

1 **Males and females differ in how their behaviour changes with age in wild crickets**

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3 Gul Makai^{1,2,3}, Rolando Rodríguez-Muñoz^{1,3}, Jelle J. Boonekamp¹, Paul Hopwood¹, Tom

4 Tregenza^{*1}

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7 (1) Centre for Ecology & Conservation, School of Biosciences, University of Exeter, Penryn
8 Campus, Penryn, U.K.

9

10 (2) Department of Zoology, Sardar Bahadur Khan Women's University Quetta, Pakistan

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12 (3) These authors contributed equally to this work

13 Received 13 September 2019

14 Initial acceptance 13 November 2019

15 Final acceptance 24 February 2020

16 MS number 19-00622R

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18 * Correspondence: T. Tregenza, Centre for Ecology & Conservation, School of Biosciences,
19 University of Exeter, Penryn Campus, Penryn TR10 9FE, U.K.

20 E-mail address: T.Tregenza@exeter.ac.uk

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22 Because females produce and lay eggs or nurture embryos, they are constrained in the timing
23 of their investment in reproduction. Males may have more opportunity to concentrate
24 reproductive investment earlier in life, mating with as many females as possible soon after
25 becoming adult. This fundamental difference leads to the prediction that because males can

26 bias allocation towards increased reproductive investment early in life, they will use up
27 resources earlier in their lives and hence senesce faster than females. A first step towards
28 testing this prediction is to determine whether there are between-sex differences in age-
29 related changes in behaviour. To do this we recorded the behaviour of crickets, *Gryllus*
30 *campestris*, in a natural population living in and around their burrows in a meadow in
31 northern Spain. Following individuals of both sexes through their adult lives, we recorded a
32 range of nonreproductive behaviours, including how often they moved in and out of their
33 burrows, how long they spent at the entrance, how long they spent outside, how quickly they
34 left a burrow after fleeing inside to escape predation and whether they fed. We found
35 evidence for substantial age-related changes in two of the movement traits in males, but not
36 in females. Males moved less often and spent less time outside their burrows as they aged,
37 whereas females showed no age-related changes in either trait. Feeding was not affected by
38 age in males, but females fed more often as they got older. Our findings are consistent with
39 the prediction that males senesce faster than females; experiments in nature will be needed to
40 determine whether this pattern arises from life history trade-offs between reproduction and
41 other traits.

42

43 **Keywords:** ageing, *Gryllus campestris*, senescence, trade-off, WildCrickets

44

45 Organisms maximize fitness by balancing their investment across the competing demands of
46 development, somatic maintenance and reproduction. Reproductive investment must be
47 traded off with development or somatic maintenance, leading to senescence: individuals
48 declining in their capacity to express physiological and other fitness-related traits as they age
49 (Kirkwood & Rose, 1991; Rose, 1991; Williams, 1957). Evidence for age-related declines in
50 trait expression have been documented across a wide variety of organisms (Nussey, Froy,

51 Lemaitre, Gaillard, & Austad, 2013; Shefferson, Jones, & Salguero-Gómez, 2017). Life
52 history theories of senescence make the clear prediction that patterns of ageing will depend
53 upon the trade-offs that determine the extent and timing of investment in reproduction and
54 other life history traits (Williams, 1957). Differences in life history between males and
55 females (Brooks & Garratt, 2017; Kirkwood & Rose, 1991; Trivers, 1972) are therefore
56 expected to affect the age at the onset and the rate at which they decline in performance with
57 age. Males may have greater potential than females to concentrate reproductive effort into a
58 short period of time because they are not constrained by having to produce eggs or nurture
59 developing embryos or offspring. Hence males may be expected to invest heavily in their
60 reproductive effort early in life, while females tend to adopt a slow and steady strategy of
61 reproductive investment (Trivers, 1972). Bonduriansky et al. (2008) suggested that the most
62 frequent outcome of this asymmetry will be a ‘live fast die young’ strategy in males but they
63 noted that numerous exceptions to this pattern are observed and that sex differences in ageing
64 rate remain poorly understood (Bonduriansky et al., 2008; Vinogradov, 1998).

65

66 Studies on birds and mammals have found consistent evidence that a higher intensity of
67 intrasexual competition in males is associated with a shorter life span relative to females
68 (Clutton-Brock & Isvaran, 2007; Cornwallis, Dean, & Pizzari, 2014; Promislow, 1992).
69 However, shorter life span is not, in itself, evidence for senescence, because life span is
70 determined not only by the age-dependent increase in mortality rate due to declining
71 performance with age, but also by the age-independent baseline mortality rate, which
72 includes environmental components of mortality (Boonekamp, Salomons, Bouwhuis,
73 Dijkstra, & Verhulst, 2014; Monaghan, Charmantier, Nussey, & Ricklefs, 2008; Péron,
74 Lemaître, Ronget, Tidière, & Gaillard, 2019). Such age-independent environmental
75 components of mortality are likely to cause sex-specific effects on life span, because males

76 might expose themselves to greater risks (for example predation) in pursuit of matings
77 (Magnhagen, 1991; Rodríguez-Muñoz, Bretman, & Tregenza, 2011).

