

# Condition Dependence of Male Lifespan and Calling Effort in a Field Cricket

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1 **Condition dependence of male lifespan and calling effort in a field cricket**

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28

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30

31 **Abstract**

32 Sexually selected traits are thought to impose survival costs on showy males. Recent empirical work  
33 found a negative relationship between male display and survival in a field cricket species (Orthoptera,  
34 Gryllidae, Gryllinae) where there is no evidence of a mating bias towards older males. In most species,  
35 however, male survival and ornamentation are positively correlated, and older males often have a mating  
36 success advantage over younger males. These findings suggest that male quality and survival are  
37 positively correlated, but more tests of this hypothesis are needed. We measured the condition  
38 dependence of male survival and mating investment (calling effort) in another grylline, *Gryllus*  
39 *pennsylvanicus*, where older males have previously been shown to have greater mating success. We  
40 varied condition by manipulating diet, and measured male lifespan and calling effort to assess the relative  
41 condition dependence of these traits. High and medium condition males survived longer than low  
42 condition males, and high condition males called more than medium and low condition males.  
43 Differences in calling effort among the condition treatments were not apparent early in life, but emerged  
44 as males aged. We discuss possible explanations for the differences between our study and contrasting  
45 results such as the previous grylline work.

46

## 47 **Introduction**

48 Darwin initially proposed the theory of sexual selection to account for male traits, like the peacock's  
49 tail, that appeared to reduce survival (Darwin 1871). He proposed that the survival cost of these  
50 extravagant male traits was compensated by the advantages that their bearers gained in mating success  
51 (Darwin 1871). Contemporaries of Darwin, including Wallace, doubted that an adaptation could ever  
52 evolve that would reduce the survival of its bearer. Wallace proposed instead that only the most vigorous  
53 and fit males could develop extravagant traits and thus the most elaborated males would also survive the  
54 longest (Cronin 1991). Darwin's hypothesis was elegantly validated in theory by Fisher (1915, 1930),  
55 who showed how a male trait could evolve past its natural selection optimum, as long as females  
56 preferred males with elaborate traits, and both preference and trait became genetically correlated in future  
57 generations. Empirical findings of a negative relationship between male ornamentation and survival are  
58 thus often taken as evidence of the Darwin-Fisher process (e.g. Brooks 2000). Wallace's view that male  
59 ornamentation and survival should be positively correlated has been supported by empirical research –  
60 most studies report that males with the most elaborate ornaments also survive longest (meta-analysis by  
61 Jennions et al. 2001). Moreover, it is often concluded that older males have an advantage in mating  
62 success (e.g. Robel 1967; Zuk 1987b, 1988; Connor 1989; Simmons and Zuk 1992; Simmons 1995;  
63 Dickinson 2001; but see Jones et al. 2000; reviewed in Brooks and Kemp 2001), suggesting that male  
64 survival may be positively correlated with male quality. However, as several authors have pointed out,  
65 indicator mechanisms like the handicap hypothesis (Zahavi 1975, 1977) do not require that ornaments and  
66 survival be correlated, only that ornaments be correlated with male quality (Grafen 1990; Getty 1998;  
67 Kokko et al. 2002; Getty 2006). Thus, for any individual species, the direction of the  
68 survival/ornamentation correlation is likely determined by details of its life history.

69 One of the hallmarks of life history theory is the assumption that individuals are faced with decisions  
70 on how to allocate resources among competing life history traits (Stearns 1992). Whether these trade-offs  
71 (e.g. survival versus ornamentation) manifest themselves at the level of the population is determined by

72 the relative variation in allocation versus acquisition of resources (van Noordwijk and de Jong 1986;  
73 Grafen 1990). For instance, if males vary widely in the rules that they use to allocate resources to either  
74 survival or ornaments, but don't vary much in how many resources they have to allocate, then the  
75 relationship will tend to be negative. On the other hand, if males vary widely in their acquisition of  
76 resources, but have similar allocation rules, then it will tend to be positive (van Noordwijk and de Jong  
77 1986). By varying the amount of resources available to males (i.e. manipulating acquisition), we may be  
78 able to reveal a trade-off between survival and ornamentation (e.g. Hunt et al. 2004), and with some  
79 caution, be able to infer which life history trait is more important in determining male fitness.

80 The resource pool that an individual has available to allocate to competing life history traits has been  
81 referred to as condition (Rowe and Houle 1996). Fitness-determining traits, i.e. those under directional  
82 selection such as male ornaments, are predicted to be condition-dependent, that is, trait development is  
83 expected to vary positively with the acquisition of condition (e.g. Andersson 1982; Nur and Hasson  
84 1984). Of the few studies that have examined the condition dependence of male ornaments  
85 experimentally (reviewed in Cotton et al. 2004), even fewer have manipulated condition and examined its  
86 effects on both male lifespan and level of male sexual traits. Male *Hygrolycosa rubrofasciata* wolf spiders  
87 fed *ad libitum* signaled (drummed their abdomens) at a higher rate than food-restricted males, and males  
88 fed *ad libitum* increased their signaling rate more than food-restricted males when in the presence of a  
89 female. In addition, as diet quality increased, so too did male survival, and there was a significant but  
90 weak positive correlation between signaling rate and survival (Kotiaho 2000). Similarly, male three-  
91 spined sticklebacks, *Gasterosteus aculeatus*, fed a diet high in carotenoids had greater red nuptial  
92 colouration and survived longer than males fed a diet low in carotenoids (Pike et al. 2007). In contrast, in  
93 the black field cricket, *Teleogryllus commodus*, males reared on a high quality diet signaled (produced  
94 calling song) at a higher rate, but died younger than males reared on a low quality diet, who signaled at a  
95 lower rate. The within treatment relationship between signaling and survival varied among diet  
96 treatments, being negative for high and medium condition males, but positive for low condition males  
97 (Hunt et al. 2004). Likewise, male ambush bugs, *Phymata americana*, fed a higher quantity of prey had

98 greater lateral colouration, but tended to have higher mortality than males fed a lower quantity of prey  
99 (Punzalan et al. in prep.). In each taxon, the male secondary sexual character is under directional positive  
100 sexual selection, either through female preferences as in the spider (Parri et al. 1997), stickleback (e.g.  
101 Bakker 1993) and cricket (Hunt et al. 2004), or through competitive advantage as in the bug (Punzalan et  
102 al. in review). However, it is not known in these organisms whether older males have higher mating  
103 success, as is the case in many other species (reviewed in Brooks and Kemp 2001).

104 We investigated the condition dependence of male lifespan and calling effort in another grylline, the  
105 fall field cricket, *G. pennsylvanicus*, a species in which older males are more attractive to females than  
106 younger males (Zuk 1987b, 1988). Female gryllines are attracted to greater calling effort (Cade and Cade  
107 1992; Crnokrak and Roff 1995, 1998a,b; Hunt et al. 2004), and males fed higher quantity or quality diets  
108 put more effort into calling (Crnokrak and Roff 1998a; Wagner and Hoback 1999; Holzer et al. 2003;  
109 Scheuber et al. 2003a,b; Hunt et al. 2004). We therefore reared individuals on high, medium and low  
110 quality diets from hatching until death, and measured the calling effort of males throughout their entire  
111 lifespan. The purpose of our study was to test whether male lifespan and/or calling effort are condition  
112 dependent, and measure the correlation between these two male traits. Because male survival and calling  
113 effort are both correlated with male fitness (Zuk 1987b, 1988; Ting et al. submitted), we do not predict a  
114 negative relationship between survival and calling effort. Additionally, the pattern of allocation to these  
115 two competing life history traits may suggest the optimal way in which males increase their fitness.

116

117

## 118 **Methods**

### 119 *Study Species*

120 *G. pennsylvanicus* is univoltine and widely distributed across the eastern half of North America  
121 (Walker and Moore 2007). Adults breed in late summer until the autumn's first severe frost, and the eggs  
122 overwinter and hatch in the spring (Alexander 1968). All individuals were second-generation offspring of

123 wild animals captured in the summer of 2004 from the grounds of the University of Toronto at  
124 Mississauga (43°32'50.51"N, 79°39'37.80"W).

