



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

Gul Makai ^{a, b, 1}, Rolando Rodríguez-Muñoz ^{a, 1}, Jelle J. Boonekamp ^a, Paul Hopwood ^a, Tom Tregenza ^{a, *}

^a Centre for Ecology & Conservation, School of Biosciences, University of Exeter, Penryn Campus, Penryn, U.K.

^b Department of Zoology, Sardar Bahadur Khan Women's University Quetta, Pakistan

ARTICLE INFO

Article history:

Received 13 September 2019
Initial acceptance 13 November 2019
Final acceptance 24 February 2020
Available online 22 April 2020
MS number 19-00622R

Keywords:

ageing
Gryllus campestris
senescence
trade-off
WildCrickets

Because females produce and lay eggs or nurture embryos, they are constrained in the timing of their investment in reproduction. Males may have more opportunity to concentrate reproductive investment earlier in life, mating with as many females as possible soon after becoming adult. This fundamental difference leads to the prediction that because males can bias allocation towards increased reproductive investment early in life, they will use up resources earlier in their lives and hence senesce faster than females. A first step towards testing this prediction is to determine whether there are between-sex differences in age-related changes in behaviour. To do this we recorded the behaviour of crickets, *Gryllus campestris*, in a natural population living in and around their burrows in a meadow in northern Spain. Following individuals of both sexes through their adult lives, we recorded a range of nonreproductive behaviours, including how often they moved in and out of their burrows, how long they spent at the entrance, how long they spent outside, how quickly they left a burrow after fleeing inside to escape predation and whether they fed. We found evidence for substantial age-related changes in two of the movement traits in males, but not in females. Males moved less often and spent less time outside their burrows as they aged, whereas females showed no age-related changes in either trait. Feeding was not affected by age in males, but females fed more often as they got older. Our findings are consistent with the prediction that males senesce faster than females; experiments in nature will be needed to determine whether this pattern arises from life history trade-offs between reproduction and other traits.

Crown Copyright © 2020 Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. All rights reserved.

Organisms maximize fitness by balancing their investment across the competing demands of development, somatic maintenance and reproduction. Reproductive investment must be traded off with development or somatic maintenance, leading to senescence: individuals declining in their capacity to express physiological and other fitness-related traits as they age (Kirkwood & Rose, 1991; Rose, 1991; Williams, 1957). Evidence for age-related declines in trait expression have been documented across a wide variety of organisms (Nussey, Froy, Lemaître, Gaillard, & Austad, 2013; Shefferson, Jones, & Salguero-Gómez, 2017). Life history theories of senescence make the clear prediction that patterns of ageing will depend upon the trade-offs that determine the extent

and timing of investment in reproduction and other life history traits (Williams, 1957). Differences in life history between males and females (Brooks & Garratt, 2017; Kirkwood & Rose, 1991; Trivers, 1972) are therefore expected to affect the age at the onset and the rate at which they decline in performance with age. Males may have greater potential than females to concentrate reproductive effort into a short period of time because they are not constrained by having to produce eggs or nurture developing embryos or offspring. Hence males may be expected to invest heavily in their reproductive effort early in life, while females tend to adopt a slow and steady strategy of reproductive investment (Trivers, 1972). Bonduriansky, Maklakov, Zajitschek, & Brooks, 2008 suggested that the most frequent outcome of this asymmetry will be a 'live fast die young' strategy in males but they noted that numerous exceptions to this pattern are observed and that sex differences in ageing rate remain poorly understood (Bonduriansky et al., 2008; Vinogradov, 1998).

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

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

¹ These authors contributed equally to this work.

Studies on birds and mammals have found consistent evidence that a higher intensity of intrasexual competition in males is associated with a shorter life span relative to females (Clutton-Brock & Isvaran, 2007; Cornwallis, Dean, & Pizzari, 2014; Promislow, 1992). However, shorter life span is not, in itself, evidence for senescence, because life span is determined not only by the age-dependent increase in mortality rate due to declining performance with age, but also by the age-independent baseline mortality rate, which includes environmental components of mortality (Boonekamp, Salomons, Bouwhuis, Dijkstra, & Verhulst, 2014; Monaghan, Charmantier, Nussey, & Ricklefs, 2008; Péron, Lemaître, Ronget, Tidière, & Gaillard, 2019). Such age-independent environmental components of mortality are likely to cause sex-specific effects on life span, because males might expose themselves to greater risks (for example predation) in pursuit of matings (Magnhagen, 1991; Rodríguez-Muñoz, Bretman, & Tregenza, 2011).