78

79 Sex differences in age-related changes in behaviour have been studied in only a small number
80 of wild animals including birds (Boonekamp et al. 2014; Holand et al. 2016) and mammals
81 (Nussey et al., 2009; Sparkman et al., 2016), and in captivity (Briga, Koetsier, Boonekamp,
82 Jimeno, & Verhulst, 2017). Studies of ageing in wild invertebrates are limited to a handful of
83 studies (Zajitschek, Zajitschek, & Bonduriansky, 2019). Our own work on *Gryllus*
84 *campestris* has identified clear evidence for both actuarial and physiological senescence
85 (Rodríguez-Muñoz, Boonekamp, Liu, Skicko, Fisher, et al., 2019; Rodríguez-Muñoz,
86 Boonekamp, Liu, Skicko, Haugland Pedersen, et al., 2019; Rodríguez-Muñoz, Hopwood, et
87 al., 2019), but has not tackled sex differences. A study of Australian field crickets,
88 *Teleogryllus commodus* (Zajitschek, Brassil, Bonduriansky, & Brooks, 2009) found no
89 differences in the rate of actuarial senescence between males and females, although a study
90 using naturalistic enclosures did find later onset, but faster, actuarial senescence in females
91 (Zajitschek, Bonduriansky, Zajitschek, & Brooks, 2009). In a study on damselflies the sexes
92 were found to differ in baseline mortality rates but were not formally compared for rate of
93 senescence (Sherratt et al. 2010) and a study of the fly *Telostylinus angusticollis* found
94 evidence for actuarial senescence in males, but not in females (Kawasaki, Brassil, Brooks, &
95 Bonduriansky, 2008).

96

97 When senescence is understood in the context of life history trade-offs, it is clear that we
98 should not expect to see a continuous decline in physiological performance, but rather a more
99 complex pattern reflecting the life history trade-offs that underpin traits. Organisms need to
100 grow and develop in order to reproduce. Even once an individual is reproductively mature,

101 we expect to see increases in the expression of some traits as the capacity to express those
102 traits develops (for instance many organisms grow continuously which affects the expression
103 of numerous traits). Trait expression may also increase because the level of reproductive
104 effort may increase in the face of diminishing remaining life expectancy (Duffield, Bowers,
105 Sakaluk, & Sadd, 2017; Williams, 1966). The combination of the requirement for
106 development and trade-offs between reproduction and somatic maintenance mean that
107 predictions about the direction of change in trait expression may depend upon the type of
108 organism in question. However, there remains a clear prediction that inherent differences in
109 the life history trade-offs faced by the two sexes should lead to differences between them in
110 age-related changes in trait expression across the adult life span. We predicted that crickets
111 would change their patterns of activity with age, and that the pattern of this change would
112 differ between the sexes. Broadly speaking, we expected males to show a more rapid
113 increase in activity as individuals completed their adult development, followed by earlier and
114 faster declines in later life. We had already found this pattern in two sexually selected male
115 traits, calling effort and success in fighting (Rodríguez-Muñoz, Boonekamp, Liu, Skicko,
116 Fisher, et al., 2019), but had not investigated whether females show the same pattern. We
117 expected both sexes to become less risk averse as they aged and their residual reproductive
118 value declined (McNamara, Merad, & Houston, 1991).

119

120 **Methods**

121 **Study system**

122 Data were extracted from the video library of WildCrickets. This is a long-term project
123 monitoring the behaviour of a wild population of the field cricket *G. campestris* in a meadow
124 in northern Spain. These crickets have a single generation each year with the first adults
125 emerging in mid to late April and the last adults dying in early to mid-July. Individuals of

126 both sexes build burrows as a refuge from predation. During the breeding season they move
127 around the meadow displacing one another from burrows and sharing burrows with a single
128 member of the opposite sex. All individuals spend most of their time in the immediate
129 vicinity of a burrow, periodically retreating into it in response to threats of predation and
130 inclement weather. Males call from their burrows to attract females but, like females, they
131 also move around in search of mates (Fisher, Rodríguez-Muñoz, & Tregenza, 2016). From
132 2006 to 2017 we used up to 133 day/night video cameras to record the activity of individually
133 identified adult crickets around their burrows for 24 h a day over the whole breeding season.
134 Details of how the meadow is managed and our monitoring protocol are available in
135 Rodríguez-Muñoz et al. (2010) and Rodríguez-Muñoz et al. (2019). The data included in this
136 study were obtained from detailed manual analysis of recordings from 2012. This allowed us
137 to quantify detailed activity patterns across the entire adult life span of individuals following
138 the methodology described below.

139

140 **Analysis of video recordings**

141 Using our pre-existing registry of general activity around cricket burrows collected by
142 watching all the video for 2012 at high speed (Rodríguez-Muñoz, Boonekamp, Liu, Skicko,
143 Haugland Pedersen, et al., 2019), we identified all the periods when individuals were alone at
144 a burrow and under camera observation. A single observer (G.M.) watched the videos of
145 these periods for each burrow (one burrow at a time) mainly at the originally recorded speed,
146 but also utilizing slower and faster playback speeds where necessary. Cricket burrows are
147 built as a refuge from predators; they are unbranching and too narrow for an individual to
148 turn around (Vrenozi, Uchman, & Muceku, 2015), so we do not expect much activity to
149 happen inside. Crickets move between burrows, but they typically do so within a few
150 minutes, so where a burrow is under a camera, most behavioural activity can be observed in

151 the area immediately outside the burrow. We are therefore able to record the complete range
152 of behaviours of crickets in our population. These include singing by males and egg laying
153 by females, which are restricted to only one sex, and behaviours such as mating and fighting,
154 which only occur when more than one cricket is present. Except for cleaning behaviours,
155 which involve small movements that we cannot observe reliably, for this study we analysed
156 the complete range of behaviours seen in solitary individuals of both sexes. To quantify
157 these, we recorded the precise time when the focal cricket changed its behaviour between the
158 following mutually exclusive categories. (1) The cricket's entire body is completely inside
159 the burrow. The mouth of the burrow is defined by a vertical line from the highest point on
160 the opening of the burrow down to the floor of the burrow below it. (2) Part of the cricket's
161 body crosses the line defining the mouth of the burrow. Crickets moving rapidly from inside
162 to outside the burrow may not be recorded as being in the burrow mouth if they move rapidly
163 through this zone. (3) The cricket's entire body is outside the burrow and it is not engaging in
164 any of the mutually exclusive activities listed below. (4) The cricket is observed physically
165 eating; this activity included chewing and holding an item of vegetation, seeds or (rarely) an
166 invertebrate and using its mandibles to consume part of the item. (5) The cricket suddenly
167 flees into the burrow in response to a perceived threat within 1 s (as opposed to slowly
168 walking into the burrow which happens frequently and which is recorded as a change from
169 category 3 to category 2 or 1).

