paired crickets to mate freely. In many
239 cricket species, males stop calling after mating until they have generated a new spermatophore and
240 are ready to mate again (Huber 1962; Loher 1974; Cade & Wyatt 1984; Wagner 2005); this is also the
241 case in *G. sigillatus* (T. Houslay, personal observation). Males transfer a 2-part spermatophore,
242 comprising the sperm ampulla and a spermatophylax 'nuptial gift' (Sakaluk 1984). While these take
243 an average of 3.25 hours to compose (Sakaluk 1985), they consist of 80-85% water and have little or
244 no nutritional value (Will & Sakaluk 1994; Warwick *et al.* 2009), and as such the metabolic costs of
245 their generation are uncertain. We anticipate that one major effect of mating will be a reduction in
246 calling, with the concomitant saving in stored resources that might otherwise be spent on calling
247 activity. Our large sample size and use of continuous (rather than categorical) treatments enable us
248 to capture diet- and calling-mediated changes in energy storage despite any additional effects of
249 mating on males.

250 **MEASURING ENERGY STORAGE**

251 We used a modified version of Foray *et al.* (2012) to measure the major components of energy
252 storage in each cricket: carbohydrates, glycogen, lipids and proteins (see Appendix S2). These can be
253 assumed to comprise an individual's entire current energy budget. Cricket flight is fuelled by lipid
254 breakdown (Zhao & Zera 2002), and the nature of the underlying pathways makes it likely that lipids
255 are the major energy store for stridulatory calling effort. Their presence is likely to be greatest in
256 males that have access to high quality resources. Glycogen is the storage form of glucose, and can be
257 broken down in quick response to the need for energy in high-intensity activity (Campbell & Farrell
258 2003). High circulating glycogen levels may indicate males that are prepared to engage in sustained
259 calling bouts, while carbohydrate content shows the existence of free sugars that can be used to fuel
260 energetically expensive signalling. Protein contains the same energy content per gram as

261 carbohydrates, but takes longer to break down and is not typically used as a short-term energy
262 source. The relative value of these energy storage forms for sexual signalling is currently unclear;
263 lipids provide more energy than sugars on a gram-for-gram basis (Campbell & Farrell 2003), yet
264 mobilisation of shorter-term energy forms is probably important for plastic responses to
265 reproductive opportunities. If males were future planners, such that low-acquisition males restrict
266 early signalling in favour of storage for use later in life, we would expect these males to show greater
267 storage of lipids relative to glycogen and carbohydrate.

268 **STATISTICAL ANALYSIS**

269 We performed all statistical analyses using R 3.1.1 (R Core Team 2014). Independence between
270 linear and quadratic forms of numeric predictors (e.g., diet and diet²) was achieved by centring the
271 input variable before squaring (Gelman & Hill 2007). Diet treatments were centred and scaled to
272 single-unit deviations, such that model coefficients show the effect on the response variable
273 equivalent to one unit of change in diet treatment. In analyses of daily calling effort (discussed
274 further below), male age post-eclosion was also centred but not scaled (coefficients show effect
275 equivalent to one day's change). Continuous covariates (e.g., measurements of energy storage when
276 used as predictors) were standardised by mean-centring and scaling (dividing by 1 standard
277 deviation), putting them on a common scale and aiding interpretation of main effects (Gelman & Hill
278 2007; Schielzeth 2010). Unless otherwise stated, we performed model simplification by dropping
279 non-significant higher-order terms (interactions and quadratic effects) from the full model
280 sequentially, and using likelihood ratio tests to compare nested models. We retained more complex
281 models whenever simplification resulted in a significant increase in model deviance. We observed no
282 cases in which non-significant main effects became significant during model simplification steps that
283 did not involve the deletion of an interaction term including that particular main effect.

284 *Daily calling decisions and effort*

285 Daily calling effort data were over-dispersed and zero-inflated; for analyses of these data, we used
286 the R package MCMCglmm (Hadfield 2010) to fit a zero-altered Poisson (ZAP) model: a two-part
287 model that includes a logistic regression for the zeroes in the data and a Poisson regression for the
288 zero-truncated counts (see Appendix S3). We accounted for repeated observations on individuals by
289 specifying a random effect of cricket ID. The ZAP model enabled us to ask two distinct questions
290 within a single statistical structure (Atkins *et al.* 2013): what factors influenced whether a male
291 called or not (*i.e.*, non-zero or zero), and, if he did call, what factors influenced the magnitude of
292 calling (Houslay *et al.* 2015)?

293 For the first week post-eclosion, the full model included predictor variables of linear and quadratic
294 terms for both diet treatment and days post-eclosion (corresponding to male age, modelled as a
295 continuous variable), and all interactions (except those between the linear and quadratic forms of
296 the same predictor, e.g. $\text{day} \times \text{day}^2$, as such interactions are not interpretable).

297 For analysis of daily calling effort across the second week post-eclosion, female-access treatment
298 could not be entered in the model as a single predictor because the differences among treatment
299 groups only become apparent as the week progresses. Instead, we use both a binary predictor of
300 'female presence' (indicating whether a male had access to a female on the current day of
301 observation) and a continuous 'prior female access' variable (the number of days prior to the current
302 one in which a male had access to females). The full model for daily calling over the second week
303 post-eclosion therefore included predictor variables of female presence (binary variable), linear and
304 quadratic terms for both diet treatment and male age (in days post-eclosion), prior female access,
305 and up to three-way interactions between these (except those featuring linear and quadratic forms
306 of the same predictor).

307 *Changes in body mass*

308 We used multiple regression to assess the linear and quadratic effects of diet treatment on changes
309 in individual body mass (using the scaled mass index, SMI; Peig and Green 2009) over the first week
310 post-eclosion. SMI is a better index of the relative size of energy reserves (Peig & Green 2010), and a
311 better correlate of standardised mass in crickets (*A. domesticus*, *G. texensis*; Kelly, Tawes &
312 Worthington 2014), than other commonly-used proxies.

313 To estimate the effects of both acquisition and allocation on the change in SMI (Δ SMI) over week 2,
314 our predictors were diet treatment and log-transformed total calling effort. We used a separate
315 model to investigate the effects on Δ SMI of diet treatment, female access treatment, and their
316 interaction. Given that our individuals had already been subject to their diet treatments for the first
317 week post-eclosion, we corrected Δ SMI over week 2 for the effect of regression to the mean, using
318 the method outlined by Kelly and Price (2005).

319 *Changes in energy storage*

320 For those individuals sacrificed at eclosion, we used linear regression models to test whether
321 carbohydrate, glycogen, lipid or protein content predicted an individual's scaled body mass (SMI).
322 We log-transformed SMI so that model residuals conformed to a normal distribution. We excluded
323 one individual because its SMI was over 4 standard deviations from the mean (all others were within
324 ± 2.2 standard deviations).