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

When senescence is understood in the context of life history trade-offs, it is clear that we should not expect to see a continuous decline in physiological performance, but rather a more complex pattern reflecting the life history trade-offs that underpin traits. Organisms need to grow and develop in order to reproduce. Even once an individual is reproductively mature, we expect to see increases in the expression of some traits as the capacity to express those traits develops (for instance many organisms grow continuously which affects the expression of numerous traits). Trait expression may also increase because the level of reproductive effort may increase in the face of diminishing remaining life expectancy (Duffield, Bowers, Sakaluk, & Sadd, 2017; Williams, 1966). The combination of the requirement for development and trade-offs between reproduction and somatic maintenance mean that predictions about the direction of change in trait expression may depend upon the type of organism in question. However, there remains a clear prediction that inherent differences in the life history trade-offs faced by the two sexes should lead to differences between them in age-related changes in trait expression across the adult life span. We predicted that crickets would change their patterns of activity with age, and that the pattern of this change would differ between the sexes. Broadly speaking, we expected males to show a more rapid increase in activity as individuals completed their adult development, followed by earlier and faster declines in later life. We had already found this pattern in two

sexually selected male traits, calling effort and success in fighting (Rodríguez-Muñoz, Liu et al., 2019), but had not investigated whether females show the same pattern. We expected both sexes to become less risk averse as they aged and their residual reproductive value declined (McNamara, Merad, & Houston, 1991).

METHODS

Study System

Data were extracted from the video library of WildCrickets. This is a long-term project monitoring the behaviour of a wild population of the field cricket *G. campestris* in a meadow in northern Spain. These crickets have a single generation each year with the first adults emerging in mid to late April and the last adults dying in early to mid-July. Individuals of both sexes build burrows as a refuge from predation. During the breeding season they move around the meadow displacing one another from burrows and sharing burrows with a single member of the opposite sex. All individuals spend most of their time in the immediate vicinity of a burrow, periodically retreating into it in response to threats of predation and inclement weather. Males call from their burrows to attract females but, like females, they also move around in search of mates (Fisher, Rodríguez-Muñoz, & Tregenza, 2016). From 2006 to 2017 we used up to 133 day/night video cameras to record the activity of individually identified adult crickets around their burrows for 24 h a day over the whole breeding season. Details of how the meadow is managed and our monitoring protocol are available in Rodríguez-Muñoz, Bretman, Slate, Walling, and Tregenza, (2010) and Rodríguez-Muñoz, Boonekamp, Liu, Skicko, Haugland Pedersen, Fisher, et al. (2019). The data included in this study were obtained from detailed manual analysis of recordings from 2012. This allowed us to quantify detailed activity patterns across the entire adult life span of individuals following the methodology described below.

Analysis of Video Recordings

Using our pre-existing registry of general activity around cricket burrows collected by watching all the video for 2012 at high speed (Rodríguez-Muñoz, Haugland Pedersen et al., 2019), we identified all the periods when individuals were alone at a burrow and under camera observation. A single observer (G.M.) watched the videos of these periods for each burrow (one burrow at a time) mainly at the originally recorded speed, but also utilizing slower and faster playback speeds where necessary. Cricket burrows are built as a refuge from predators; they are unbranching and too narrow for an individual to turn around (Vrenozi, Uchman, & Muceku, 2015), so we do not expect much activity to happen inside. Crickets move between burrows, but they typically do so within a few minutes, so where a burrow is under a camera, most behavioural activity can be observed in the area immediately outside the burrow. We are therefore able to record the complete range of behaviours of crickets in our population. These include singing by males and egg laying by females, which are restricted to only one sex, and behaviours such as mating and fighting, which only occur when more than one cricket is present. Except for cleaning behaviours, which involve small movements that we cannot observe reliably, for this study we analysed the complete range of behaviours seen in solitary individuals of both sexes. To quantify these, we recorded the precise time when the focal cricket changed its behaviour between the following mutually exclusive categories. (1) The cricket's entire body is completely inside the burrow. The mouth of the burrow is defined by a vertical line from the highest point on the opening of the burrow down to the floor of the burrow below it. (2) Part of the