170

171 The timing of changes in activity was recorded to a precision of 1 min for categories 1–4, and
172 to the nearest 1 s for the onset of fleeing (5) and for the subsequent category (1 or 2) when the
173 cricket re-emerged from its burrow. To examine age-related variation in behaviour, we
174 needed a standardized measure of the expression of behaviours on as many days of each
175 individual's life as possible. Crickets frequently spend less than a whole day at a burrow

176 (Rodríguez-Muñoz, Hopwood, et al., 2019), and movement among burrows disrupts the
177 typical behaviours exhibited at a burrow. We could not simply use whatever portion of the
178 day an individual was at a burrow under observation because time of day has a large effect on
179 behaviours (Jacot, Scheuber, Holzer, Otti, & Brinkhof, 2008). Therefore, for the analyses in
180 this study we only included observations made between 0700 and 1200 hours. This is the part
181 of the day when crickets are most active, and levels of activity are fairly uniform across the
182 period. By using a 5 h period, rather than 24 h, there were more days per individual where
183 data were available for the whole of the observational period. It is of course possible that in
184 doing so we may have missed some differences between the sexes that are more obvious at
185 other times of day, but our study still has much more comprehensive monitoring of
186 individuals than is normally possible in nature. We continuously monitored the air
187 temperature using a weather station in the centre of the meadow. Our previous work
188 (Rodríguez-Muñoz, Boonekamp, Liu, Skicko, Fisher, et al., 2019; Rodríguez-Muñoz,
189 Boonekamp, Liu, Skicko, Haugland Pedersen, et al., 2019) shows that in males, senescence in
190 calling effort and fighting success does not typically manifest itself as absolute declines in
191 performance until after around 15 days of age. Longer-lived individuals are unlikely to be a
192 random sample of the population (Vaupel, Manton, & Stallard, 1979). However, our aim was
193 to investigate the potential for senescent declines to differ between the sexes. Such declines
194 cannot take place in individuals predated at very young ages. Since collecting data on
195 individual behaviour on a minute-by-minute basis is extremely time consuming, we only
196 collected the very detailed time budgets needed for this study for individuals living at least 20
197 days. This ensured that a period of 5 days after the 15-day threshold after which declines in
198 other traits were observed in males was included for all individuals.
199

200 **Quantifying age-dependent changes in behaviour**

201 Using the times of the events described in the previous section, for every day of observation
202 we calculated a score for each cricket for the following behavioural traits: Moves: how often
203 the cricket moved between the inside of the burrow, the mouth of the burrow and outside the
204 burrow; Waiting: how long the cricket spent at the entrance of the burrow; Outside: how long
205 the cricket spent outside the burrow (including time spent feeding); Re-emerging: the time
206 taken for the cricket to move back outside the burrow after a fleeing event; Feeding: whether
207 the cricket was observed feeding on a given day, recorded as a binomial trait (we did not use
208 the total time spent feeding as days with no observed feeding are common meaning that these
209 data have a very skewed distribution).

210

211 Our prediction was that crickets would change their patterns of activity with age and this
212 pattern would differ between males and females. However, other than an expectation of
213 declines in activity in old age and decreasing sensitivity to risk with age, current theory does
214 not make specific predictions about the shape of the relationship between age and the
215 expression of particular traits. Therefore, our analytical approach was to identify the models
216 with the best fit to the relationship between age and the expression of the traits discussed
217 above. We then used these models to examine the evidence for a difference between the
218 sexes, with the potential for this to include differences in the pattern of any senescent declines
219 in trait expression. To examine potential correlations between behaviours, we calculated the
220 coefficient of determination for each pair of response variables by running separate mixed
221 models for each sex with one of them as predictor and the other as response and then using
222 the piecewiseSEM R package (Lefcheck, 2016).

223

224 We started the analysis by comparing the fit of mixed models with different levels of
225 complexity including individual age (Age), sex (Sex), duration of the observation period
226 (TotalTime) and temperature (Temp) as fixed effects, and cricket identity (ID) as a random
227 effect on each of the behaviours. We included age as both a linear and a quadratic term and
228 their interactions with sex. The fit of these models was compared using their relative Akaike
229 information criterion scores (ΔAICc), calculated using the MuMIn R package (Barton, 2019).
230 Following Burnham et al. (2011), we consider the fit of models with a $\Delta\text{AICc} < 7$ as similarly
231 good, in which case we selected the simpler model. There is no consensus on which ΔAICc
232 to use; we prefer the more conservative approach advocated by Burnham et al. (2011) who
233 argued that models where Δ is in the 2–7 range have some support and should rarely be
234 dismissed. We tested all the models using the function lmer included in the lme4 R package
235 (Bates, Mächler, Bolker, & Walker, 2015) running on RStudio (v 1.0.153), with the only
236 exception being feeding activity, which was analysed using glmer and a binomial
237 distribution. Before running the analyses, we applied the standard normal transformation to
238 our age data (subtracting the overall mean from each value and then dividing it by the overall
239 standard deviation) and all the response variables were square root transformed (except the
240 binomial feeding activity).