125

### 126 *Nymph Husbandry*

127 At hatching, we isolated individuals in separate containers (9 cm diameter) with their own food (one  
128 of three diets, see below), cotton-plugged water vial, and egg carton shelter. Over the course of six weeks  
129 we isolated 1566 hatchlings and assigned each to one of three diet treatments. All crickets were housed in  
130 an environmental chamber that maintained 12 hours light: 12 hours dark, 25°C and 70% relative  
131 humidity. We replaced food and water once a week, and the cardboard shelter and container every four  
132 weeks. After six weeks of development, nymphs were checked daily for the presence of newly moulted  
133 adults. No cricket moulted to adulthood before six weeks.

134

### 135 *Condition Manipulation*

136 We haphazardly assigned hatchlings to one of three experimental diets composed of different  
137 proportions of: 1) rabbit food (Martin “Little Friends” Rabbit Food;  
138 <http://www.martinmills.com/littleRabbit.htm>), and 2) white bran, which are known to be of high and low  
139 quality respectively (KAJ unpubl. data). The three diets were as follows: high quality (90% rabbit food:  
140 10% bran), medium quality (50% rabbit food: 50% bran), and low quality (10% rabbit food: 90% bran).  
141 Rabbit food and bran were ground up and passed through a 1 mm mesh sieve, combined in the above  
142 ratios based on weight, and mixed in a blender. For the first two weeks of life we gave nymphs the ground  
143 and blended food that they could easily ingest (presented on a small section of egg carton). After two  
144 weeks, all individuals were given the hard pellet form. Pellets were formed by mixing each diet with  
145 water until it was a viscous paste, which was then spread onto a Plexiglas sheet into which many uniform  
146 1 cm-diameter holes had been drilled (see Hunt et al. 2004). We placed these molds containing the diet



147 pastes into a 55°C drying oven for 24 hours, after which the food pellets could be removed. This  
148 technique resulted in food pellets that were highly consistent in size (KAJ unpubl. data).

149

### 150 ***Adult Husbandry***

151 Newly moulted adults were weighed and given new food, water, egg carton shelter and container on  
152 the day following their moult to adulthood (i.e. one day old) to prevent handling injuries when their  
153 exoskeleton had not fully hardened. We changed food and water, and cleaned the containers of all adults  
154 every five days thereafter (i.e. 6, 11, 16, etc.) until death. Males were weighed every five days until death  
155 to assess the relationship between calling effort and body mass throughout life, whereas females were  
156 weighed every five days up to a maximum of 31 days old to investigate the effect of the diet  
157 manipulation. We did not mate females unlike the previous experiment on *T. commodus* (see Hunt et al.  
158 2005). Every day, we checked all adults. Date of death was noted and all dead crickets were preserved in  
159 70% ethanol for morphological measurement.

160

### 161 ***Measurement of Calling Effort***

162 Starting at six days post-adult moult, when most male *G. pennsylvanicus* have reached sexual  
163 maturity (Cade and Wyatt 1984), males had their calling effort measured every five days until death. We  
164 measured calling effort using microcassette recorders with auto voice record (AVR) (General Electric  
165 model 3-5377). Each recorder came with a small lapel microphone that we suspended from the inside lid  
166 of a Styrofoam box (interior dimensions: 17 cm wide, 21.5 cm long, 16 cm high). During calling effort  
167 measurement, the lid of each male's individual container was replaced with a lid with a mesh screen  
168 window to afford better acoustic access to his song. We placed the male's container inside the Styrofoam  
169 box so that the lapel microphone was suspended approximately 1 cm above the mesh screen. Males were  
170 left for 15 minutes to acclimate to the Styrofoam box before recording was started using the automatic

171 voice record (AVR) function. AVR turned on the recording when the microphone detected sound and shut  
172 off the recording following approximately six seconds of silence. Thus, recording occurred only when  
173 males called continuously (i.e. in a sample of males recorded in the field, the maximum interchirp interval  
174 was less than 0.7 s during bouts of calling song; KAJ unpubl. data) and stopped when there was a  
175 sustained break in singing. Because the maximum duration of our microcassette tapes was 90 min, we  
176 halted all recorders after 90 min and then used the tape counter to determine how much time the recorder  
177 had been turned on. We then calculated a male's calling effort as a percentage of 90 minutes.

178 All recorders were checked during the 15-minute acclimation period before each trial to ensure that  
179 they did not turn on when the male was not singing. In addition, our recorders were sensitive to an  
180 artificial chirp with a carrier frequency of 5000 Hz (mean carrier frequency of lab-reared individuals from  
181 this population, KAJ unpubl. data) broadcast at a sound pressure level of  $69.4 \pm 0.4$  dB (mean  $\pm$  SE, N =  
182 22, re 20  $\mu$ Pa, measured with a Radio Shack<sup>®</sup> digital sound level meter, model 33-2055). This is below  
183 the average amplitude of male calling song in this population (KAJ pers. obs.) indicating that the  
184 recorders were sufficiently sensitive to male song. However, during the 15-minute acclimation period, if  
185 we noticed that a male was singing without the recorder turning on, we increased the gain on his recorder  
186 to reduce the threshold sensitivity until the recorder turned on when the male sang. The proportion of  
187 males that had the gain adjusted at least once did not differ among the diet treatments (low: 52/170,  
188 medium: 46/187, high: 44/190; chi-squared contingency analysis:  $\chi^2 = 2.85$ , df = 2, p = 0.241).

189 We had enough recorders to measure the calling effort of 22 males simultaneously. However, due to  
190 a combination of high juvenile and adult survival (see below) and large sample sizes, we had more than  
191 22 males to measure on many days. Consequently, we often had to conduct multiple runs of the recorder  
192 array in one day. When we did so, we selected a random sample of males for each run of the array. The  
193 median start time for calling effort measurements was 9:06 pm (N = 5203, interquartile range = 7:06 -  
194 11:18 pm). Although calling in crickets is known to change with the time of day (Alexander 1968), we  
195 did not correct our measurements of calling effort for time of day because Julian time of day explained

196 only 6% of the variation in male calling effort (cubic regression: adjusted  $R^2 = 0.059$ ,  $p < 0.001$ ) and  
197 corrected calling effort measurements gave the same results as uncorrected values (KAJ unpubl. data).

198 In addition to the condition dependence of calling effort, past experiments have also examined  
199 dietary effects on carrier frequency (e.g. Hunt et al. 2004). For logistical reasons we were unable to  
200 measure other features of *G. pennsylvanicus* calling song.

201

## 202 ***Morphological Measurement***

203 Using the program NIH Image (Version 1.62 for Macintosh), we measured pronotum length on all  
204 crickets to the nearest 0.01 mm. Pronotum length is a good overall measure of body size in *G.*  
205 *pennsylvanicus* (KAJ unpubl. data).

206

## 207 ***Statistical Analysis***

208 Our data for male calling effort were highly right-skewed, with the mode of our 5203 measurements  
209 lying at the smallest value. As a result, we calculated a median (as opposed to average) for each male as a  
210 measure of his daily investment in calling effort. Although we were able to transform these data to  
211 approximate a normal distribution ( $[\arcsine(\text{calling effort})^{(1/2)}]^{(1/3)}$ ), for reasons of clarity we choose to  
212 present more conservative non-parametric rather than parametric analyses (in all but one analysis, see  
213 below). In all cases the non-parametric and parametric analyses detected the same effects, but  
214 interpretation of the response variable is less complicated in the non-parametric analyses.

215 We conducted all statistical analyses using SPSS 10 for Windows. All tests are two-tailed and have  
216 an *a priori* Type I error rate of 5%.

217

218

## 219 **Results**

### 220 *Survivorship and Body Size*

221 Of the initial 522 hatchlings isolated for each diet, 346 low, 376 medium and 383 high condition  
222 individuals survived to reach adulthood (total = 1105). We used Kaplan-Meier survival analysis to test for  
223 an effect of diet on survival to adulthood since the Cox regression assumption of proportionality of  
224 hazards (effect of the predictor is constant over time) was violated. Although there was a trend for  
225 individuals reared on the low quality diet to be more likely to die before reaching adulthood, this was not  
226 statistically significant (Log Rank test statistic = 4.96, df = 2, p = 0.084).

227 The adult sex ratio showed a male-biased trend for all three diets, with 178 males: 168 females, 195  
228 males: 181 females and 198 males: 184 females for the low, medium and high quality diets respectively  
229 (there was one intersex individual [Johnstone 1975] in the high quality diet). Diet had no significant effect  
230 on the sex ratio at the adult moult (Heterogeneity Chi-square [Zar 1996]:  $\chi^2 = 0.015$ , df = 2, p = 0.993),  
231 and the pooled sex ratio did not differ significantly from an equal ratio of males to females ( $\chi^2 = 1.308$ , df  
232 = 1, p = 0.253).