cricket's body crosses the line defining the mouth of the burrow. Crickets moving rapidly from inside to outside the burrow may not be recorded as being in the burrow mouth if they move rapidly through this zone. (3) The cricket's entire body is outside the burrow and it is not engaging in any of the mutually exclusive activities listed below. (4) The cricket is observed physically eating; this activity included chewing and holding an item of vegetation, seeds or (rarely) an invertebrate and using its mandibles to consume part of the item. (5) The cricket suddenly flees into the burrow in response to a perceived threat within 1 s (as opposed to slowly walking into the burrow which happens frequently and which is recorded as a change from category 3 to category 2 or 1).

The timing of changes in activity was recorded to a precision of 1 min for categories 1–4, and to the nearest 1 s for the onset of fleeing (5) and for the subsequent category (1 or 2) when the cricket re-emerged from its burrow. To examine age-related variation in behaviour, we needed a standardized measure of the expression of behaviours on as many days of each individual's life as possible. Crickets frequently spend less than a whole day at a burrow (Rodríguez-Muñoz, Hopwood, et al., 2019), and movement among burrows disrupts the typical behaviours exhibited at a burrow. We could not simply use whatever portion of the day an individual was at a burrow under observation because time of day has a large effect on behaviours (Jacot, Scheuber, Holzer, Otti, & Brinkhof, 2008). Therefore, for the analyses in this study we only included observations made between 0700 and 1200 hours. This is the part of the day when crickets are most active, and levels of activity are fairly uniform across the period. By using a 5 h period, rather than 24 h, there were more days per individual where data were available for the whole of the observational period. It is of course possible that in doing so we may have missed some differences between the sexes that are more obvious at other times of day, but our study still has much more comprehensive monitoring of individuals than is normally possible in nature. We continuously monitored the air temperature using a weather station in the centre of the meadow. Our previous work (Rodríguez-Muñoz, Liu et al., 2019; Rodríguez-Muñoz, Haugland Pedersen et al., 2019) shows that in males, senescence in calling effort and fighting success does not typically manifest itself as absolute declines in performance until after around 15 days of age. Longer-lived individuals are unlikely to be a random sample of the population (Vaupel, Manton, & Stallard, 1979). However, our aim was to investigate the potential for senescent declines to differ between the sexes. Such declines cannot take place in individuals predated at very young ages. Since collecting data on individual behaviour on a minute-by-minute basis is extremely time consuming, we only collected the very detailed time budgets needed for this study for individuals living at least 20 days. This ensured that a period of 5 days after the 15-day threshold after which declines in other traits were observed in males was included for all individuals.

Quantifying Age-dependent Changes in Behaviour

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

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

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

Ethical Note

The study is based on video observations from a natural population of crickets. The only manipulation we did with the wild insects was removing them from the meadow for a maximum of a few hours during which time we take a small haemolymph sample, remove the tip of one of the hindlegs and attach a plastic tag by gluing it to the pronotum. The death of crickets during this process is very unusual (about 1–2%), and they start behaving in a natural way on being released after they have been tagged. Our tagged crickets live out their natural lives in the meadow.