241

242 **Ethical note**

243

244 The study is based on video observations from a natural population of crickets. The only
245 manipulation we did with the wild insects was removing them from the meadow for a
246 maximum of a few hours during which time we take a small haemolymph sample, remove the
247 tip of one of the hindlegs and attach a plastic tag by gluing it to the pronotum. The death of
248 crickets during this process is very unusual (about 1–2%), and they start behaving in a natural

249 way on being released after they have been tagged. Our tagged crickets live out their natural
250 lives in the meadow.

251

252 **Results**

253 Summary statistics for the number of movements we observed and the time that males and
254 females spent on the activities we measured are shown in Fig. 1. Subsequent analyses do not
255 include the time that individuals spent inside their burrows because this is the remainder of
256 the time spent on other activities. The other activities are predominantly independent of one
257 another (Table 1); the only moderate correlation is between the number of movements that
258 females made and the total time that they spent outside their burrow.

259

260 Age was included in the best model for four of the five traits, the only exception being the
261 time taken for the cricket to re-emerge after fleeing down its burrow; for this trait the simplest
262 model had the best fit (Table 2). The best model describing the time spent outside the burrow
263 (Outside) included a linear interaction between age and sex (Table 2). For time spent at the
264 entrance (Waiting), the best model included age but not sex (Table 2). For how often the
265 cricket moved in and out the burrow (Moves) and whether it fed or not during the observation
266 period (Feeding), the best supported model included a quadratic age term, but neither model
267 including the main term of sex, nor models including the interaction term of sex*age were
268 supported (Table 2). The quadratic term of age means that there is a nonlinear change in the
269 expression of the trait with age. To determine whether this results in a peak of expression at
270 some point in the life span, we used threshold models (Douhard, Gaillard, Pellerin, Jacob, &
271 Lemaître, 2017; Rodríguez-Muñoz, Boonekamp, Liu, Skicko, Haugland Pedersen, et al.,
272 2019). These models allowed us to establish whether a peak was present, and if it was, at
273 what age the trait reached its peak value. Males showed a clear peak for the two traits (10.2

274 days for moves and 38.4 days for feeding) but there was no evidence of a peak in females
275 (Fig. 2). This suggests that the quadratic relationship identified in our original models (which
276 include both males and females) are likely to be driven predominantly by the males in the
277 data set. To investigate this, we carried out another run of model selection with separate
278 models for each sex. This confirmed the pattern identified in the threshold models. For males,
279 the best model included a quadratic relationship between age and the expression of both traits
280 (Table 3). For females, no quadratic relationship was present; feeding was best explained as
281 having a linear relationship with age, whereas for movement, age was not included (Table 3).
282

283 Analysing the effect of age in observational studies is complicated by the fact that differences
284 between age classes can occur because of within-individual declines, or because individuals
285 surviving to older ages may not be a random sample of the population (Vaupel et al., 1979).
286 To investigate whether age effects identified in the models described previously are artefacts
287 of this selective disappearance, we performed additional analyses including age as two
288 separate components on an individual basis: mean age (μAge ; the mean age across all
289 observation periods) and delta age (ΔAge ; the difference between age measured at each
290 observation period and μAge ; Van de Pol & Wright, 2009). This allowed us to separate
291 within-individual effects from among-individual effects, i.e. the relationship between age and
292 the expression of the trait within individuals from any potential age-related selective
293 mortality. For the two traits where males showed a nonlinear relationship with age (Moves
294 and Feeding) we only analysed the life span portion after the peak, as this is the period when
295 trait expression is declining. We included TotalTime, Temp and ID in the analyses of the four
296 traits, and we included or excluded Sex on the basis of the results of our previous tests for
297 model selection (Tables 2 and 3), Therefore, Moves was analysed only for males (postpeak),
298 Waiting was analysed for both sexes separately, and Outside included both sexes and the Sex

299 interaction with Δ Age. We had to remove males from the analysis of Feeding because the
300 peak of the quadratic relationship between this variable and age in males happened so late in
301 life that insufficient data were available. Sufficient data were available in females if we
302 removed female ID as a random effect and ran the test using a general linear model.

303

304 Males declined in the number of times they moved in and out of their burrows with Δ Age,
305 and in the time they spent outside (Table 4). However, the time spent waiting at the entrance
306 was not affected by age in either sex, and the probability of feeding in females increased with
307 age (Table 4). The combined analyses of the time spent outside including both sexes showed
308 an interaction between Sex and Δ Age. Males spent less time outside with Δ Age, but females
309 did not (Table 4, Fig. 1).

310 <H1>Discussion

311 We found evidence for age-related changes in the expression of all but one of the traits that
312 we examined. In two of these traits (the frequency of movements through the entrance of the
313 burrow (Moves) and the time spent outside (Outside)) we found a decline in their expression
314 with age in males but not in females (Table 4). Because the relationship between the
315 expression of these traits and fitness is unknown, we cannot unequivocally describe a decline
316 in their expression as being consistent with senescence. However, movement in and out of the
317 burrow requires energy and males can only gain fitness via attracting and mating with
318 females which can only occur outside the burrow. Hence declines in these traits are very
319 likely to reflect declines in expression of energetically costly behaviour and reproductive rate.
320 This is consistent with our previous findings of age-related increases in probability of
321 mortality and declines in male singing in later life (Rodríguez-Muñoz, Boonekamp, Liu,
322 Skicko, Fisher, et al., 2019; Rodríguez-Muñoz, Boonekamp, Liu, Skicko, Haugland Pedersen,
323 et al., 2019). We found direct evidence for an interaction between sex and age both in

324 relation to the proportion of time that individuals spent outside their burrows and in whether
325 individuals fed or not (Table 4). Table 4 and Fig. 3 reveal that the interaction involving sex
326 and age explaining time spent outside the burrow was caused by a consistent decline with age
327 in males which contrasts with the lack of an effect of age in females. For whether an
328 individual fed or not, the figure suggests an increase in expression in females and no pattern
329 in males (Table 4, Fig. 3).