233 Both diet quality and sex had significant effects on adult body size (Diet Quality:  $F_{2, 1092} = 36.601$ , p  
234 < 0.001; Sex:  $F_{1, 1092} = 617.470$ , p < 0.001; Diet \* Sex:  $F_{2, 1092} = 0.113$ , p = 0.893). Crickets reared on the  
235 high and medium quality diets did not differ (Tukey HSD: p = 0.135), but had larger pronotum lengths  
236 than crickets reared on the low quality diet (Tukey HSD: both p < 0.001) (Fig. 1). Females were larger  
237 than males (Tukey HSD: p < 0.001) (Fig. 1).

238 There was a significant interaction between diet quality and sex in the amount of mass gained early  
239 in life (Diet \* Sex: Days 1 to 6 post adult eclosion:  $F_{2, 1034} = 16.819$ , p < 0.001) so we analyzed the sexes  
240 separately. Males reared on the different diets did not differ in the amount of mass gained between days 1  
241 and 6 post adult eclosion ( $F_{2, 535} = 1.763$ , p = 0.172), whereas females did ( $F_{2, 499} = 24.304$ , p < 0.001).  
242 Females reared on the high quality diet gained more mass than females on both the medium and low  
243 quality diets (high: mean + SE = 113 ± 4 mg; medium: mean + SE = 94 ± 4 mg; low: mean + SE = 73 ± 3

244 mg; Tukey HSD<sub>high vs medium</sub>:  $p = 0.001$ ; Tukey HSD<sub>high vs low</sub>:  $p < 0.001$ ), and females reared on the medium  
245 quality diet gained more weight than females on the low quality diet (Tukey HSD<sub>medium vs low</sub>:  $p = 0.001$ ).

246 Diet quality, sex and their interaction were entered as categorical covariates in a Cox regression to  
247 test for the effect of diet quality and sex on adult survival. The Diet \* Sex interaction was not significant  
248 (Wald = 4.246, df = 2,  $p = 0.120$ ) so the interaction term was removed and the data reanalyzed. Diet  
249 quality had a significant effect on adult survival (Wald = 345.757, df = 2,  $p < 0.001$ ). Crickets raised on  
250 the high and medium quality diets lived longer than crickets raised on the low quality diet (Wald<sub>high vs low</sub> =  
251 276.031, df = 1,  $p < 0.001$ ; Wald<sub>medium vs low</sub> = 267.787, df = 1,  $p < 0.001$ ), but did not differ from each  
252 other (Wald<sub>high vs medium</sub> = 0.032, df = 1,  $p = 0.858$ ) (Fig. 2). And males lived slightly longer than females  
253 (Wald<sub>males vs females</sub> = 5.248, df = 1,  $p = 0.022$ ) (Fig. 2).

254 *G. pennsylvanicus* in our experiment lived longer than the oldest individuals found in a wild  
255 population (20 days, Zuk 1987a). However, this difference likely does not affect the interpretation of our  
256 results for three reasons. First, differences among our three diet treatments in adult survival were  
257 significant even if we only consider mortality up to 20 days post-adult moult, and longer-lived individuals  
258 are treated as right-censored data (results not shown). Second, treatment differences in daily calling effort  
259 were significant at 11 days post-adult moult (see Fig. 4 below), which is within the age range found in the  
260 wild (Zuk 1987a). Thirdly, 20 days may be an underestimate for the maximum age of *G. pennsylvanicus*  
261 in the wild, due to the error inherent in estimating age using daily growth rings in insect cuticle (see Fig. 1  
262 in Zuk 1987a).

263

## 264 ***Calling Effort***

265 Diet affected a male's daily calling effort (Kruskal-Wallis:  $\chi^2 = 29.149$ , df = 2,  $p < 0.001$ ). High  
266 condition males called more per day than both low (Mann-Whitney U = 11016.5,  $p < 0.001$ ) and medium  
267 condition males (Mann-Whitney U = 13699.0,  $p < 0.001$ ), which did not differ from one another (Mann-  
268 Whitney U = 14634.0,  $p = 0.195$ ) (median calling effort [interquartile range]: high = 14.5% [2.4 –

269 40.1%], medium = 6.7% [1.1 – 24.9%], low = 4.8% [1.0 – 16.9%]). Combined with the differences in  
270 adult lifespan between the diet treatments (see above), these daily effort differences resulted in a strong  
271 effect of diet on lifetime calling effort (lifetime effort = [median daily calling effort] \* [lifespan];  
272 Kruskal-Wallis:  $\chi^2 = 52.056$ ,  $df = 2$ ,  $p < 0.001$ ). High condition males had higher lifetime calling effort  
273 than medium (Mann-Whitney  $U = 13901.5$ ,  $p < 0.001$ ) and low condition males (Mann-Whitney  $U =$   
274  $8954.5$ ,  $p < 0.001$ ), and medium condition males had greater lifetime calling effort than low condition  
275 males (Mann-Whitney  $U = 12536.0$ ,  $p < 0.001$ ) (median lifetime calling effort [interquartile range]: high =  
276 9.17 days [1.28 – 22.72 days], medium = 3.48 days [0.66 – 13.94 days], low = 1.55 days [0.37 – 6.82  
277 days]).

278

### 279 *Age-dependent Calling Effort*

280 Given that diet had an effect on adult lifespan, we tested whether it also had an effect on how males  
281 invested in calling effort throughout their lives. To do this, we considered only three calling effort  
282 measurements from each male: the first (at six days post-adult eclosion) and last (within 5 days of death)  
283 measurements, as well as one measurement from the mid-point of each male's adult lifespan (i.e. the  
284 measurement closest [ $\pm 3$  days] in time to the exact halfway point in the male's adult lifespan). These  
285 measurements were classified as early, late and middle life calling effort, respectively. This procedure  
286 eliminated any differences amongst the three diet treatments in lifespan, and allowed us to examine  
287 calling effort differences as the crickets aged, without the complicating factor of dwindling sample sizes.  
288 We detected no significant effect of diet on calling effort in early life (Kruskal-Wallis:  $\chi^2 = 1.395$ ,  $df = 2$ ,  
289  $p = 0.498$ ) (Fig. 3). However, diet had an effect on calling effort at both middle life (Kruskal-Wallis:  $\chi^2 =$   
290  $15.284$ ,  $df = 2$ ,  $p < 0.001$ ) and late life (Kruskal-Wallis:  $\chi^2 = 14.473$ ,  $df = 2$ ,  $p = 0.001$ ). At both life  
291 stages, high condition males called more than both medium (Mann-Whitney  $U_{\text{middle life}} = 14772$ ,  $p = 0.012$ ;  
292 Mann-Whitney  $U_{\text{late life}} = 14992$ ,  $p = 0.020$ ) and low condition males (Mann-Whitney  $U_{\text{middle life}} = 11598.5$ ,  
293  $p < 0.001$ ; Mann-Whitney  $U_{\text{late life}} = 11682$ ,  $p < 0.001$ ) (Fig. 3). Medium condition males did not call for a

294 significantly greater proportion of time than low condition males at either middle life (Mann-Whitney U =  
295 13541.5,  $p = 0.169$ ) or late life (Mann-Whitney U = 13470.5,  $p = 0.143$ ) (Fig. 3). We also compared  
296 calling effort amongst life stages within diet treatments using nonparametric Friedman tests. Calling effort  
297 significantly changed throughout the lives of males on all three diets (low quality:  $\chi^2 = 45.138$ ,  $df = 2$ ,  $p <$   
298  $0.001$ ; medium:  $\chi^2 = 45.441$ ,  $df = 2$ ,  $p < 0.001$ ; high:  $\chi^2 = 33.959$ ,  $df = 2$ ,  $p < 0.001$ ; Fig. 3). For all three  
299 diets, early calling effort did not differ from mid-life calling effort (all  $p > 0.240$ ), but calling effort  
300 significantly declined in late life (mid-life vs late life: low:  $\chi^2 = 30.716$ ,  $df = 1$ ,  $p < 0.001$ ; medium:  $\chi^2 =$   
301  $41.286$ ,  $df = 1$ ,  $p < 0.001$ ; high:  $\chi^2 = 31.077$ ,  $df = 1$ ,  $p < 0.001$ ; Fig. 3).