325 We also used linear regression models to investigate the causes of variation in energy storage
326 components at the end of the first week post-eclosion. For each response variable (protein, lipid,
327 glycogen and carbohydrate), we estimated approximate changes over this period by subtracting the
328 mean concentration of each storage form at eclosion from every individual's measurements. We
329 then tested for the effect of diet treatment on these changes. The values representing changes in
330 carbohydrates, glycogen and lipids were log-transformed prior to analysis. We also tested whether
331 the changes in each form of energy storage predicted changes in SMI.

332 We estimated approximate changes in energy storage components over the second week by
333 subtracting the diet-specific mean content of each storage form at the end of week 1 from each
334 individual's measurements. We then tested whether these estimated changes in energy storage
335 were associated with individual changes in SMI. We also tested whether individual energy storage
336 measurements at the end of week 2 predicted SMI at the same stage.

337

338 *Results*

339 As expected (because treatments began after males reached eclosion), there were no significant
340 differences between diet or female-access treatment groups in pronotum length, raw body mass, or
341 scaled body mass (scaled mass index, SMI) at eclosion (all $P > 0.37$). Of the four energy storage forms
342 measured, only lipids were a significant predictor of SMI at eclosion (lipid coefficient = 0.065 ± 0.030 ,
343 $t_{1,50} = 2.19$, $P = 0.033$).

344 **MANIPULATION OF RESOURCE ACQUISITION IN EARLY ADULTHOOD**

345 *The likelihood of calling and calling effort both increase with diet quality and age*

346 The simplified ZAP model for days 2-7 post-eclosion included predictor variables of diet, linear and
347 quadratic terms for the day of calling (i.e., the age of an individual post-eclosion), and an interaction
348 between diet and the linear day term. The likelihood of calling increased significantly along with
349 both nutritional diet content and age over the first week (Table 1, Fig. 2(a)). The age-related increase
350 in the likelihood of calling was less pronounced towards the end of the week. When males did call,
351 there was a significant two-way interaction between day and diet on the amount of calling effort:
352 effort increased over the course of the week, especially when males were fed higher quality diets
353 (Table 1, Fig. 2(b)). The main effects of age and diet were to increase calling effort during this period,
354 age acted in a non-linear manner. This non-linear effect of age can be seen in the change in the

355 intercept (centred at 48% diet) across panels in Fig. 2(b): the age-related change in the intercept
356 does not increase at a constant rate, with the rate of increase dropping at higher values of male age.

357 *Greater resource acquisition leads to increases in body mass and energy storage*

358 The change in SMI among individuals increased with improving dietary nutrition, although this
359 increase levelled off at higher diets (negative quadratic effect of diet; Table 2(a)). We estimated
360 changes in energy storage content by comparing individual measurements of each storage
361 component to averages taken from the subset of crickets sacrificed at eclosion, enabling us to
362 investigate the underlying physiological response to our dietary manipulation. Improving dietary
363 nutrition significantly increased carbohydrate, glycogen and lipid reserves, but not protein (Table
364 2(b)). Separate models also showed that the estimated changes in lipid and glycogen were significant
365 predictors of changes in SMI over the first week post-eclosion (carbohydrate = 0.015 ± 0.004 , $t_{1,43} =$
366 1.70 , $P = 0.096$; glycogen = 0.008 ± 0.003 , $t_{1,47} = 2.30$, $P = 0.026$; lipid = 0.008 ± 0.003 , $t_{1,46} = 2.34$, $P =$
367 0.024 ; protein $< -0.001 \pm 0.003$, $t_{1,48} = -0.01$, $P = 0.992$).

368 *Relationship between calling and change in body mass is dependent on resource acquisition*

369 The significant interaction term (Table 3) indicated that the relationship between total calling effort
370 and change in SMI over week 1 was strongly dependent upon diet, switching from a negative to a
371 positive relationship as diet improved (Figure 3): increased dietary nutrition meant males that called
372 more were also better able to increase body mass.

373 **MANIPULATION OF RESOURCE ACQUISITION AND ACCESS TO POTENTIAL MATES**

374 In the first part of our study, males on lower quality diets called less often and less intensely than
375 those on higher-quality diets (Fig. 2). While total calling effort and storage appeared to covary
376 negatively among those low-acquisition males, those males did not invest more in energy reserves
377 relative to higher-acquisition individuals (Fig. 3). To demonstrate 'future planning', low-acquisition

378 males should remain less likely to call even in the presence of females, instead conserving energy
379 reserves for greater calling later in life.

380 *Males are more likely to call when females are present*

381 The simplified ZAP model for daily calling effort during the female-access treatment period included
382 predictor variables of diet, female presence on the current day, the age of an individual at the time
383 of measurement (in days post-eclosion), and prior female access (the number of days the male had
384 access to a female prior to the current measurement). Multiple interactions were retained in the
385 model, including a three-way interaction between prior female access, diet, and day of
386 measurement.

387 Female presence significantly increased the likelihood of calling (Table 4, Fig. 4(a)). Males were less
388 likely to call as the week progressed, but this decrease was not observable when females were
389 present ('Female presence × day' interaction in Table 4; Fig. 4(a)). Finally, call likelihood was
390 significantly reduced in males that had greater access to females prior to the current measurement
391 ('Prior female access', Table 4). Diet had no effect on the likelihood of calling: low-acquisition males
392 were just as likely to call as high-acquisition males.

393 *The positive effect of diet on calling effort is reduced by greater prior access to females*

394 Calling effort increased significantly when a female was present, but the effect decreased over the
395 week ('Female presence × day' interaction term in Table 4; Fig. 4(b)). Dietary nutrition also
396 significantly increased calling effort (Fig. 5), but this effect was reduced in males with greater access
397 to females as the week progressed ('Prior female access × diet × day' interaction in Table 4; Fig. 5).
398 These effects are visualised in Fig. 5, which shows the relationship between diet treatment and
399 calling effort for the first (left panels) and final (right panels) days of the female-access manipulation,
400 for those given no female access (lower panels) or daily female access (upper panels).

401 *Diet-related increase in body mass is reduced by access to females*

402 Having excluded males that did not call or that cannibalised females during the female-access
403 treatment period, we found that increased total calling effort during week 2 was associated with
404 decreased SMI (log total calling = -0.0018 ± 0.0007 , $t_{1,307} = -2.55$, $P = 0.011$). Diet treatment increased
405 individual SMI, but this effect was reduced at higher diets (diet = 0.0021 ± 0.0006 , $t_{1,307} = 3.51$, $P <$
406 0.001 ; diet² = -0.0018 ± 0.0003 , $t_{1,307} = -3.76$, $P < 0.001$). Separately, we found no effect of diet on the
407 frequency with which males cannibalised females during the female access treatment period ($\chi^2_6 =$
408 1.10 , $P = 0.98$).