330

331 Two of the traits that changed with age, Moves and Feeding, showed a quadratic relationship
332 with age. We investigated this relationship using threshold models (Douhard et al., 2017).
333 This revealed that there was clear evidence of a peak age in relation to the expression of both
334 traits in males but not for females (shown in Fig. 2) by the sharply lower AICc value for the
335 males' model, with a peak at around 10 and 38 days, respectively, and no evidence of a peak
336 in females. This apparent sex difference is supported by the separate models of ageing in
337 males and females shown in Table 3, where the best fitting model includes a quadratic effect
338 of age in males, but not in females. There is something of a contradiction between this
339 observation of an apparent sex difference in age trajectories in the analyses in Fig. 2 and
340 Table 3 and the lack of a significant interaction between sex and age in our original model
341 selection procedure for these traits (Table 2). This might be due to the low power of the
342 quadratic models to detect these differences in the absence of a clear peak of expression. For
343 Moves, the portion of life postpeak showed a significant decline in males, whereas in females
344 there was no evidence that Moves was affected by age. For Feeding, our results are
345 inconclusive. We could not analyse the postpeak portion in males, although the existence of a
346 peak indicates that at least there was a continuously decelerating effect of age. In females the
347 relationship was positive over their whole life, but because we do not have female data for
348 ages after the peak age of males, it is unclear whether there is really any sex difference in the

349 expression of this trait. The lack of data for very old females in this subset of our population
350 is not reflected in the population as a whole where males and females have very similar
351 average life spans (Rodríguez-Muñoz, Boonekamp, Liu, Skicko, Haugland Pedersen, et al.,
352 2019).

353

354 Sex differences in senescence have been documented in a relatively small number of wild
355 animals. Sparkmann et al. (2016) found that in red wolves, *Canis rufus*, there was no
356 evidence of a relationship between maternal age and the production of adult offspring
357 whereas males showed a steep decline in their success in siring recruits to the population.
358 Similarly, in red deer, *Cervus elaphus*, Nussey et al. (2009) identified faster declines in
359 breeding success in males than females. They also observed a rapid decline in the number of
360 days that males spent rutting even though individual reproductive traits varied in their
361 patterns of senescence, with some male secondary sexual traits apparently declining more
362 slowly than some female traits. Beirne et al. (2015) identified a sex difference in the rate of
363 late-life decline in body mass in European badgers, *Meles meles*. They were able to show
364 that this sex difference was a direct result of intrasexual competition between males, and only
365 occurred in groups where males experienced high levels of competition early in adulthood.
366 We cannot definitively identify the reason why male crickets in our population appear to
367 show steeper declines with age in the expression of some behaviours compared to females.
368 However, we have previously identified an increase in mortality rate with age (actuarial
369 senescence), and in the rate of decline in male calling effort (behavioural senescence) in years
370 when the sex ratio is more male biased (Rodríguez-Muñoz, Boonekamp Jelle, Fisher,
371 Hopwood, & Tregenza, 2019). This suggests that intrasexual competition plays a role in
372 male senescence in this species. However, we would need to repeat the analysis described in
373 this paper across multiple years of our study to directly examine this relationship. The data

374 included in this study were extracted from a year with a female-biased sex ratio, when calling
375 effort showed no decline with age (in contrast to more even sex ratio years; Rodríguez-
376 Muñoz, Boonekamp Jelle, et al., 2019); this suggests that greater sex differences might be
377 apparent if we analysed video from years in which the proportion of males in the population
378 was more even.

379 The only trait that did not show a change in expression with age in either sex was the time it
380 took individuals to re-emerge from their burrows after a predator fleeing event. Hiding in the
381 burrow is a risk avoidance strategy that carries the cost of reducing the time available for
382 reproduction. Therefore, our prediction was that as individuals aged and their future
383 reproductive potential decreased, they would be more likely to take risks (McNamara et al.,
384 1991). We did not observe this effect. This might indicate that it is absent, or that senescent
385 declines in speed of movement balance out a greater willingness to re-emerge. This latter
386 possibility does not seem very likely, however, because re-emergence only involves the
387 cricket slowly reversing out of the burrow which is within the capacity of even very old
388 crickets. Closely related to this is our finding that the time spent at the entrance of the burrow
389 increased with age in a similar way for both sexes. This might be indicative of senescence, as
390 it means that they take more time to move between being inside or outside of their burrows.

391
392 Overall, our study confirms our earlier findings of a general pattern of age-related declines in
393 performance in wild crickets. We found evidence for sex differences in how traits change
394 with age. These differences manifested as divergent patterns of age-dependent changes in
395 trait expression. Males showed significant peaks of expression during adulthood in two of
396 the behaviours we studied, with subsequent declines in old age, whereas in females there was
397 no conclusive evidence for quadratic forms of variation in trait expression. Neither sex
398 appeared to become less risk averse with age. Our results are consistent with life history

399 theories of senescence, which predict that selection for sex-specific differences in
400 reproductive strategies might result in differences in the patterns of senescence between the
401 sexes.