302 These patterns were echoed in examinations of change in calling effort with age for the three diets.  
303 However, due to declining sample sizes with advancing age, we were unable to analyze this dataset using  
304 repeated measures. Instead, we tested whether males reared on the three diets differed in their calling  
305 effort as they aged by conducting Kruskal-Wallis tests at each age until numbers declined to 90% of the  
306 initial sample size for each treatment (after which values fluctuated due to small sample sizes). These  
307 were followed by post-hoc Mann-Whitney tests comparing each pair of diets. The overall result of these  
308 tests indicate that high condition males were able to sustain greater calling effort for longer periods than  
309 medium condition males, who in turn sustained greater calling than low condition males (Fig. 4).

310 Because our calling effort recorders were sometimes triggered by external noise, when noting calling  
311 effort measurements we reviewed low effort recordings and found that when measured calling effort was  
312 1% or less, males usually had not called. For this reason we defined a male to have not called when his  
313 calling effort was 1% or less. At every age, males were categorized as either calling ( $>1\%$  calling effort)  
314 or not calling ( $\leq 1\%$  calling effort) and the proportion of calling males was calculated for each diet for: 1)  
315 each life stage, and 2) each age until 90% of males in each treatment had died (after which proportions  
316 fluctuated widely due to small sample sizes). We tested whether the diet treatments differed in the  
317 proportion of calling males by conducting chi-squared tests at each: 1) life stage or 2) age, and then  
318 following each with a series of post-hoc Fisher's exact tests for each pair of diets. The diets differed in the  
319 proportion of calling males at middle ( $\chi^2 = 9.779$ ,  $p = 0.008$ ) and late ( $\chi^2 = 18.560$ ,  $p < 0.001$ ) but not

320 early life ( $\chi^2 = 1.145$ ,  $p = 0.564$ ). High condition males were more likely than medium or low condition  
321 males to call at middle (high vs low:  $\chi^2 = 9.889$ ,  $p = 0.002$ ; high vs medium:  $\chi^2 = 4.816$ ,  $p = 0.037$ ) and  
322 late life (high vs low:  $\chi^2 = 18.132$ ,  $p < 0.001$ ; high vs medium:  $\chi^2 = 7.882$ ,  $p = 0.005$ ), but medium and  
323 low condition males did not differ in their probability of calling (middle life:  $\chi^2 = 1.031$ ,  $p = 0.351$ ; late  
324 life:  $\chi^2 = 2.460$ ,  $p = 0.120$ ) (Fig. 5). We found qualitatively similar results for the proportion of calling  
325 males after 11 days post-adult moult (Fig. 6).

326 We also examined diet effects on the time course of investment in calling effort by conducting linear  
327 and polynomial regressions of calling effort versus adult age for every male that had more than one  
328 calling effort measurement. Due to high variability and low sample sizes for many males, very few of  
329 these regressions were statistically significant. However, this procedure (sensu Brooks and Endler 2001)  
330 gave us two summary measures that we could compare amongst the three diet treatments. Both the linear  
331 and polynomial regression coefficients were normally distributed, so we proceeded to test for an effect of  
332 diet on these two measures using a multivariate GLM with diet as a fixed factor and both the standardized  
333 linear and nonlinear regression coefficients as response variables. The mean linear and nonlinear  
334 regression coefficients were significantly less than zero for males on all three diets (one sample t-tests: all  
335  $p < 0.011$ ). However, diet did not have an effect on the linear or nonlinear relationship between calling  
336 effort and age (Pillai's trace = 0.012,  $F_{4, 1060} = 1.585$ ,  $p = 0.176$ ), although there was a trend for linear  
337 regression coefficients to become less negative as diet quality increased (mean linear coefficient  $\pm$  SE:  
338 low =  $-0.217 \pm 0.038$ , medium =  $-0.148 \pm 0.029$ , high =  $-0.116 \pm 0.028$ ).

339

#### 340 *Lifespan and Daily Calling Effort*

341 We tested for a significant relationship between calling effort and male lifespan. First we tested for  
342 homogeneity of slopes for the three diets by conducting an ANCOVA with male lifespan as the response  
343 variable, transformed daily calling effort ( $[\arcsine(\text{calling effort})^{(1/2)}]^{(1/3)}$ ) as the covariate, and diet as the  
344 independent factor. We interpret a significant covariate by factor interaction as evidence that the



345 relationship between lifespan and daily calling effort varied among the three diets. The interaction  
346 between transformed daily calling effort and diet was not statistically significant, although there was a  
347 trend ( $F_{2, 541} = 2.637$ ,  $df = 2$ ,  $p = 0.073$ ), so we conducted a regression between lifespan and transformed  
348 daily calling effort. There was a statistically significant positive relationship between lifespan and daily  
349 calling effort ( $F_{1, 545} = 8.034$ ,  $p = 0.005$ ), however, calling effort only explained 1.3% of the variation in  
350 male lifespan (adjusted  $R^2$ ) (Fig. 7). We also tested for a linear relationship between early calling effort  
351 (at six days post-adult moult) and male lifespan. ANCOVA revealed no significant differences among the  
352 three diets in the slope of the lifespan versus transformed early calling effort ( $[\arcsine(\text{calling}$   
353  $\text{effort})^{(1/2)}]^{(1/3)}$ ) relationship (interaction:  $F_{2, 529} = 0.834$ ,  $p = 0.435$ ). The regression of lifespan on  
354 transformed early calling effort was marginally non-significant ( $F_{1, 533} = 3.234$ ,  $p = 0.073$ ).

355

356

## 357 **Discussion**

358 We manipulated condition in *G. pennsylvanicus*, where older males have a mating advantage over  
359 younger males (Zuk 1987b, 1988). We predicted that as diet quality increased, males would both live  
360 longer and invest more in sexual signaling (calling effort). Males reared on high and medium quality diets  
361 did not differ in their adult lifespan, but both lived longer than males reared on the low quality diet (Fig.  
362 2). And males on a high quality diet invested in daily calling effort more than those on either medium or  
363 low quality diets, who did not differ from one another, a result that is broadly consistent with previous  
364 work on the condition dependence of grylline calling song (Crnokrak and Roff 1998a, Wagner and  
365 Hoback 1999; Holzer et al. 2003; Scheuber et al. 2003a,b; Hunt et al. 2004). We found no evidence for  
366 age-specific investment in calling varying with diet quality: at sexual maturity (six days post-adult moult)  
367 there were no differences among the three diet treatments in either daily calling effort (Figs. 3 and 4) or  
368 the proportion of males that called (Figs. 5 and 6). Differences among the three treatments grew apparent  
369 as males aged (after six days post-adult moult); a greater proportion of high condition males were able to

370 sustain high levels of calling effort longer than medium condition males, both of which by virtue of their  
371 longer lifespans maintained calling effort longer than low condition males (Figs. 3 to 6). Along with a  
372 strong effect of diet quality on lifespan and calling effort, there was an indication that longer-lived males  
373 called more with the significant (albeit weak) positive correlation between median daily calling effort and  
374 male lifespan (Fig. 7). There was no significant relationship between calling effort early in life and  
375 lifespan.