409 Table 5 shows the minimum adequate model for a separate analysis of the effects of our
410 experimental manipulations on the change in SMI over week 2 (again, excluding males that
411 cannibalised females). The effect of diet depended on female-access treatment; in the absence of
412 females, males on high-nutrition diets tended to gain more body mass during this period than those
413 on low diets; however, high-nutrition males with consistent access to potential mates lost more
414 mass ('Diet × Female-access' interaction term in Table 5; Fig. 6).

415 *Changes in body mass are associated with changes in carbohydrate and glycogen reserves*

416 We found that the estimated change in carbohydrate and glycogen reserves were significant
417 predictors of changes in individual SMI over the second week post-eclosion (carbohydrate = $0.0045 \pm$
418 0.0008 , $t_{1,143} = 5.52$, $P < 0.001$; glycogen = 0.0039 ± 0.0009 , $t_{1,145} = 4.56$, $P < 0.001$; lipid = $-0.0006 \pm$
419 0.0009 , $t_{1,142} = -0.72$, $P = 0.470$; protein = 0.0007 ± 0.0009 , $t_{1,139} = 0.70$, $P = 0.486$).

420 We also tested whether any of our energy storage measurements correlated with individual SMI at
421 the end of week 2; only lipid content significantly predicted SMI (lipid = 0.014 ± 0.005 , $t_{1,142} = 2.96$, P
422 = 0.004).

423 **EFFECTS OF RESOURCE ACQUISITION AND ACCESS TO POTENTIAL MATES ON SURVIVAL**

424 Due to the high proportions of deaths in the two lowest diet treatments (100% and 60.5%
425 respectively), we excluded individuals in those treatments from our analysis of the likelihood of

426 dying during the female-access period. Greater female access significantly increased the risk of death
427 during this period, while diet significantly reduced it (diet = -0.225 ± 0.113 , $t_{1,377} = -1.99$, $P = 0.047$;
428 female-access = 0.226 ± 0.074 , $t_{1,377} = 3.04$, $P = 0.002$; Fig. S2). A model retaining the excluded diet
429 treatments gave qualitatively similar results, which are not presented here.

430 Our female-access treatment had a significant effect on lifespan after the conclusion of the female
431 access treatment period (i.e., after the end of the second week post-eclosion); males with greater
432 access to females during week 2 had shorter lifespans (female-access = -3.913 ± 0.937 days, $t_{1,145} = -$
433 4.18 , $P = 0.001$; Fig. S3(a)). Lifespan was significantly increased by greater dietary nutrition, although
434 this effect disappeared at higher quality diets (diet = 11.823 ± 1.734 days, $t_{1,145} = 6.82$, $P < 0.001$; diet²
435 = -2.491 ± 0.869 , $t_{1,145} = -2.87$, $P = 0.005$; Fig. S3(b)).

436

437 *Discussion*

438 Male sexual signals are often condition-dependent, with trait expression closely associated with the
439 size of the resource budget (e.g. Andersson 1994; Johnstone 1995). Few studies have simultaneously
440 manipulated resource acquisition and access to reproductive opportunities while also examining the
441 resultant patterns of energy storage and use (Kotiaho 2000). Recently, it has become clear that traits
442 used to measure condition are themselves condition-dependent (and are built using the resources
443 that make up condition), meaning that traits reflecting condition must inevitably trade-off with one
444 another (Tomkins *et al.* 2004; Houslay & Bussière 2012). This fact prescribes careful interpretation of
445 covariances between proxies for condition and other life history traits, and highlights the need for
446 more direct measurements of energy reserves (Morehouse 2014; Wilder *et al.* 2015). Despite the
447 inherent challenges, identifying relationships between trait investment and stored energy reserves
448 can illuminate mechanisms leading to changes in resource storage and use, and therefore help

449 clarify the adaptive significance of variation in resource allocation among males as well as the
450 consequences of energetic trade-offs for honesty in sexual trait expression.

451 By manipulating dietary nutrition in male crickets, we showed that greater resource acquisition led
452 to an increase in both the likelihood and amount of signalling in early adulthood (Table 1, Fig. 2), as
453 well as greater investment in energy stores (lipid, glycogen and carbohydrate) during this period
454 (Table 2). The relationship between allocation to scaled body mass (as scaled mass index, SMI) and
455 calling effort depended on diet quality, switching from negative covariance when diet quality was
456 low to positive covariance when high (Table 3, Fig. 3). While low-acquisition males called less often,
457 and less intensely, during this period than did higher-acquisition males, we found no evidence that
458 such a suppression of signalling effort led to increased energy reserves. If low calling effort among
459 low-acquisition males was due to energy constraints rather than future planning, we predicted that
460 these males would respond to the presence of potential mates by investing more in calling instead
461 of saving energy for the future.

462 Sexual trait expenditure was highly plastic depending on the availability of a potential mate: males
463 responded strongly to the presence of a female by increasing both the likelihood of calling and time
464 spent calling (Table 4, Fig. 4). During the female-access treatment period, diet did not affect the
465 probability of signalling on any given day. It did, however, have a strong positive effect on the
466 amount of time spent calling (Fig. 5), mediated by female-access: the positive effect of diet on calling
467 effort decreased with greater exposure to females over the course of the week (Fig. 5). The change
468 in male scaled body mass (SMI) as a function of diet during this period was non-linear and also
469 depended on access to females (Table 5, Fig. 6). In the absence of females, males fed higher
470 nutrition diets tended to increase or maintain body mass more than those on lower-nutrition diets.
471 However, greater female-access effectively reversed this relationship: males on high-nutrition diets
472 tended to lose more SMI than those on lower-nutrition diets when given daily access to females over
473 the treatment period. Diminishing calling effort by the end of week 2, even by males on high-quality

474 diets in the presence of females, suggests an exhaustion of available resources over this period (Fig.
475 5).

476 Indeed, the change in male body mass over week 2 covaried negatively with total calling effort, and
477 the likelihood of calling decreased as previous exposure to females increased (Fig. 4(a), Table 4) –
478 both results irrespective of diet. Greater exposure to potential mates also increased the risk of dying
479 during week 2, although this effect was mitigated by diet quality (Fig. S2). There were lasting
480 consequences of our experimental manipulations: longevity following week 2 was increased by
481 dietary nutritional quality, and decreased by greater prior exposure to females (Fig. S3). However,
482 this reduced viability cannot be considered a true cost unless it is accompanied by a net decrease in
483 fitness, because any decrease in lifespan may be offset in fitness terms by increased early
484 reproductive success (Kotiaho 2001; Hunt et al. 2004a,b).