RESULTS

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

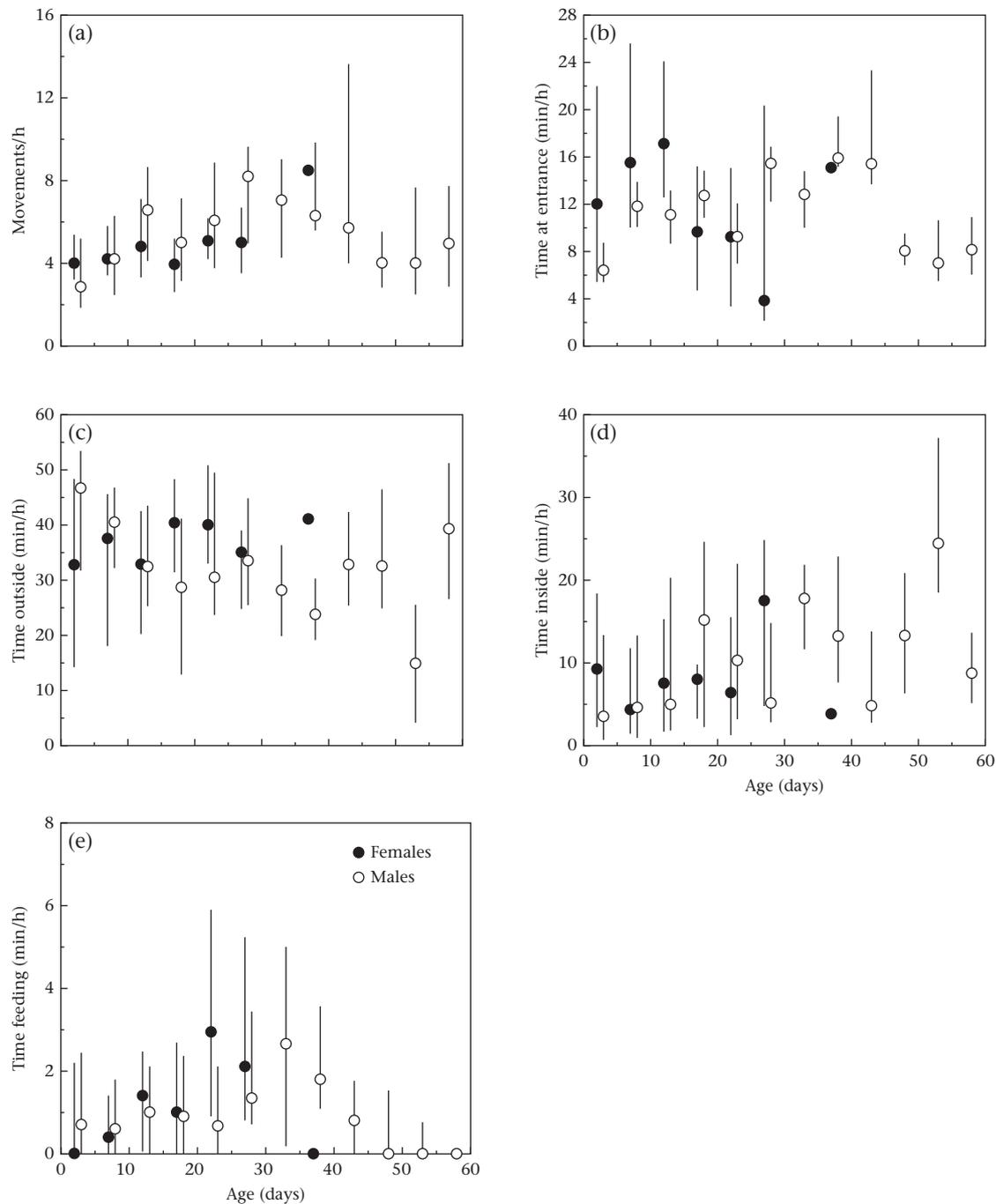


Figure 1. Relationship between age and five behavioural traits in female and male crickets (medians and quartiles) of (a) number of movements, (b) time spent at the entrance of the burrow, (c) time spent outside, (d) time spent inside the burrow and (e) time spent feeding. Values have been binned into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

Age was included in the best model for four of the five traits, the only exception being the time taken for the cricket to re-emerge after fleeing down its burrow; for this trait the simplest model had the best fit (Table 2). The best model describing the time spent outside the burrow (Outside) included a linear interaction between age and sex (Table 2). For time spent at the entrance (Waiting), the best model included age but not sex (Table 2). For how often the cricket moved in and out the burrow (Moves) and whether it fed or not during the observation period (Feeding), the best supported model included a quadratic age term, but neither model including the main term of sex, nor models including the interaction term of

sex*age were supported (Table 2). The quadratic term of age means that there is a nonlinear change in the expression of the trait with age. To determine whether this results in a peak of expression at some point in the life span, we used threshold models (Douhard, Gaillard, Pellerin, Jacob, & Lemaître, 2017; Rodríguez-Muñoz, Haugland Pedersen et al., 2019). These models allowed us to establish whether a peak was present, and if it was, at what age the trait reached its peak value. Males showed a clear peak for the two traits (10.2 days for moves and 38.4 days for feeding) but there was no evidence of a peak in females (Fig. 2). This suggests that the quadratic relationship identified in our original models (which