376 Sexual selection theory predicts that investment in sexual signaling by high quality males can be  
377 sufficiently high that they die younger than low quality males (Darwin 1871; Fisher 1915, 1930; Grafen  
378 1990; Getty 1998; Kokko 1998; Kokko et al. 2002; Getty 2006). Work on a grylline field cricket, *T.*  
379 *commodus* (Hunt et al. 2004), was the first experimental support for this prediction. High condition males  
380 signaled more, but died younger than low condition males (Hunt et al. 2004). Furthermore, within diets,  
381 males reared on a low quality diet showed a positive correlation between signaling and lifespan; whereas  
382 high and medium condition males that signaled more, died younger (Hunt et al. 2004). In contrast, we  
383 found in our grylline, *G. pennsylvanicus*, that males reared on a high quality diet both lived longer and  
384 invested more effort in sexual signaling than males on a low quality diet. In addition, there was a weak  
385 positive correlation between lifespan and daily calling effort that did not differ among treatments (Fig. 7).  
386 Studies of other taxa have also shown varying support for the basic Darwinian hypothesis. Similar to our  
387 *G. pennsylvanicus*, male *H. rubrofasciata* wolf spiders fed at a high level, signaled (drummed their  
388 abdomens) more and survived longer than males fed at a low level (Mappes et al. 1996; Kotiaho 2000).  
389 There was a weak positive relationship between drumming rate and male survival when females were  
390 present, but not when they were absent (Kotiaho 2000). And in three-spined sticklebacks, *Gasterosteus*  
391 *aculeatus*, males fed a diet high in carotenoids had greater red nuptial colouration (which is preferred by  
392 females) and survived longer than males fed a diet low in carotenoids (Pike et al. 2007). In contrast, and  
393 similar to *T. commodus*, recent work on an ambush bug, *Phymata americana*, found that adult males fed a  
394 higher quantity of prey had greater lateral colouration (a sexually selected trait) but tended not to live as  
395 long as males fed a lower quantity of prey (Punzalan et al. in prep.). Thus, although the balance of

396 correlative evidence showing that male ornamentation and survival are positively correlated suggests that  
397 a negative correlation is not a common occurrence (meta-analysis by Jennions et al. 2001), the question of  
398 how often males of other species invest in secondary sexual characters to the detriment of their survival  
399 remains open and awaits further testing.

400       Why do males of some species (e.g. *T. commodus*, *P. americana*) invest in sexual ornaments to the  
401 detriment of survival, whereas males of others (e.g. *H. rubrofasciata*, *G. aculeatus*, *G. pennsylvanicus*) do  
402 not? A comparison of the two most closely related species (the gryllines) may shed some light on this  
403 question. Differences between *T. commodus* and *G. pennsylvanicus* in the relationship between signaling  
404 and lifespan may be due to life history differences. First, these two gryllines differ in terms of seasonality:  
405 northern hemisphere *G. pennsylvanicus* breed over several weeks from mid-summer to the first severe  
406 frost (Alexander 1968) whereas breeding appears to be episodic in Australian *T. commodus* (Jennions et  
407 al. 2004). Thus, *G. pennsylvanicus* and *T. commodus* may represent prolonged and explosive breeders  
408 respectively. In prolonged breeders, males have the opportunity to monopolize matings over the course of  
409 the breeding season. However, female availability is often high and synchronous in explosive breeders,  
410 reducing the potential for males to monopolize matings (Wells 1977). In the wild, the peak of female *G.*  
411 *pennsylvanicus* activity-density (an index of abundance) occurs approximately two weeks after the peak  
412 in male activity-density (Carmona et al. 1999; see also Ritz and Köhler 2007 for similar data for *G.*  
413 *campestris*). Under these conditions it may be adaptive for male *G. pennsylvanicus* to invest substantially  
414 in both survival and signaling. Although comparable data for *T. commodus* are unavailable, males of this  
415 grylline may invest primarily in signaling if endurance contributes little to male mating success.  
416 Latitudinal variation in the length of the breeding season within a single species (see Walker and Masaki  
417 1989) could provide a model system in which to test this hypothesis.

418       In *T. commodus*, the allocation of condition altered with increases in condition acquisition (Hunt et  
419 al. 2004), whereas in *G. pennsylvanicus* the pattern of allocation did not change drastically with increased  
420 acquisition (Fig. 7) This could be the result of selection for the ability of male *T. commodus* to adjust  
421 allocation of condition depending on local resource availability, whereas *G. pennsylvanicus* may be under

422 selection to maintain a specific allocation pattern. Putatively different selective regimes such as these  
423 might be a result of inhabiting unstable versus stable environments. *T. commodus* is recognized as a pest  
424 and exists in “large, eruptive populations” (Jennions et al. 2004, p 2475), which suggests high  
425 environmental variability and selection for the ability to take advantage of fluctuations in resources.  
426 However, we currently do not know how stable the environment of *G. pennsylvanicus* is. If it is stable,  
427 then male *G. pennsylvanicus* genetic quality may be reflected in genetic variance for resource acquisition,  
428 whereas genetic quality in male *T. commodus* may be based on genetic variance for resource allocation.

429 Another reason for the difference between *G. pennsylvanicus* and *T. commodus* may be that male *G.*  
430 *pennsylvanicus* are better able to buffer the metabolic demands of calling than male *T. commodus*. Our *G.*  
431 *pennsylvanicus* are micropterous (KAJ pers. obs.) whereas *T. commodus* are macropterous (Alexander  
432 and Otte 1983). Micropterous individuals have reduced or absent flight muscles (Harrison 1980), which  
433 not only have lower maintenance costs (Mole and Zera 1993) but can also lead to both the flight muscle  
434 space being filled with a fat body (reported in beetles: Jackson 1952) and greater fecundity than with  
435 macroptery (reviewed in Roff 1984). Moreover, the energetic costs of calling with short chirps  
436 (Alexander 1957) may be lower for *G. pennsylvanicus* males than *T. commodus* males with their longer  
437 chirp-trills (Loher and Rence 1978) (Prestwich 1994). Thus, due to microptery, *G. pennsylvanicus* males  
438 may be more able to live longer than *T. commodus* males while signaling at a high rate. *G. pennsylvanicus*  
439 reared on all three diets attained greater levels of calling effort in our study (high = 25.7%, medium =  
440 14.0%, low = 9.9%; Fig. 7) than *T. commodus* reared on the corresponding diets (high = 10.4%, medium  
441 = 3.7%, low = 3.0%; proportions calculated from Hunt et al. 2004 Fig. 2b based on a 15 hour [54000 s]  
442 observation period). In wing-polymorphic *G. firmus*, micropterous males call more than macropterous  
443 males (Crnokrak and Roff 1995, 1998a,b). However, it is unknown whether males of the two wing  
444 morphs differ in lifespan (but see Roff 1984 who did not detect a difference between micropterous and  
445 macropterous *G. firmus* females). Further progress on the question of the relative importance of  
446 investment in sexual signaling versus survival is likely to be made by studying North American gryllines

447 given the both a well-supported phylogeny (Huang et al. 2000) and within-species variation in life history  
448 parameters (e.g. Harrison 1979; Walker and Masaki 1989; Roff et al. 2003).

449 Females are generally attracted to greater amounts of sexual signal (reviewed in Ryan and Keddy-  
450 Hector 1992; gryllines: e.g. Cade and Cade 1992; Crnokrak and Roff 1995, 1998a,b; Hunt et al. 2004). In  
451 *G. pennsylvanicus*, high condition males call more (this study), so females choosing males investing in  
452 greater calling effort are likely to pick a high quality mate, but not necessarily an older mate. Zuk (1987b)  
453 suggested that female *G. pennsylvanicus* are attracted to older males or to some quality that is correlated  
454 with male survival. Our results indicate that females do not prefer old males *per se*, but instead choose  
455 high quality males. Furthermore, there is little evidence that male age can be predicted from his song  
456 (Ciceran et al. 1994; KAJ unpubl. data). Previous work showing that female *G. pennsylvanicus* prefer  
457 mating with older males (Zuk 1987b, 1988) either did not assess male calling effort (Zuk 1988) or did so  
458 using a relatively imprecise measure (see Zuk 1987b p1243). Interestingly, Zuk (1987b) found calling  
459 effort to be positively correlated with the number of females attracted, although this relationship was not  
460 statistically significant.

461 Calling effort in six-day-old males did not differ among any of our three diet quality treatments.  
462 Treatment differences in calling effort only became apparent in older males as medium condition males  
463 reduced their calling effort, and low condition males both reduced their calling effort and died. Thus, low  
464 condition males were weeded out of the population and high condition males were distinguishable by  
465 their greater signaling effort. These results are consistent with a model by Proulx et al. (2002), in which  
466 females prefer older males because they signal their quality more reliably than younger males. However,  
467 we found no evidence that males increased their calling effort with age (Figs. 3 and 4, and see Cade and  
468 Wyatt 1984), which is a prediction of reliable signaling by older males in species with multiple  
469 reproductive bouts (Proulx et al. 2002). Uncertainty about the timing of the first severe killing frost may  
470 enforce maximal signaling by males of all qualities immediately after maturing.