485 **FUTURE PLANNING OR BUDGET CONSTRAINTS?**

486 Crickets are ideal for testing hypotheses concerning age-related reproductive effort because we can
487 precisely quantify sexual advertisement effort by males. Several studies have manipulated resource
488 acquisition to investigate its effects on life history traits, with largely consistent results: males fed
489 higher-quality diets typically increase their calling effort with age, and longer-lived males call more
490 (Judge *et al.* 2008; Maklakov *et al.* 2008; Zajitschek *et al.* 2009, 2012; Houslay *et al.* 2015). One
491 exception is the study of Hunt et al. (Hunt *et al.* 2004a), in which males fed a high-protein diet called
492 earlier and far more intensely than those fed lower protein diets; high-protein diet males also
493 suffered survival costs such that they died earlier than low-protein diet males. This pattern of age-
494 related allocation may reflect status-dependent plasticity in allocation to reproduction and survival
495 in some cases (Kokko 1997, 1998; Höglund & Sheldon 1998; Vinogradov 1998). In particular, low-
496 condition males can benefit from suppressing signalling at early ages and investing in longevity and
497 sexual advertisement later in life (Kokko 1997). If this adaptive plasticity in investment applied to *G.*

498 *sigillatus*, males restricted to lower-nutrient diets should have allocated resources preferentially to
499 energy storage instead of early signalling.

500 Males fed lower nutrition diets in our study called less, and the correlation between allocation to
501 storage (individual change in SMI) and calling effort was negative during week 1 among males on
502 lower-quality diets (Table 2, Fig. 3). However, while diet-restricted males were less likely to call over
503 the first week (Table 1, Fig. 2(a)), this effect was not evident during week 2 (Table 4). If males on
504 low-quality diets had continued to show a depressed propensity to call, and had increased body
505 mass over this period, that would be more consistent with crickets suppressing advertisement in
506 favour of increased future investment. Instead, it appears more likely that variation in calling effort
507 was due simply to budget constraints: i.e., having less energy to allocate to signalling. The non-
508 adaptive explanation for this variation among males is given further credence by dietary nutrition
509 being a strong predictor of survival, with males fed lower-nutrient diets suffering reduced longevity.
510 The fact that a male's current signalling effort is primarily governed by his acquisition ability and
511 previous expenditure also supports previous assertions that energetic trade-offs provide a
512 mechanism for maintaining honesty on average in male behavioural display traits (Kokko 1997).

513 **VARIATION IN USAGE AND IMPORTANCE OF ENERGY STORAGE FORMS**

514 Increased resource acquisition from higher-nutrient diets enabled male crickets to allocate more
515 resources to storage after eclosion in the forms of greater lipid, glycogen, and carbohydrate content
516 (Table 2(b)). These appear to represent the major forms of energy stores; protein levels did not vary
517 over the three time points that these stores were measured, indicating that males seem to maintain
518 protein content rather than increase it (although the nutrient ratio in our diet treatment was heavily
519 in favour of carbohydrate rather than protein, the variation in total nutrient content would enable
520 individuals to differ in allocation if required). We hypothesised that 'future planning' would result in
521 low-acquisition males prioritising storage in the form of lipids; the positive effect of diet on this form
522 indicates that this was not the case. Our results further corroborate findings in other cricket species,

523 in which calling effort covaried with the ability to acquire, metabolise and mobilise these three
524 storage forms (Bertram *et al.* 2011; Thomson *et al.* 2014).

525 Males tended to lose scaled body mass (SMI) over week 2 (Table 5), and individual SMI change in this
526 period was associated with estimated changes in glycogen and carbohydrate reserves – both of
527 which are quick-release forms of energy. Absolute SMI at the end of that period was associated with
528 current lipid reserves. Together, these results suggest that glycogen and carbohydrate are more
529 freely expendable forms of energy, while lipids are more carefully conserved. Such variation in the
530 conservation of storage forms indicates that lipids differ from carbohydrate and glycogen in usage
531 and importance, and highlights the importance of estimating multiple metabolic reserves when
532 examining life-history trade offs. The patterns of change in individual body mass and energy reserves
533 over weeks one and two suggest that resource acquisition early in adulthood tended to be mobilised
534 for fuelling calling effort as soon as the social circumstances favour it.

535 **ACQUISITION CAN AFFECT COVARIANCES BETWEEN EXPENSIVE LIFE HISTORY TRAITS**

536 Variation in resource acquisition ability among individuals can lead to positive correlations between
537 life history traits, as predicted by Van Noordwijk and De Jong (1986) and often found in nature
538 (Jennions *et al.* 2001). Fig. 3 demonstrates clearly how such a correlation can arise when some males
539 have acquired a greater amount of resources and can then allocate to two competing traits.
540 Increased nutrient availability can mask any negative correlation between two traits because
541 individuals have more resources to allocate to both, as seen in the increasingly positive relationship
542 between calling effort and body mass when dietary nutrition increases. We found that the mean
543 change in body mass also increased with diet and with total calling effort, indicating that individuals
544 allocate more resources to both storage and current reproductive effort as acquisition increases.
545 These results have implications for how males are likely to sample their social environment through
546 calling effort: males probably call irregularly early in life, and the extent to which this activity affects
547 the accumulation of resources depends on nutrient intake. The accumulation of body mass with

548 increases in both diet and total calling effort may be due partly to those individuals on higher quality
549 diets having a greater resource intake, and also because of the smaller marginal costs of increased
550 advertisement to higher condition males, as predicted by models of sexual selection under
551 condition-dependence (Grafen 1990; Rowe & Houle 1996). These findings mirror interspecific (Judge
552 *et al.* 2008) and intraspecific (Hunt *et al.* 2004a) differences in the covariance between expensive
553 traits under contrasting conditions, although it is not clear the extent to which our results are related
554 to selection in the lab rather than in the wild. We hope to see more studies in more taxa that directly
555 assess the storage and use of multiple energy forms over time – particularly in the face of varying
556 resource acquisition regimes, and with varying reproductive opportunities.