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

	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	

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

Table 2
Relative AICc values ($\Delta AICc$) for comparisons among models to explain variation 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

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

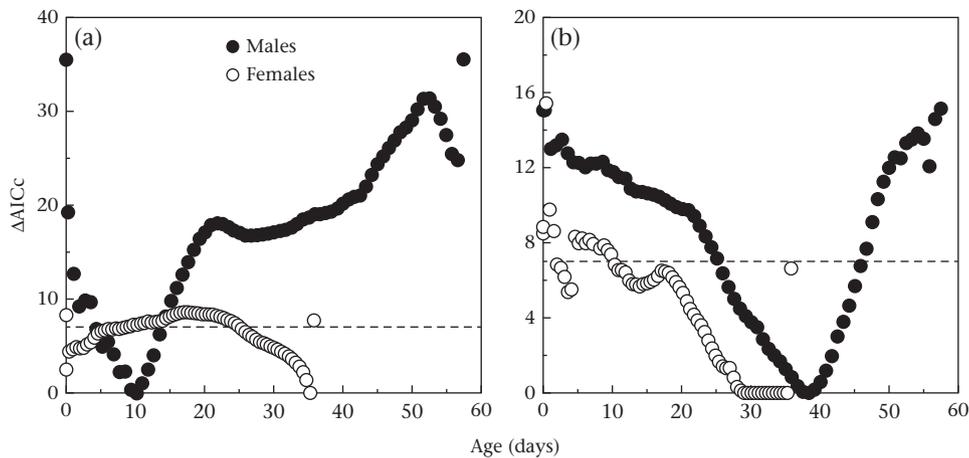


Figure 2. $\Delta AICc$ (increment in corrected Akaike information criterion) values obtained after running threshold models (Douhard et al., 2017) to identify the peak age in the expression of three traits for both sexes. (a) Moves; (b) Feeding. The broken line shows the position of $\Delta AICc = 7$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

include both males and females) are likely to be driven predominantly by the males in the data set. To investigate this, we carried out another run of model selection with separate models for each sex. This confirmed the pattern identified in the threshold models. For males, the best model included a quadratic relationship between age and the expression of both traits (Table 3). For females, no quadratic relationship was present; feeding was best explained as having a linear relationship with age, whereas for movement, age was not included (Table 3).

Analysing the effect of age in observational studies is complicated by the fact that differences between age classes can occur because of within-individual declines, or because individuals surviving to older ages may not be a random sample of the population

Table 3
Relative AICc values ($\Delta AICc$) for comparisons between models to explain variation in two behavioural traits treating males and females independently

Model	Moves		Feeding	
	Males	Females	Males	Females
TotalTime + ID	35.5	0.0	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	0.0
TotalTime + Temp + Age + Age ² + ID	0.0	10.4	0.0	0.1

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

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

	Moves			Waiting			Outside			Feeding		
	C	SD	P									
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	N	V	SD	N	V	SD	N			N
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				

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

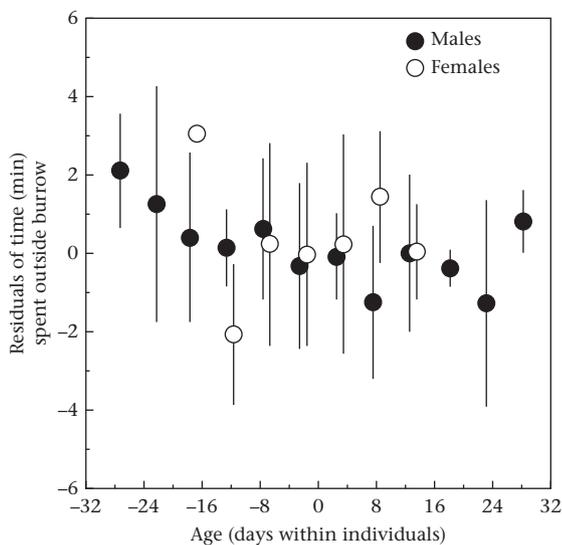


Figure 3. Changes in the time individual crickets spent outside their burrows during the daily 5 h observation period in relation to their age relative to their mean age (Δ Age). Values have been binned into age classes.