471 Our finding that male crickets on a high quality diet called more is broadly consistent with previous  
472 work on the condition-dependence of grylline calling song (Crnokrak and Roff 1998a, Wagner and

473 Hoback 1999; Holzer et al. 2003; Scheuber et al. 2003a,b; Hunt et al. 2004). In studies that manipulated  
474 adults, males that received higher quality or more food called more, whereas other call characteristics,  
475 such as carrier frequency, were unaffected (Crnokrak and Roff 1998a, Wagner and Hoback 1999; Holzer  
476 et al. 2003; Scheuber et al. 2003a). However, studies that manipulated juvenile diet have found  
477 inconsistent effects on calling. In *G. campestris*, food-stressed late-instar nymphal males moulted with  
478 smaller harps (the membranous area of the forewings that radiates song) and consequently produced calls  
479 with a higher carrier frequency (Scheuber et al. 2003b). In contrast, *T. commodus* males that had been  
480 reared from hatching on a poor quality diet were small as adults but carrier frequencies (and by  
481 implication harp areas [Simmons 1995; Scheuber et al. 2003a]) were unaffected (Hunt et al. 2004). This  
482 suggests that carrier frequency is under stabilizing selection in *T. commodus* (see Brooks et al. 2005,  
483 Bentsen et al. 2006). In future, it would be highly informative to directly compare the condition-  
484 dependence of calling effort with both temporal and spectral characteristics of male *G. pennsylvanicus*  
485 calling song.

486       The pattern of allocation to survival and calling effort in *G. pennsylvanicus* suggests that males gain  
487 fitness from initially investing more in survival than calling effort. An increase in diet quality from low to  
488 medium was associated with an increase in survival, but a further increase in diet quality brought no  
489 change in survival. However, high condition males invested significantly more resources into calling  
490 effort than medium condition males, who tended to invest more than low condition males. These results  
491 suggest a hierarchy to allocation decisions made by *G. pennsylvanicus*. Investment into survival may  
492 plateau because uncertainty over the onset of killing frost may weaken selection to increase male lifespan.  
493 Latitudinal variation in growing season within many North American gryllines, as well as variation in  
494 hatch date (e.g. Harrison 1985, KAJ pers. obs.) may have important impacts on this selection. Increasing  
495 investment in calling effort will have increasingly positive fitness returns due to the multiplicative effects  
496 of survival and ornamentation on male fitness (Grafen 1990; Getty 2006). It remains to be seen whether  
497 variation in growing season, environmental stability or some other ecological factor can switch the pattern  
498 of allocation and cause male *G. pennsylvanicus* to invest in calling effort at the expense of survival.

499

500

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512

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657

658 **Figure Legends**

659

660 Figure 1: Mean ( $\pm$  SE) pronotum length for males and females reared on low (light grey triangles),  
661 medium (dark grey squares) and high (black circles) quality diets.

662

663 Figure 2: Plot of: a) adult male, and b) adult female survival for individuals reared on low (dotted light  
664 grey line), medium (dashed dark grey line) and high (black solid line) quality diets.

665

666 Figure 3: Calling effort by life stage. Symbols represent medians and error bars are interquartile ranges.  
667 The three diet treatments are represented as follows: low quality – light grey triangles and dotted line,  
668 medium quality – dark gray squares and dashed line, and high quality – black circles and solid line.

669

670 Figure 4: Calling effort by age. The three diet treatments are represented as follows: low quality – light  
671 grey dotted line, medium quality – dark gray dashed line, and high quality – black solid line. Due to  
672 dwindling sample sizes with age, curves extend only to the age at which 90% of the males in a diet  
673 treatment had died. Treatments with the same letter on the same day are not statistically different at  $\alpha =$   
674 0.05 following sequential Bonferroni correction (Holm 1979).

675

676 Figure 5: Proportion of calling males by life stage. The three diet treatments are represented as follows:  
677 low quality – light grey dotted line, medium quality – dark gray dashed line, and high quality – black  
678 solid line.

679

680 Figure 6: Proportion of calling males by age. The three diet treatments are represented as follows: low  
681 quality – light grey dotted line, medium quality – dark gray dashed line, and high quality – black solid  
682 line. Due to dwindling sample sizes with age, curves extend only to the age at which 90% of the males in

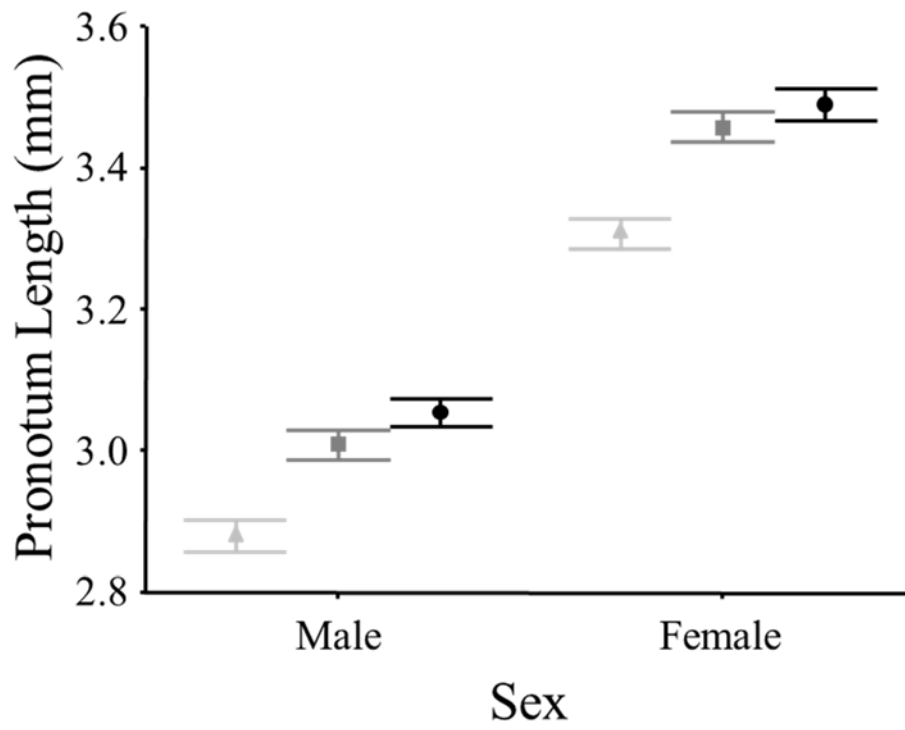
683 a diet treatment had died. Treatments with the same letter on the same day are not statistically different at  
684  $\alpha = 0.05$  following sequential Bonferroni correction (Holm 1979).

685

686 Figure 7: Plot of male lifespan versus transformed daily calling effort. The three diet treatments are  
687 represented as follows: low quality – light grey triangles, medium quality – dark gray squares, and high  
688 quality –black circles. The line represents the common regression slope for all three diets.