557 **SOCIALLY MEDIATED PLASTICITY IN REPRODUCTIVE EFFORT**

558 Male decorated crickets responded strongly to female presence, with significant increases in both
559 the likelihood and the time spent calling. To date, most work on male responses to the social
560 environment in crickets have focused on adaptive plasticity for anticipating future conditions
561 (Kasumovic & Brooks 2011): manipulations of juveniles' perceived density and future competition
562 can affect adult life history traits (*T. oceanicus*, Bailey *et al.* 2010; *T. commodus*, Kasumovic *et al.*
563 2012a,b). Manipulations of the social environment in adult crickets have thus far been less common.
564 Callander *et al.* (2013) measured the calling effort of male Australian black field crickets (*T.*
565 *commodus*) that were either kept isolated or housed with a rival male after reaching maturity.
566 However, all males in that study were isolated for the measurement period itself, which might
567 explain the lack of behavioural plasticity across treatments (Callander *et al.* 2013). The extreme
568 phenotypic flexibility of behavioural traits means individuals can adjust trait expression rapidly in
569 response to social cues (Ghalambor, Angeloni & Carroll 2010; Bretman *et al.* 2011); indeed, female
570 presence has previously been shown to affect the frequency and timing of cricket calling (Simmons
571 1986; Burpee & Sakaluk 1993; although see Bertram, Orozco & Bellani 2004). Storage of resources in
572 'quick-release' form as sugars (carbohydrate and glycogen) may provide male crickets the flexibility

573 to signal more effectively in the presence of females, explaining the increased calling effort by males
574 on higher-quality diets during our female-access treatment period.

575 **HOW STRONG IS THE EVIDENCE FOR ADAPTIVE PLASTICITY IN AGE-SPECIFIC REPRODUCTIVE**
576 **EFFORT?**

577 An unresolved question from our study relates to the decrease in calling effort over the second week
578 due to greater previous exposure to females (Fig. 5). Early theoretical models concluded that
579 reproductive investment should increase with age (Williams 1966), but recent studies using game
580 theory and life history theory paint a more complex picture (Kokko 1997, 1998; Lindström *et al.*
581 2009). Kokko (1998) illustrated three phenomena that can prevent positive correlations between life
582 history traits: 1) trade-offs acting over lifetimes, such that fitness benefits accrued early in life
583 outweigh late life fitness (Hansen & Price 1995); 2) increasing marginal gains in fecundity could
584 favour decreased survival and intense sexual advertisement for high-quality males; and/or, 3)
585 suboptimal allocation. The last point is of particular interest: if individuals can plastically vary trait
586 expression in heterogeneous environments, and trait expression is under selection, shouldn't we
587 generally expect adaptive plasticity for continuous traits (Scheiner & Holt 2012)? One explanation for
588 suboptimal allocation is that the genetic and regulatory machinery required for controlling allocation
589 across traits and over time is expensive to maintain, and may not confer a sufficiently high selection
590 advantage over a simpler set of rules: spend resources if you have them, and if not, focus on
591 acquiring more resources instead. The differences we find in individuals that signal at high and low
592 levels early in life may be primarily determined by budget constraints, as opposed to adaptive
593 perception of future opportunities.

594

595 **AUTHOR CONTRIBUTIONS**

596 TMH, LFB and JH conceived the ideas and designed the experiment; JR advised on design and
597 created the artificial diets; TMH performed the experiment and collected the data; KFH performed
598 the energy storage estimation assays; TMH analysed the data; TMH, LFB and JH led the writing of the
599 manuscript. All authors contributed critically to manuscript drafts and gave final approval for
600 publication.

601

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609

610 **DATA ARCHIVING**

611 All data will be uploaded to Dryad upon acceptance of this manuscript.

612

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813 and flight capability in a wing-polymorphic cricket. *Proceedings of the National Academy of*
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816 **Figures**

817 Figure 1: A male *Gryllodes sigillatus* calls to a female (photograph by T. Houslay).

818 Figure 2: The effects of diet treatment (x-axis) and day of measurement (equivalent to male age
819 post-eclosion; modelled as a continuous variable and shown here as distinct panels) on male sexual
820 advertisement during the first week post-eclosion. (a) The likelihood of male calling, with fitted
821 regression line taken from coefficients from the zero-altered part of the daily calling analysis; (b) the
822 amount of calling effort (plotted on log-scale y-axis), given a male called, with fitted regression line
823 from the Poisson part of the daily calling analysis. The first day post-eclosion was excluded from the
824 analysis as no males called.

825 Figure 3: The relationship between total calling effort over the first week post-eclosion (log-
826 transformed) and the change in scaled mass index (SMI) during this period, plotted separately for
827 each diet treatment (note that diet was modelled as a continuous predictor). Lines are predicted
828 slopes from a linear regression model, and shaded areas represent 95% confidence intervals.

829 Figure 4: The partial effect of day of measurement (equivalent to male age post-eclosion) on male
830 sexual advertisement during week 2, plotted separately for whether a female was absent or present
831 on the day of measurement. (a) The likelihood of male calling, with fitted regression line taken from
832 coefficients from the zero-altered part of the daily calling analysis; (b) the amount of calling effort
833 (plotted on log-scale y-axis), given a male called, with fitted regression line from the Poisson part of
834 the daily calling analysis. Measurements from males fed 12% nutrition diet have been excluded.

835 Figure 5: 'Small multiples' show how the relationship between diet and daily calling effort changes as
836 a function of day and female access treatment. Each individual panel plots the predicted slope from
837 the Poisson part of our MCMCgIimm ZAP model of daily calling effort against dietary nutrition (24-
838 84%). Here we present a subset of panels, showing how the effect of diet on calling effort (plotted
839 on log-scale y-axis) changes from the first to last day of the female access treatment period (male

840 ages of 8 and 14 days post-eclosion, overall horizontal axis), among males that had either no access
841 to females (lower panels) or daily access to females (upper panels). See text for model details; Figure
842 S1 presents the complete set of panels for all combinations of day and female availability treatment.

843 Figure 6: Predicted quadratic slopes from a linear regression model show the effect of diet
844 treatment on the change in individual scaled mass index (SMI) over week 2, separately for each
845 female access treatment. All males on the lowest nutrition (12%) diet died before the end of the
846 week and were thus excluded; we also excluded males that cannibalised females. Shaded areas
847 represent 95% confidence intervals. Values for the change in SMI have been corrected for the effect
848 of regression to the mean.

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850

851 **Tables**

852 Table 1: MCMCglmm zero-altered Poisson (ZAP) analysis of male nightly calling effort over the first
 853 week post-eclosion. Day 1 was excluded from the analysis as no males called.

Fixed effects		Estimate	95% CI (lower, upper)	pMCMC
Likelihood of calling	(Intercept)	-5.636	(-5.926, -5.374)	<0.001
	Diet	0.187	(0.081, 0.297)	<0.001
	Day	0.420	(0.306, 0.540)	<0.001
	Day ²	-0.147	(-0.198, -0.088)	<0.001
	Diet × day	0.036	(-0.006, 0.082)	0.120
<hr/>				
Calling effort	(Intercept)	3.636	(3.391, 3.876)	<0.001
	Diet	0.183	(0.094, 0.276)	<0.001
	Day	0.191	(0.115, 0.265)	<0.001
	Day ²	-0.074	(-0.108, -0.042)	<0.001
	Diet × day	0.060	(0.033, 0.089)	<0.001
<hr/>				
Variance components		Estimate	95% CI (lower, upper)	
Likelihood of calling	ID	1.128	(1.009, 1.258)	
<hr/>				
Calling effort	ID	1.559	(1.190, 1.979)	
	Residual	5.000	(3.990, 6.086)	

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856 Table 2: Linear regression models showing the effect of diet over the first week post-eclosion on (a)
 857 individual changes in body mass, as scaled mass index (SMI), and (b) approximated changes in four
 858 different energy reserve forms. Values representing changes in carbohydrate, glycogen and lipid
 859 were log-transformed prior to analysis.