(Vaupel et al., 1979). To investigate whether age effects identified in the models described previously are artefacts of this selective disappearance, we performed additional analyses including age as two separate components on an individual basis: mean age (μ Age; the mean age across all observation periods) and delta age (Δ Age; the difference between age measured at each observation period and μ Age; Van de Pol & Wright, 2009). This allowed us to separate within-individual effects from among-individual effects, i.e. the relationship between age and the expression of the trait within individuals from any potential age-related selective mortality. For the two traits where males showed a nonlinear relationship with age (Moves and Feeding) we only analysed the life span portion after the peak, as this is the period when trait expression is declining. We included TotalTime, Temp and ID in the analyses of the four traits, and we included or excluded Sex on the basis of the results of our previous tests for model selection (Tables 2 and 3). Therefore, Moves was analysed only for males (postpeak), Waiting was analysed for both sexes separately, and Outside included both sexes and the Sex interaction with Δ Age. We had to remove males from the analysis of Feeding because the peak of the quadratic relationship between this variable and age in males happened so

late in life that insufficient data were available. Sufficient data were available in females if we removed female ID as a random effect and ran the test using a general linear model.

Males declined in the number of times they moved in and out of their burrows with Δ Age, and in the time they spent outside (Table 4). However, the time spent waiting at the entrance was not affected by age in either sex, and the probability of feeding in females increased with age (Table 4). The combined analyses of the time spent outside including both sexes showed an interaction between Sex and Δ Age. Males spent less time outside with Δ Age, but females did not (Table 4, Fig. 3).

DISCUSSION

We found evidence for age-related changes in the expression of all but one of the traits that we examined. In two of these traits (the frequency of movements through the entrance of the burrow (Moves) and the time spent outside (Outside)) we found a decline in their expression with age in males but not in females (Table 4). Because the relationship between the expression of these traits and fitness is unknown, we cannot unequivocally describe a decline in their expression as being consistent with senescence. However, movement in and out of the burrow requires energy and males can only gain fitness via attracting and mating with females which can only occur outside the burrow. Hence declines in these traits are very likely to reflect declines in expression of energetically costly behaviour and reproductive rate. This is consistent with our previous findings of age-related increases in probability of mortality and declines in male singing in later life (Rodríguez-Muñoz, Liu et al., 2019; Rodríguez-Muñoz, Haugland Pedersen et al., 2019). We found direct evidence for an interaction between sex and age both in relation to the proportion of time that individuals spent outside their burrows and in whether individuals fed or not (Table 4). Table 4 and Fig. 3 reveal that the interaction involving sex and age explaining time spent outside the burrow was caused by a consistent decline with age in males which contrasts with the lack of an effect of age in females. For whether an individual fed or not, the figure suggests an increase in expression in females and no pattern in males (Table 4, Fig. 3).

Two of the traits that changed with age, Moves and Feeding, showed a quadratic relationship with age. We investigated this relationship using threshold models (Douhard et al., 2017). This revealed that there was clear evidence of a peak age in relation to the expression of both traits in males but not for females (shown in Fig. 2) by the sharply lower AICc value for the males' model, with a

peak at around 10 and 38 days, respectively, and no evidence of a peak in females. This apparent sex difference is supported by the separate models of ageing in males and females shown in Table 3, where the best fitting model includes a quadratic effect of age in males, but not in females. There is something of a contradiction between this observation of an apparent sex difference in age trajectories in the analyses in Fig. 2 and Table 3 and the lack of a significant interaction between sex and age in our original model selection procedure for these traits (Table 2). This might be due to the low power of the quadratic models to detect these differences in the absence of a clear peak of expression. For Moves, the portion of life postpeak showed a significant decline in males, whereas in females there was no evidence that Moves was affected by age. For Feeding, our results are inconclusive. We could not analyse the postpeak portion in males, although the existence of a peak indicates that at least there was a continuously decelerating effect of age. In females the relationship was positive over their whole life, but because we do not have female data for ages after the peak age of males, it is unclear whether there is really any sex difference in the expression of this trait. The lack of data for very old females in this subset of our population is not reflected in the population as a whole where males and females have very similar average life spans (Rodríguez-Muñoz, Haugland Pedersen et al., 2019).