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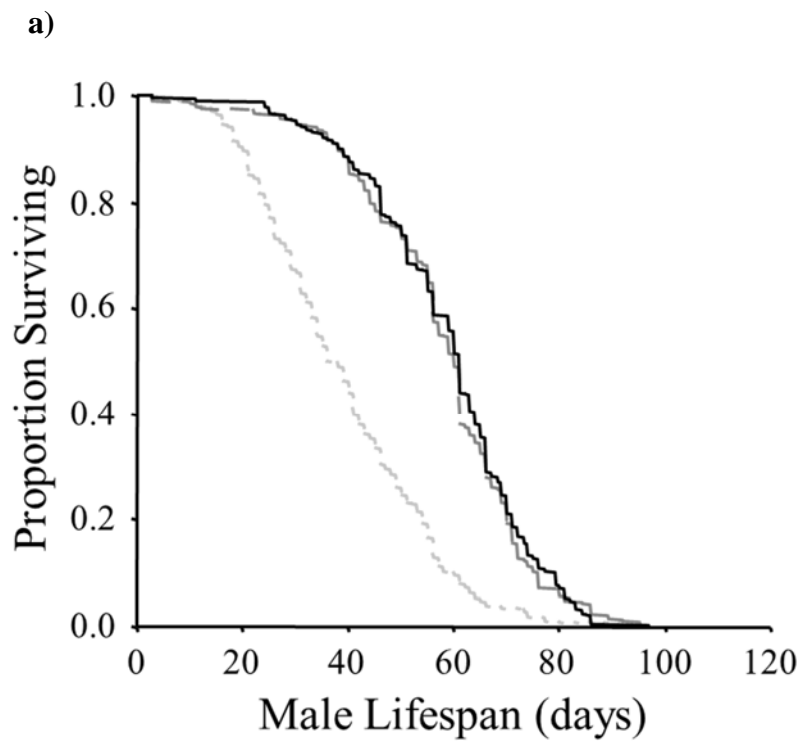
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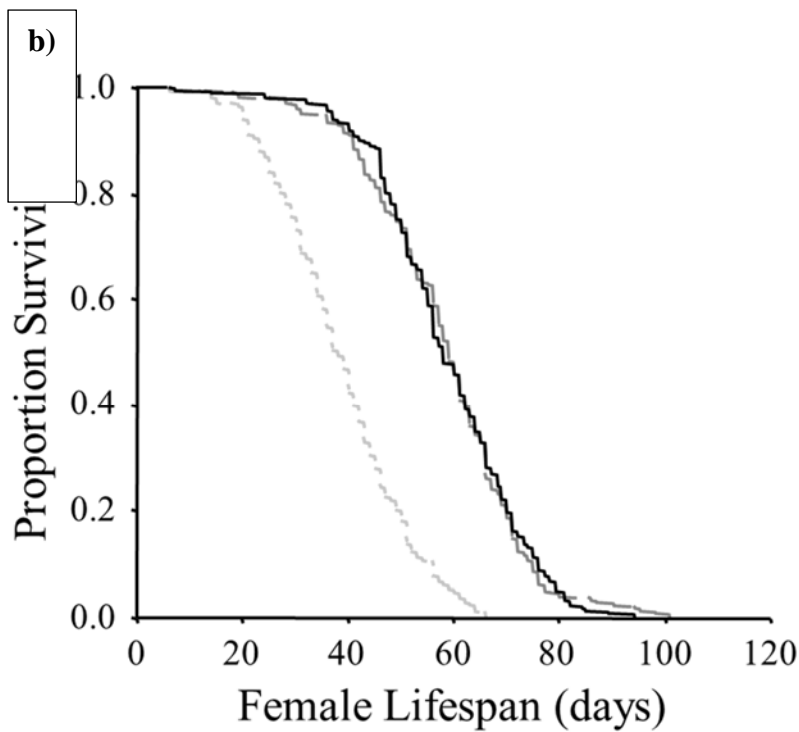
693 Judge et al. Fig. 1

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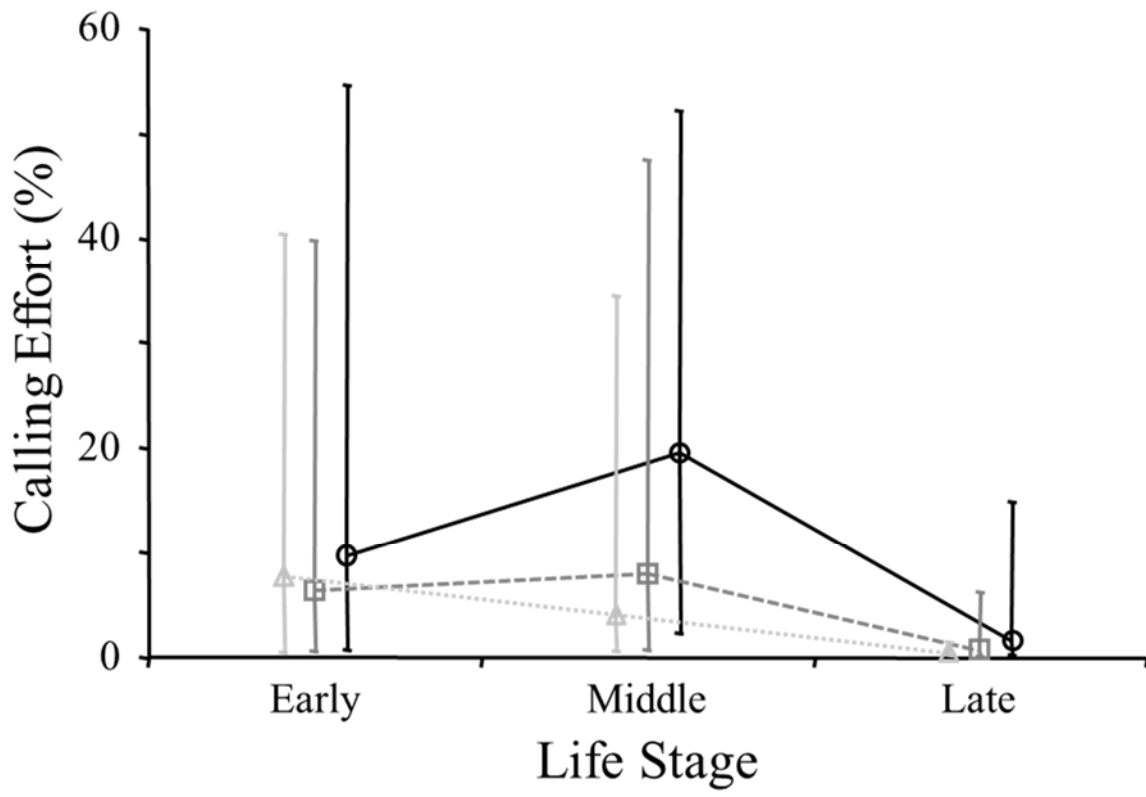
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697 Judge et al. Fig. 2

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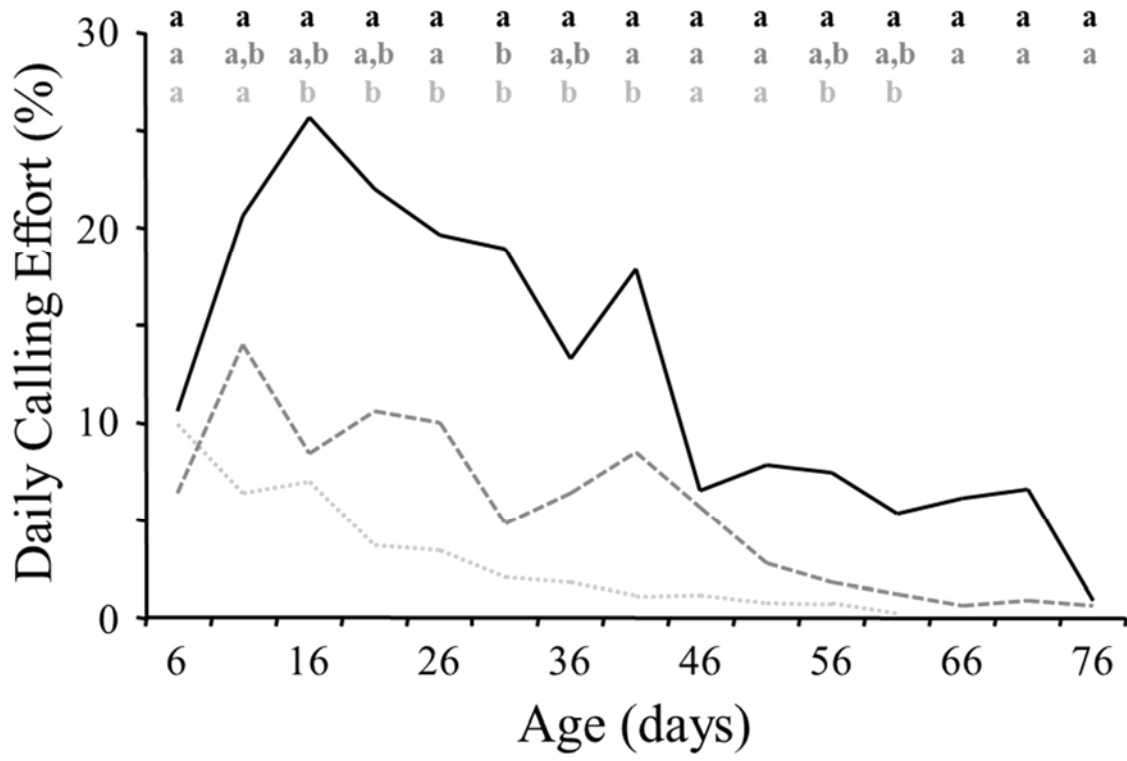