402

403 **Data Availability**

404 Data supporting the results are archived in ORE.

405

406 **Acknowledgments**

407 We thank L. Rodríguez and M.C. Muñoz for unconditional support, providing access to
408 facilities including the WildCrickets study meadow. Carlos Rodríguez del Valle and David
409 Fisher contributed to video processing and data recording. We also thank www.icode.co.uk
410 for developing their i-catcher video recording package to optimize it for behavioural research.
411 Jon Slate has been a constant partner in the development of the project. The manuscript was
412 improved by comments from five referees, including Jean-François Lemaître and from the
413 editor Peter Schausberger. This work was supported by the Natural Environment Research
414 Council (NERC); standard grants: NE/E005403/1, NE/H02364X/1, NE/L003635/1,
415 NE/R000328/1; and studentships: European Union's Horizon 2020 research and innovation
416 programme under the Marie Skłodowska-Curie grant agreement, CONSENT 792215
417 (Boonekamp) and the Leverhulme Trust. G.M. was supported by a grant from Sardar
418 Bahadur Khan Women's University, Quetta, Pakistan.

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568 Table 1. Correlations between response variables for females (above the diagonal) and males
569 (below the diagonal)

570

	No. of movements	Time at the entrance	Time outside	Feeding activity
No. of movements		0.04	0.35	0.06
Time at burrow entrance	0.13		0.01	0.00
Time outside burrow	0.09	0.00		0.08
Feeding activity	0.10	0.00	0.07	

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572 The table shows the marginal coefficient of determination (i.e. including only fixed effects)
573 between pairs of variables calculated using the piecewiseSEM R package (Lefcheck, 2016).

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589 Table 2. Relative AICc values (ΔAICc) for comparisons among models to explain variation
 590 in five behavioural traits

Model	Moves	Waiting	Outside	Re-emerging	Feeding
TotalTime + ID	32.0	7.1	17.7	0.0	38.5
TotalTime + Temp + ID	14.0	8.3	8.3	4.9	26.8
TotalTime + Temp + Age + ID	18.7	6.3	8.9	5.2	27.0
TotalTime + Temp + Sex + Age + ID	21.9	6.1	9.0	6.5	28.1
TotalTime + Temp + Age + Age ² + ID	0.0	6.4	13.0	8.8	0.0
TotalTime + Temp + Sex*Age + ID	25.4	5.6	0.0	6.6	16.4
TotalTime + Temp + Sex + Age + Age ² + ID	3.1	6.1	13.2	10.1	1.1
TotalTime + Temp + Sex*Age + Sex*Age ² + ID	0.7	0.0	0.3	8.8	3.3

591
 592 Values show ΔAICc (increment in corrected Akaike information criterion) as compared to the
 593 value of the model with the lowest AICc (best fit). Fits with $\Delta\text{AICc} < 7$ are considered as
 594 similar (Burnham et al., 2011). The simplest model among those with similar smaller AICc
 595 values is highlighted in bold italics. Each record in the data set includes the values for 1 day
 596 of observation. TotalTime: duration of the observation period each day; Temp: mean ambient
 597 temperature during the observation period; Age: age of the cricket; ID: individual identifier.
 598 Moves is the number of times the cricket changed between being inside, at the entrance or
 599 outside the burrow. Waiting and Outside are the total time spent at the entrance or outside
 600 the burrow, Re-emerging is the time taken to move outside the burrow after rapidly fleeing
 601 inside. Feeding is whether the cricket fed or not during the observation period that day.
 602 TotalTime, Temp and Age are continuous fixed effects, Sex is a fixed factor and ID is a
 603 random factor. TotalTime was not included in the analysis of Re-emerging, as there is no way
 604 it can have an effect.

605

606 Table 3. Relative AICc values (ΔAICc) for comparisons between models to explain variation
 607 in two behavioural traits treating males and females independently

608

Model	Moves		Feeding	
	Males	Females	Males	Females
TotalTime + ID	35.5	<i>0.0</i>	16.1	19.0
TotalTime + Temp + ID	19.0	3.0	9.6	16.2
TotalTime + Temp + Age + ID	23.9	5.7	11.4	<i>0.0</i>
TotalTime + Temp + Age + Age ² + ID	<i>0.0</i>	10.4	<i>0.0</i>	0.1

609

610 Values show ΔAICc (increment in corrected Akaike information criterion) as compared to the
 611 value of the model with the lowest AICc. The simplest model among those with similar
 612 smaller AICc values is highlighted in bold italics. Fits with $\Delta\text{AICc} < 7$ are considered similar
 613 (Burnham et al., 2011). TotalTime, Temp and Age are continuous fixed effects and ID is a
 614 random factor.

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617

618 Table 4. The relationship between age relative to the mean age of each individual (Δ Age) and
 619 four behavioural traits
 620

	Moves			Waiting			Outside			Feeding		
	C	SD	<i>P</i>									
Fixed effects												
Intercept	1.149	0.830	0.168	4.290	1.089	<0.001	-1.247	1.235	0.314	-3.560	1.553	0.021
TotalTime	0.332	0.067	<0.001	1.134	0.110	<0.001	2.016	0.123	<0.001	0.553	0.195	0.004
Temperature	0.119	0.037	0.002	-0.122	0.048	0.011	0.221	0.054	<0.001	0.095	0.065	0.140
Δ Age	-0.538	0.148	<0.001	0.495	0.185	0.006	0.503	0.519	0.333	0.760	0.268	0.005
SexM							0.359	0.493	0.476			
μ Age	-0.534	0.501	0.312	-0.508	0.585	0.395	-0.008	0.441	0.986	1.489	0.421	<0.001
Δ Age: SexM							-1.094	0.551	0.048			
Samples	153			403			403			150		
Random effects												
	V	SD	<i>N</i>	V	SD	<i>N</i>	V	SD	<i>N</i>			<i>N</i>
ID	0.650	0.806	13	2.217	1.489	28	0.498	0.706	28			15
Residual	1.326	1.152		7.302	2.702		9.334	3.055				