	Response	Predictor	df	t	Estimate \pm S.E.	<i>P</i>
a)	Δ SMI	Diet	1,536	13.97	0.0062 \pm 0.0004	<0.001
		Diet ²	1,536	-3.62	-0.0009 \pm 0.0002	<0.001
b)	Δ Carbohydrate	Diet	1,43	3.39	0.050 \pm 0.015	0.001
	Δ Glycogen	Diet	1,47	3.90	0.135 \pm 0.035	0.003
	Δ Lipid	Diet	1,49	2.67	0.075 \pm 0.028	0.010
	Δ Protein	Diet	1,48	0.53	0.100 \pm 0.189	0.597

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862 Table 3: Multiple regression showing how individual change in body condition over the first week of
 863 adulthood (SMI day 7 – SMI at eclosion) is affected by how much a male called over week 1 (log-
 864 transformed and standardised) and diet.

	t	Estimate ± S.E.	<i>P</i>
(Intercept)	16.34	0.0143 ± 0.0009	<0.001
Log week 1 total calling effort	1.80	0.0016 ± 0.0009	0.073
Diet	12.87	0.0058 ± 0.0004	<0.001
865 Log week 1 total calling effort × diet	2.88	0.0013 ± 0.0004	0.004

866

867 Table 4: MCMCgImm zero-altered Poisson (ZAP) analysis of male nightly calling over the second
 868 week post-eclosion. Males fed the 12% nutrition diet were excluded as they all died prior to the end
 869 of the week. Also excluded were males that cannibalised a female during the female-access
 870 treatments.

Fixed effects		Estimate	95% CI (lower, upper)	pMCMC
Likelihood of calling	(Intercept)	-4.617	(-5.034, -4.179)	<0.001
	Female presence	3.007	(2.491, 3.564)	<0.001
	Diet	0.031	(-0.149, 0.196)	0.732
	Day	-0.120	(-0.244, -0.005)	0.058
	Prior female access	-0.647	(-0.871, -0.429)	<0.001
	Female presence × day	0.779	(0.566, 1.001)	<0.001
	Prior female access × diet	0.055	(-0.018, 0.144)	0.185
	Prior female access × day	0.014	(-0.041, 0.067)	0.607
	Prior female access × diet × day	0.017	(-0.010, 0.044)	0.223
Calling effort	(Intercept)	4.065	(3.717, 4.381)	<0.001
	Female presence	0.742	(0.498, 0.971)	<0.001
	Diet	0.385	(0.281, 0.489)	<0.001
	Day	-0.195	(-0.264, -0.130)	<0.001
	Prior female access	-0.080	(-0.214, 0.058)	0.247
	Female presence × day	-0.210	(-0.335, -0.082)	0.001
	Prior female access × diet	0.024	(-0.012, 0.058)	0.191
	Prior female access × day	0.054	(0.028, 0.079)	<0.001
	Prior female access × diet × day	-0.020	(-0.032, -0.007)	<0.001
Variance components		Estimate	95% CI (lower, upper)	
Likelihood of calling	ID	5.365	(3.982, 6.876)	
Calling effort	ID	2.108	(1.694, 2.553)	
	Residual	1.283	(1.183, 1.394)	

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874 Table 5: Simplified multiple regression model showing factors affecting individual change in scaled
 875 body mass over the second week of adulthood (SMI day 14 – SMI day 7, corrected for the effect of
 876 regression to the mean). Males that cannibalised a female during this period were excluded from the
 877 analysis.

878

	t	Estimate ± S.E.	<i>P</i>
(Intercept)	1.34	0.0019 ± 0.0014	0.182
Diet	3.5	0.0031 ± 0.0008	<0.001
Female-access	0.09	0.0001 ± 0.0003	0.927
Diet ²	-3.72	-0.0011 ± 0.0003	<0.001
879 Diet × Female-access	-2.16	-0.0004 ± 0.0002	0.032