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701 Judge et al. Fig. 3

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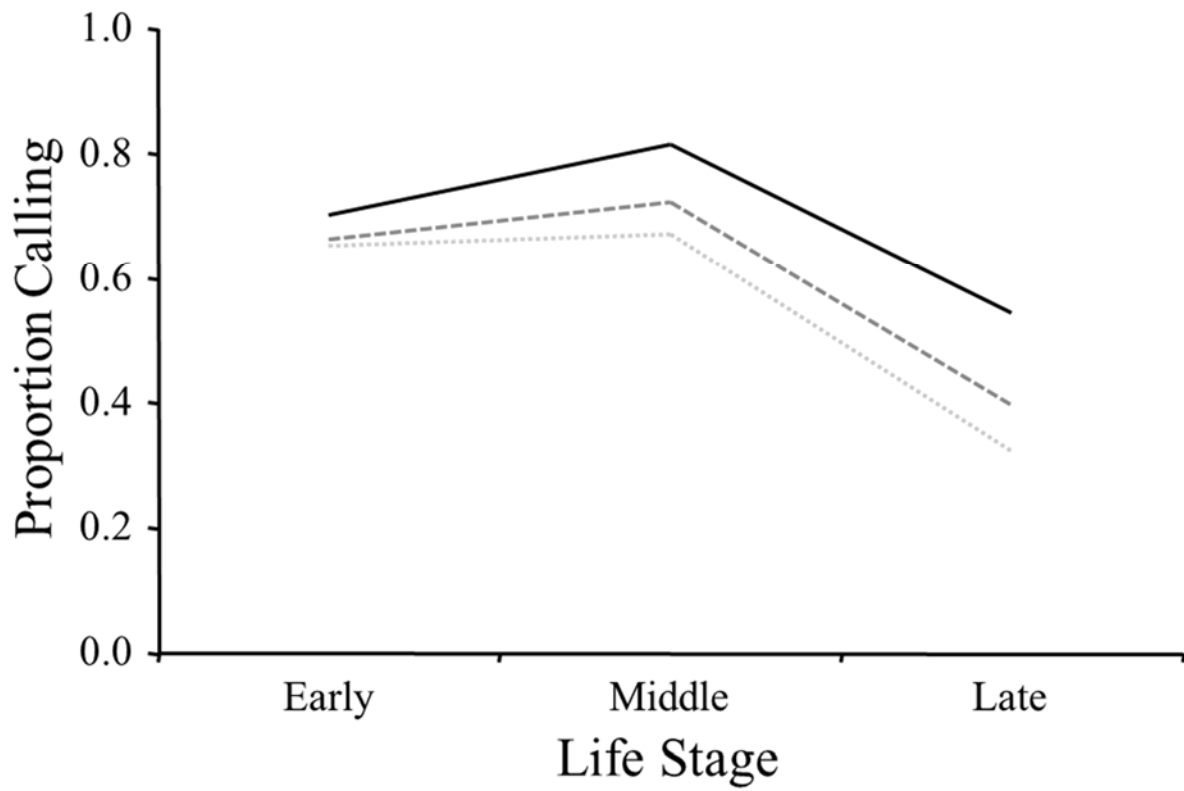


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705 Judge et al. Fig. 4

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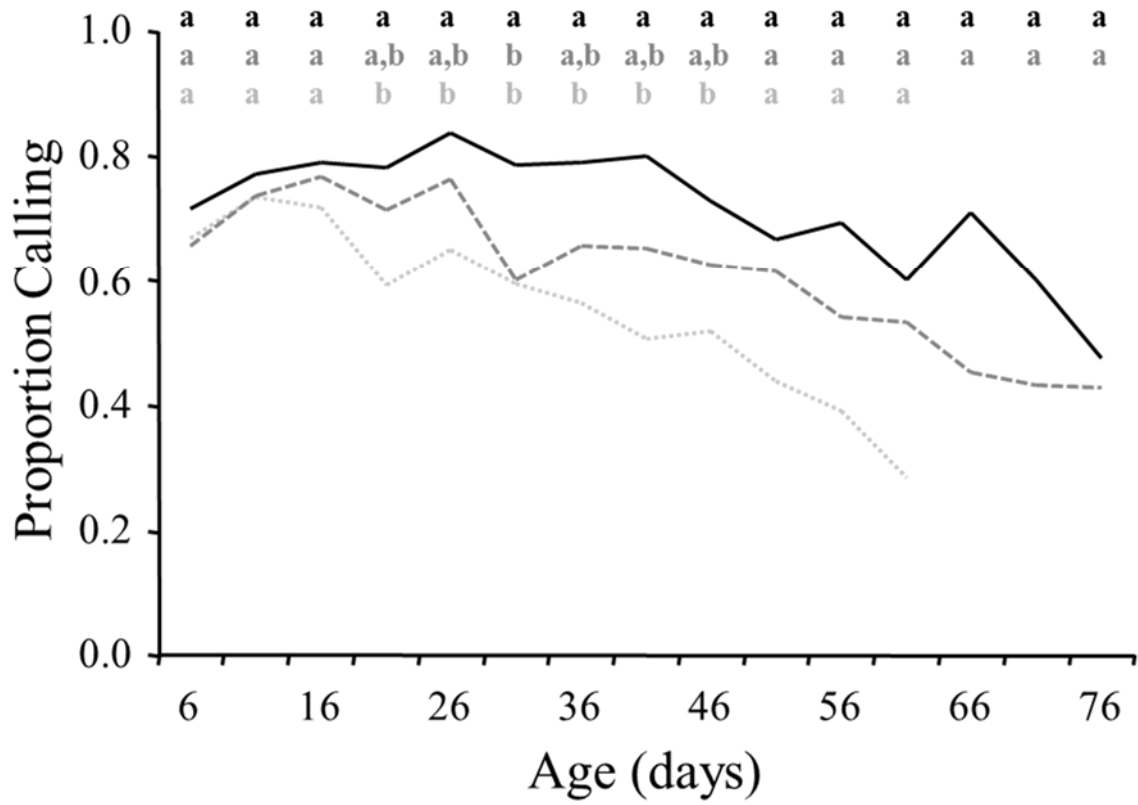


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709 Judge et al. Fig. 5

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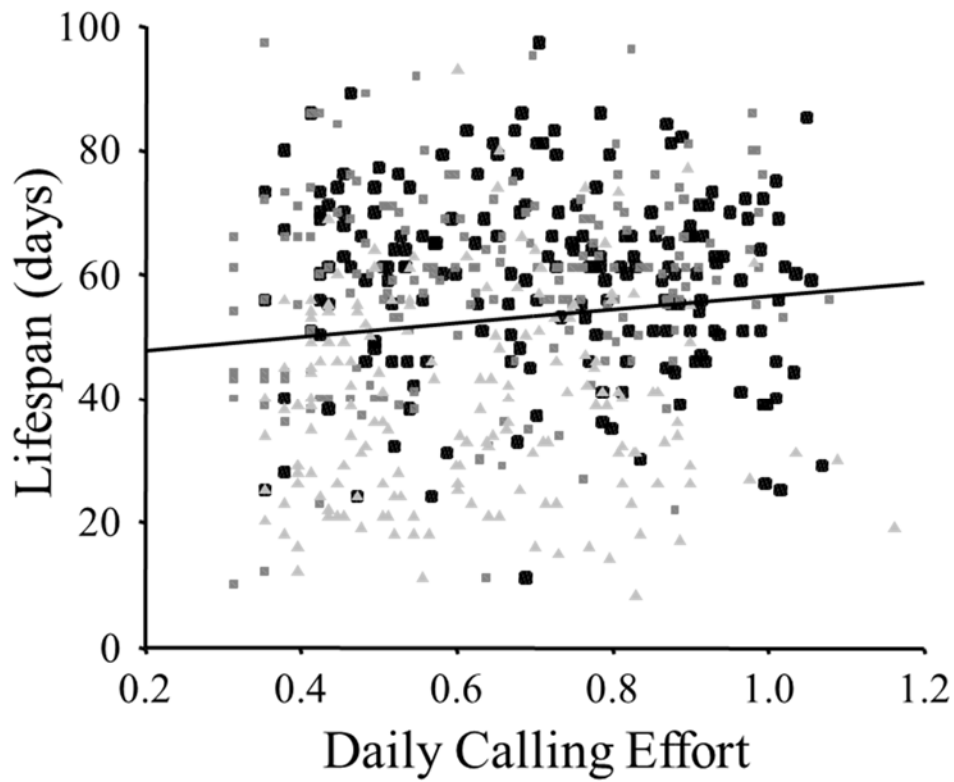


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713 Judge et al. Fig. 6

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717 Judge et al. Fig. 7