621
 622 C: coefficient; V: variance. The table shows the results of a mixed model using the lme4 R
 623 package with a normal (Moves, Waiting and Outside) or binomial (Feeding) distribution.
 624 Coefficients with significant *P* values are highlighted in bold italics. We only analysed the
 625 sex and trait combinations where our previous analyses identified changes with age (Moves
 626 for males only, Waiting for both sexes independently, Outside for both with sex included and
 627 Feeding for females only; see Methods and Results).
 628

629 Figure 1. Relationship between age and five behavioural traits in female and male crickets
630 (medians and quartiles) of (a) number of movements, (b) time spent at the entrance of the
631 burrow, (c) time spent outside, (d) time spent inside the burrow and (e) time spent feeding.
632 Values have been binned into 5-day age classes. We recorded 3088 switches between
633 categories of behaviour in females and 5306 in males. We observed 15 females for a total of
634 647 h and 13 males for a total of 991 h.

635

636 Figure 2. $\Delta AICc$ (increment in corrected Akaike information criterion) values obtained after
637 running threshold models (Douhard et al., 2017) to identify the peak age in the expression of
638 three traits for both sexes. (a) Moves; (b) Feeding. The broken line shows the position of
639 $\Delta AICc = 7$ under which different models are considered equally good (Burnham et al., 2011).

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641 Figure 3. Changes in the time individual crickets spent outside their burrows during the daily
642 5 h observation period in relation to their age relative to their mean age (ΔAge). Values have
643 been binned into age classes.

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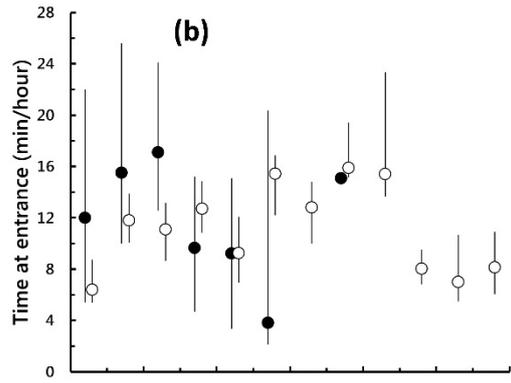
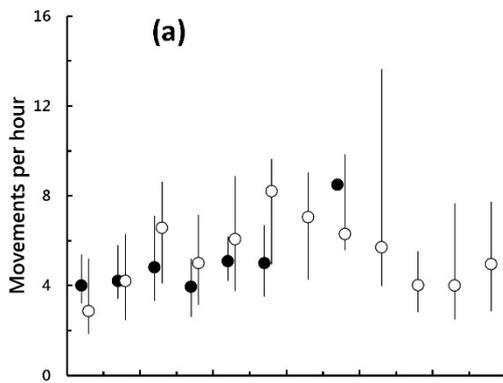
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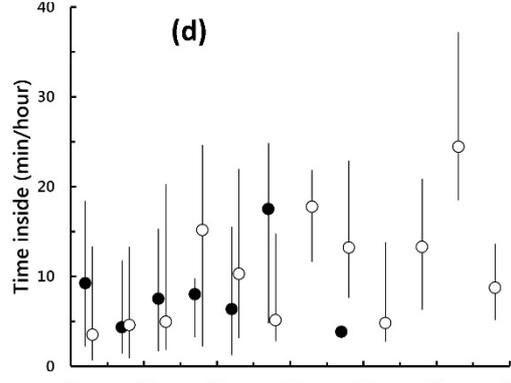
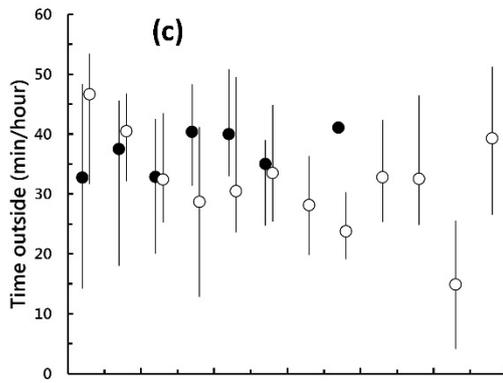


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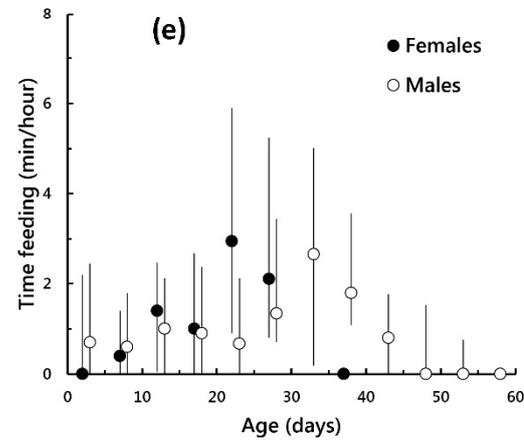
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Figure 1