880

881 **Supporting information**

882 Appendix S1: Specifications for the creation of artificial diets.

883 Appendix S2: Details of methods used for estimating energy storage components.

884 Appendix S3: MCMCglmm Zero-Altered Poisson (ZAP) model specification for the analysis of daily
885 calling effort.

886 Figure S1: The effect of diet on calling effort as a function of day and female-access treatment.

887 Figure S2: The effects of diet and female access on the likelihood of death during female-access
888 period.

889 Figure S3: The effects of diet and female access on male lifespan.

890

Figure 1



Figure 2

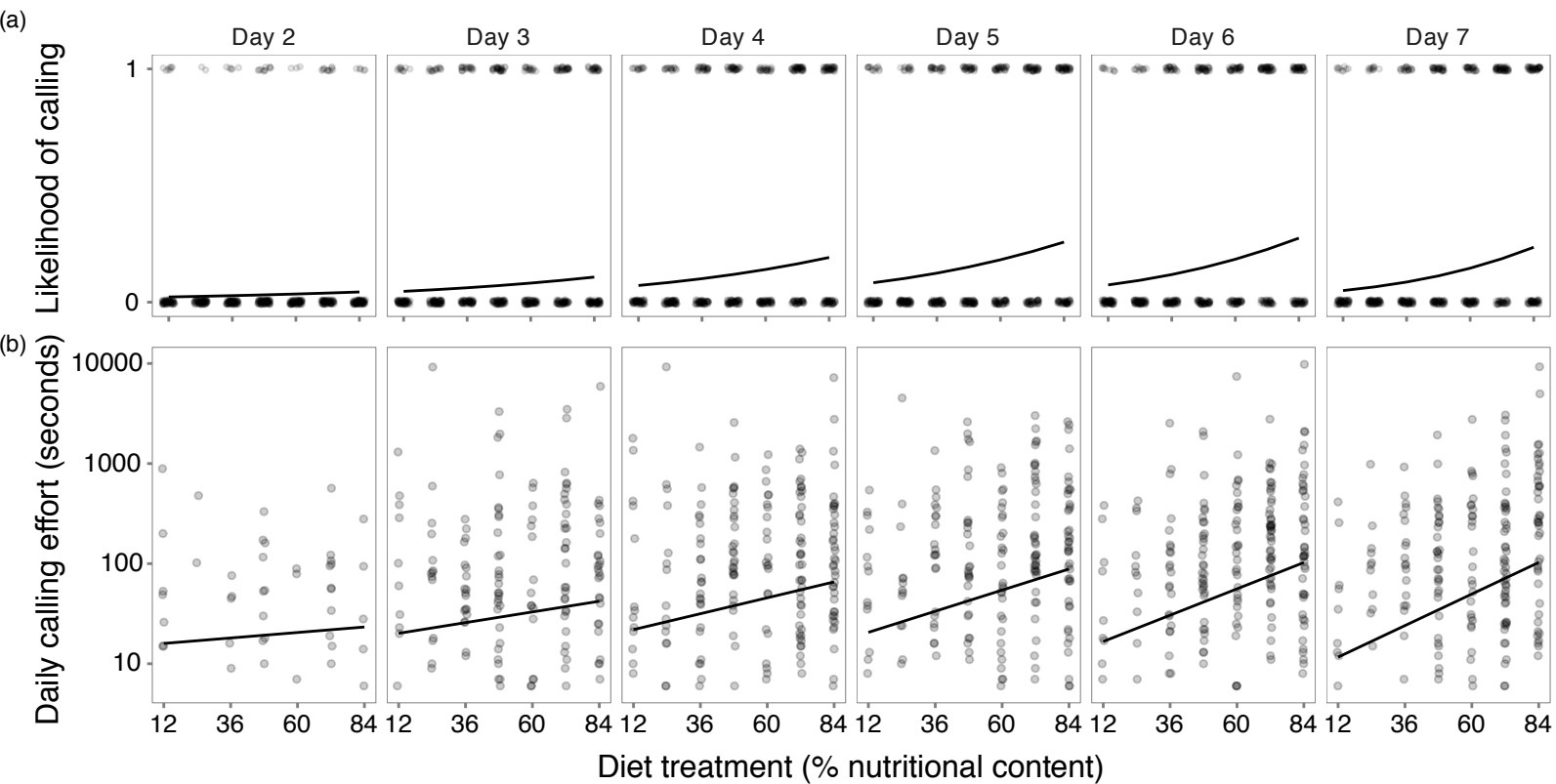


Figure 3

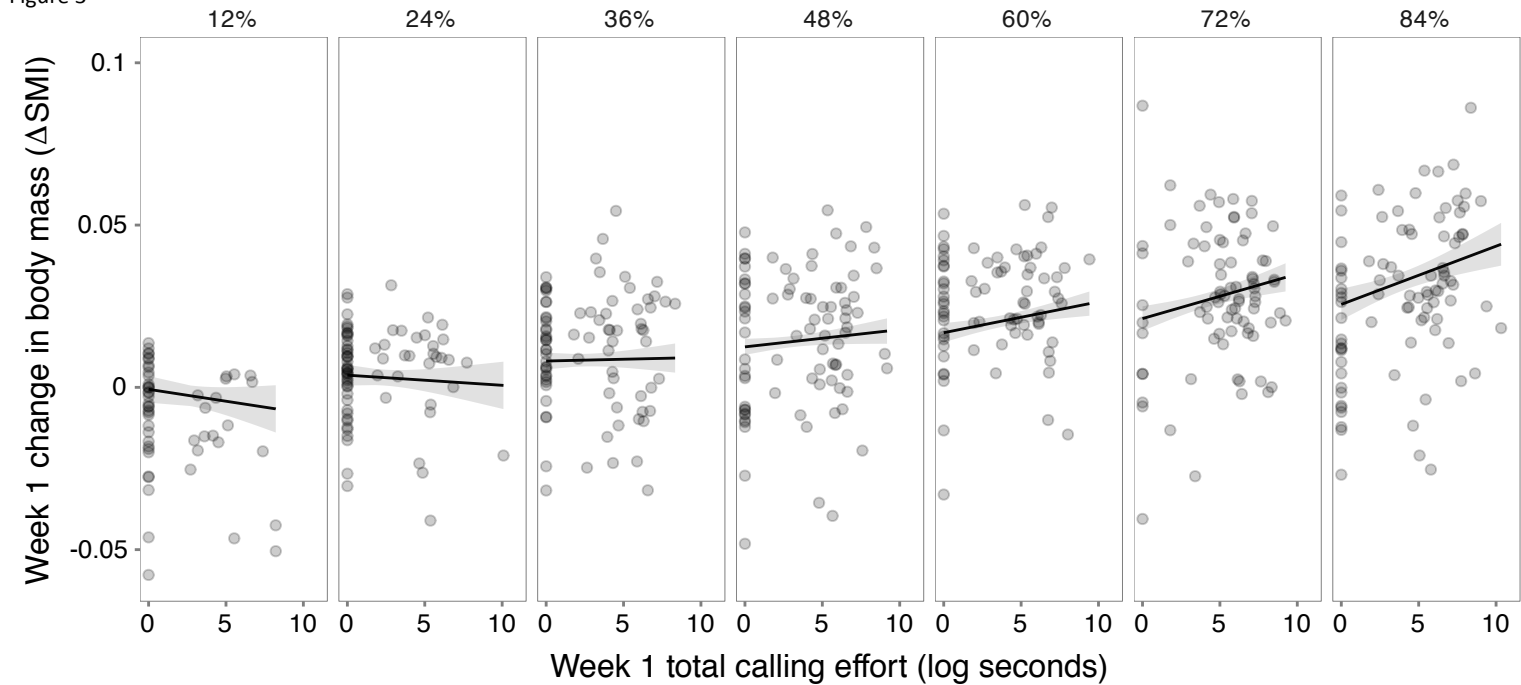


Figure 4

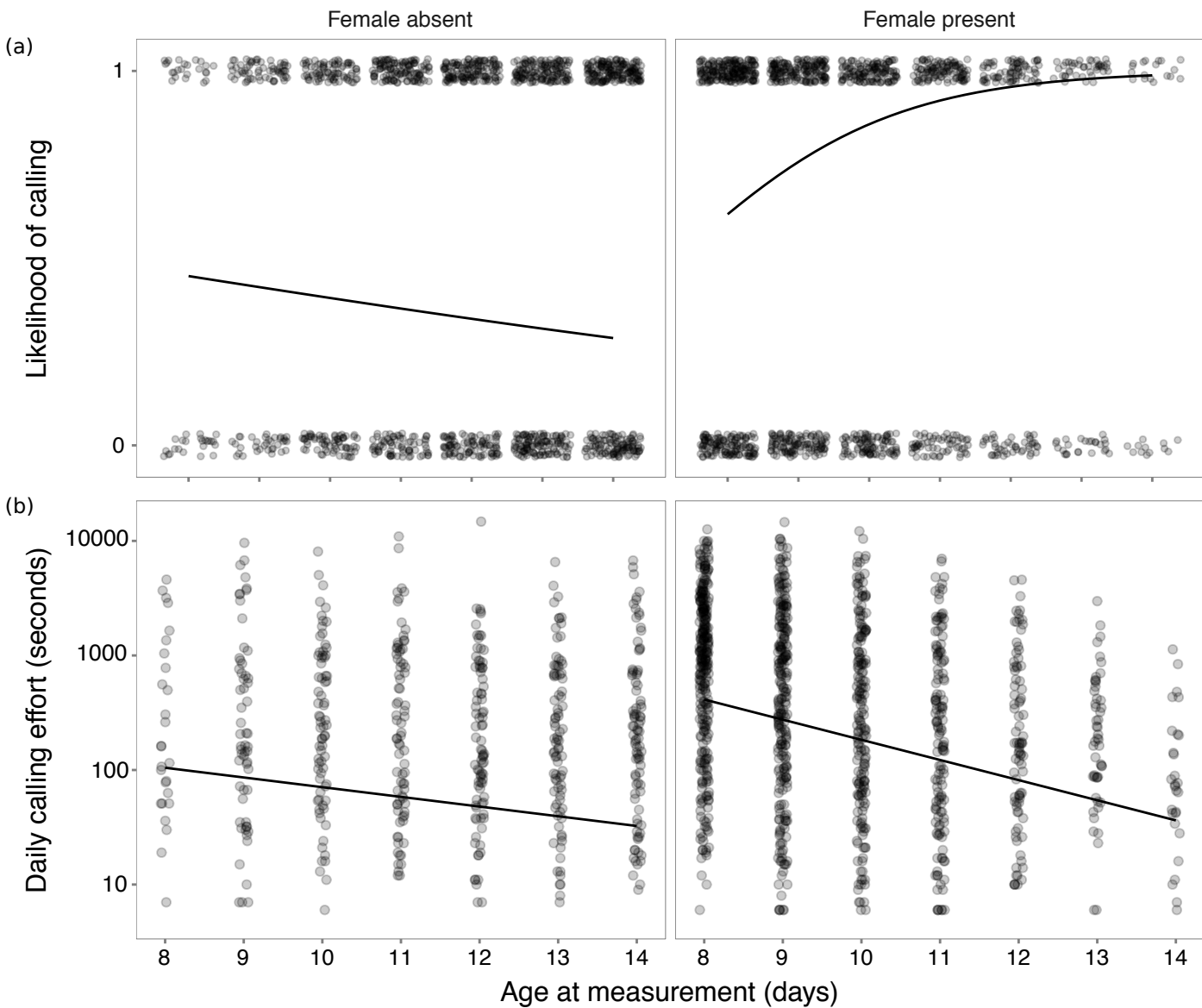


Figure 5

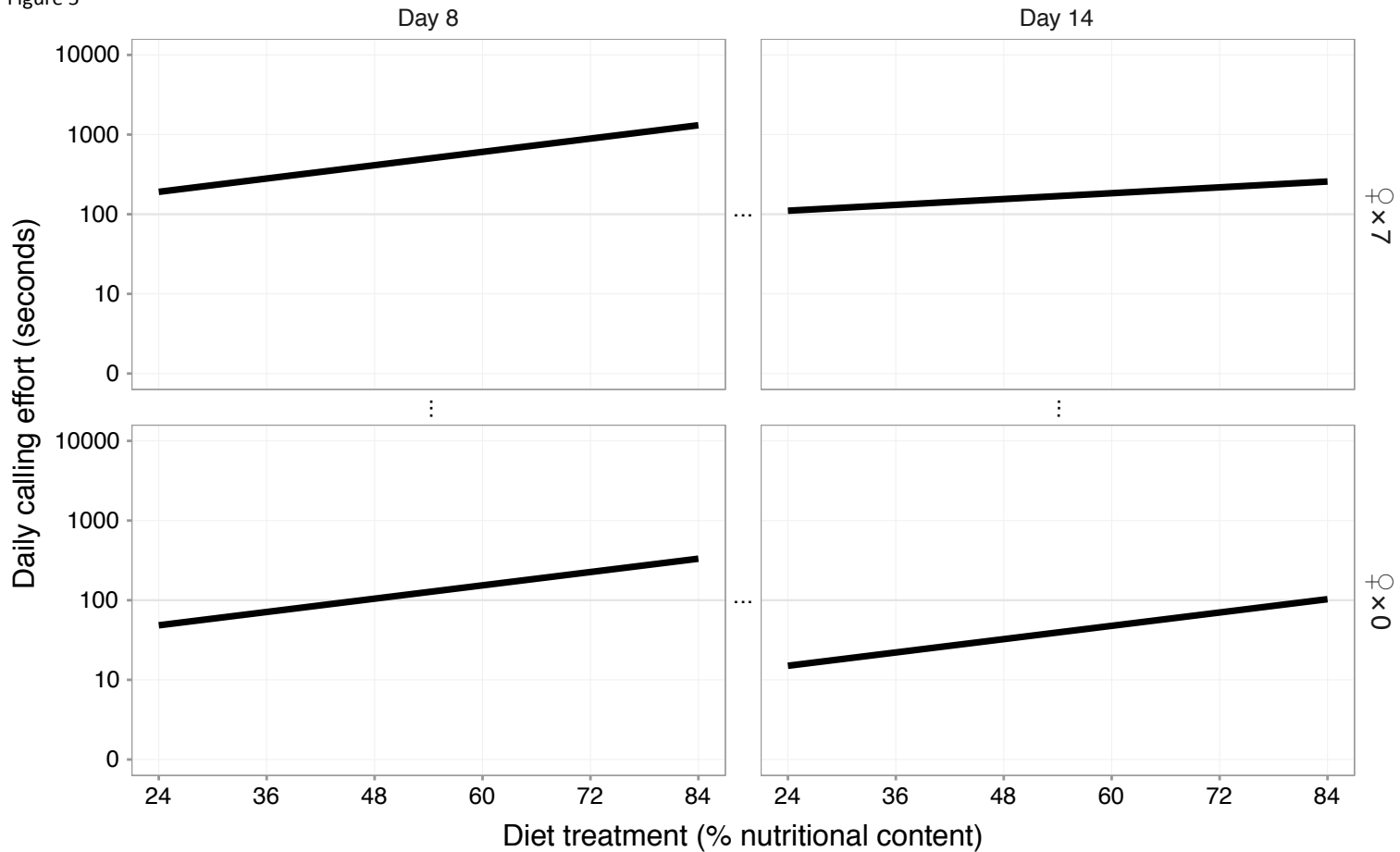


Figure 6