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

The only trait that did not show a change in expression with age in either sex was the time it took individuals to re-emerge from their burrows after a predator fleeing event. Hiding in the burrow is a risk avoidance strategy that carries the cost of reducing the time available for reproduction. Therefore, our prediction was that as individuals aged and their future reproductive potential decreased, they would be more likely to take risks (McNamara et al., 1991). We

did not observe this effect. This might indicate that it is absent, or that senescent declines in speed of movement balance out a greater willingness to re-emerge. This latter possibility does not seem very likely, however, because re-emergence only involves the cricket slowly reversing out of the burrow which is within the capacity of even very old crickets. Closely related to this is our finding that the time spent at the entrance of the burrow increased with age in a similar way for both sexes. This might be indicative of senescence, as it means that they take more time to move between being inside or outside of their burrows.

Overall, our study confirms our earlier findings of a general pattern of age-related declines in performance in wild crickets. We found evidence for sex differences in how traits change with age. These differences manifested as divergent patterns of age-dependent changes in trait expression. Males showed significant peaks of expression during adulthood in two of the behaviours we studied, with subsequent declines in old age, whereas in females there was no conclusive evidence for quadratic forms of variation in trait expression. Neither sex appeared to become less risk averse with age. Our results are consistent with life history theories of senescence, which predict that selection for sex-specific differences in reproductive strategies might result in differences in the patterns of senescence between the sexes.

Data Availability

Data are archived at the University of Exeter Repository: <https://ore.exeter.ac.uk/repository/>

Acknowledgments

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

References

- Barton, K. (2019). *MuMIn: Multi-Model Inference*. R package, version 1.43.6 <https://CRAN.R-project.org/package=MuMIn>.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 48. <https://doi.org/10.18637/jss.v067.i01>.
- Beirne, C., Delahay, R., & Young, A. (2015). Sex differences in senescence: The role of intra-sexual competition in early adulthood. *Proceedings of the Royal Society B: Biological Sciences*, 282. Retrieved from <http://rspb.royalsocietypublishing.org/content/282/1811/20151086.abstract>.
- Bonduriansky, R., Maklakov, A., Zajitschek, F., & Brooks, R. (2008). Sexual selection, sexual conflict and the evolution of ageing and life span. *Functional Ecology*, 22(3), 443–453. <https://doi.org/10.1111/j.1365-2435.2008.01417.x>.
- Boonekamp, J. J., Salomons, M., Bouwhuis, S., Dijkstra, C., & Verhulst, S. (2014). Reproductive effort accelerates actuarial senescence in wild birds: An experimental study. *Ecology Letters*, 17(5), 599–605.
- Briga, M., Koetsier, E., Boonekamp, J. J., Jimeno, B., & Verhulst, S. (2017). Food availability affects adult survival trajectories depending on early developmental conditions. *Proceedings of the Royal Society B: Biological Sciences*, 284(1846).