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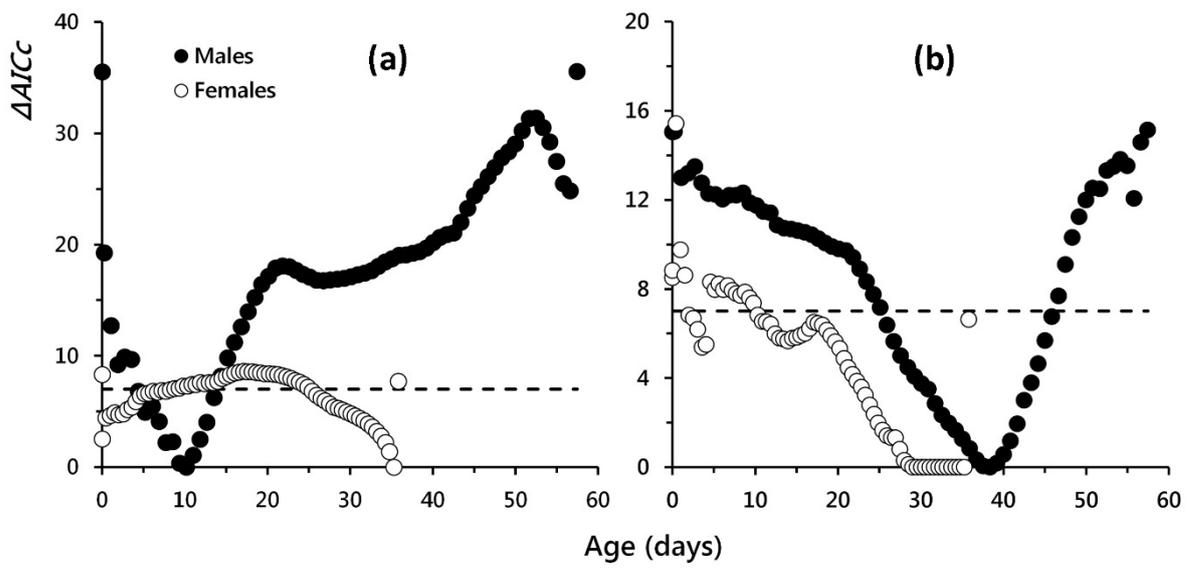


Figure 2

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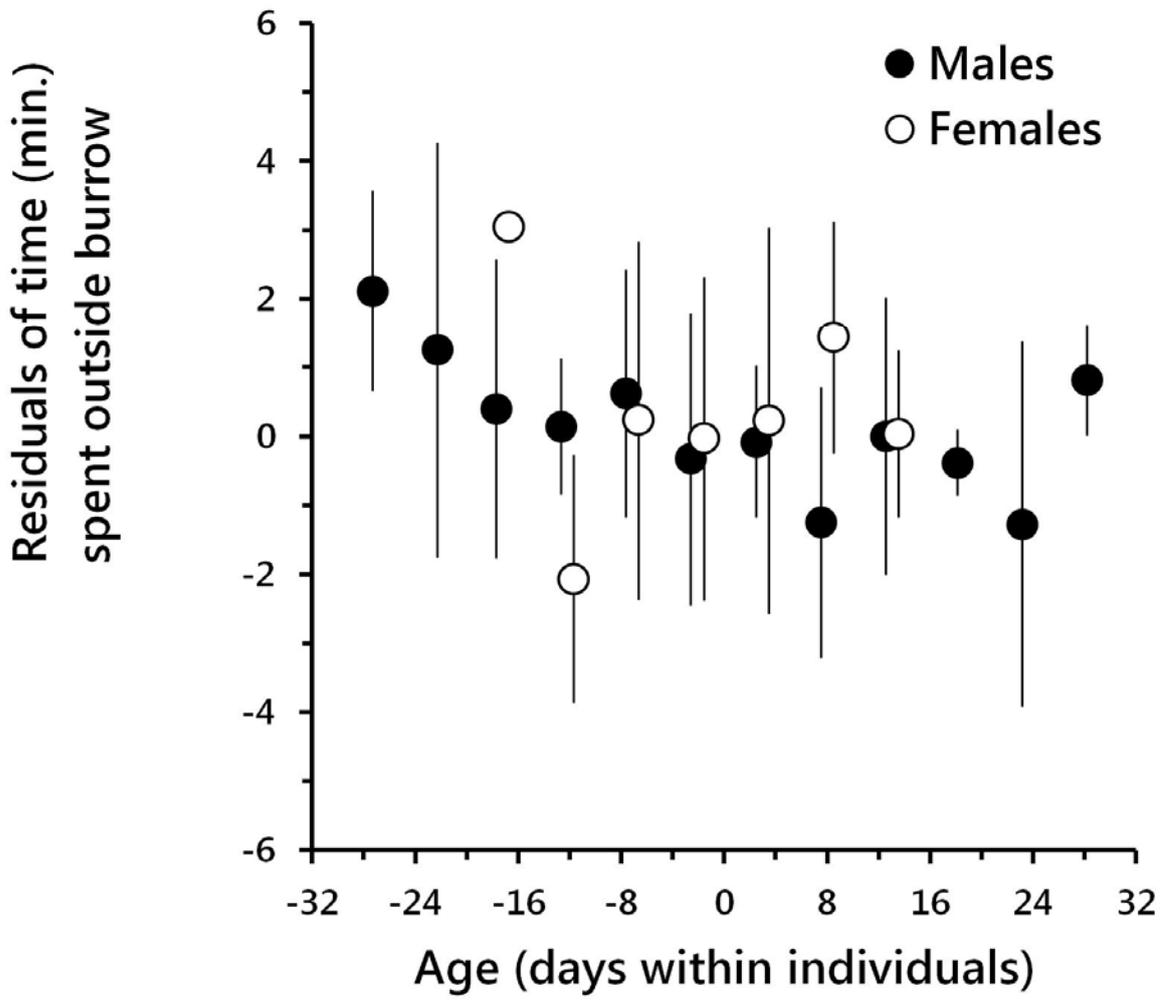


Figure 3