- Retrieved from <http://rspb.royalsocietypublishing.org/content/284/1846/20162287.abstract>.
- Brooks, R. C., & Garratt, M. G. (2017). Life history evolution, reproduction, and the origins of sex-dependent aging and longevity. *Annals of the New York Academy of Sciences*, 1389(1), 92–107. <https://doi.org/10.1111/nyas.13302>.
- Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, 65(1), 23–35. <https://doi.org/10.1007/s00265-010-1029-6>.
- Clutton-Brock, T., & Isvaran, K. (2007). Sex differences in ageing in natural populations of vertebrates. *Proceedings of the Royal Society of London B Biological Sciences*, 274(1629), 3097–3104.
- Cornwallis, C. K., Dean, R., & Pizzari, T. (2014). Sex-specific patterns of aging in sexual ornaments and gametes. *American Naturalist*, 184(3), E66–E78. <https://doi.org/10.1086/677385>.
- Douhard, F., Gaillard, J.-M., Pellerin, M., Jacob, L., & Lemaître, J.-F. (2017). The cost of growing large: Costs of post-weaning growth on body mass senescence in a wild mammal. *Oikos*, 126(9), 1329–1338. <https://doi.org/10.1111/oik.04421>.
- Duffield, K. R., Bowers, E. K., Sakaluk, S. K., & Sudd, B. M. (2017). A dynamic threshold model for terminal investment. *Behavioral Ecology and Sociobiology*, 71(12), 185. <https://doi.org/10.1007/s00265-017-2416-z>.
- Fisher, D. N., Rodríguez-Muñoz, R., & Tregenza, T. (2016). Wild cricket social networks show stability across generations. *BMC Evolutionary Biology*, 16. <https://doi.org/10.1186/s12862-016-0726-9>.
- Holand, H., Kvalnes, T., Gamelon, M., Tufto, J., Jensen, H., Pärn, H., Ringsby, T. H., & Sæther, B.-E. (2016). Spatial variation in senescence rates in a bird metapopulation. *Oecologia*, 181, 865–871. <https://doi.org/10.1007/s00442-016-3615-4>.
- Jacot, A., Scheuber, H., Holzer, B., Ottili, O., & Brinkhof, M. W. G. (2008). Diel variation in a dynamic sexual display and its association with female mate-searching behaviour. *Proceedings of the Royal Society Biological Sciences*, 275(1634), 579–585. <https://doi.org/10.1098/rspb.2007.1500>.
- Kawasaki, N., Brassil, C. E., Brooks, R. C., & Bonduriansky, R. (2008). Environmental effects on the expression of life span and aging: An extreme contrast between wild and captive cohorts of *Telostylinus angusticollis* (Diptera: Neriidae). *American Naturalist*, 172(3), 346–357.
- Kirkwood, T. B. L., & Rose, M. R. (1991). Evolution of senescence: Late survival sacrificed for reproduction. *Philosophical Transactions of the Royal Society: Biological Science*, 332(1262), 15–24. Retrieved from <http://www.jstor.org/stable/55487>.
- Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7(5), 573–579. <https://doi.org/10.1111/2041-210x.12512>.
- Magnhagen, C. (1991). Predation risk as a cost of reproduction. *Trends in Ecology & Evolution*, 6(6), 183–186. [https://doi.org/10.1016/0169-5347\(91\)90210-O](https://doi.org/10.1016/0169-5347(91)90210-O).
- McNamara, J. M., Merad, S., & Houston, A. I. (1991). A model of risk-sensitive foraging for a reproducing animal. *Animal Behaviour*, 41(5), 787–792. [https://doi.org/10.1016/S0003-3472\(05\)80345-8](https://doi.org/10.1016/S0003-3472(05)80345-8).
- Monaghan, P., Charmantier, A., Nussey, D. H., & Ricklefs, R. E. (2008). The evolutionary ecology of senescence. *Functional Ecology*, 22(3), 371–378.
- Nussey, D. H., Froy, H., Lemaître, J.-F., Gaillard, J.-M., & Austad, S. N. (2013). Senescence in natural populations of animals: Widespread evidence and its implications for bio-gerontology. *Ageing Research Reviews*, 12(1), 214–225.
- Nussey, D. H., Kruuk, L. E., Morris, A., Clements, M. N., Pemberton, J. M., & Clutton-Brock, T. H. (2009). Inter- and intrasexual variation in aging patterns across reproductive traits in a wild red deer population. *American Naturalist*, 174(3), 342–357.
- Péron, G., Lemaître, J.-F., Ronget, V., Tidière, M., & Gaillard, J.-M. (2019). Variation in actuarial senescence does not reflect life span variation across mammals. *PLoS Biology*, 17(9), e3000432. <https://doi.org/10.1371/journal.pbio.3000432>.
- Promislow, D. (1992). Costs of sexual selection in natural populations of mammals. *Proceedings of the Royal Society Biological Sciences*, 247(1320), 203–210. <https://doi.org/10.1098/rspb.1992.0030>.
- Rodríguez-Muñoz, R., Boonekamp, J. J., Fisher, D., Hopwood, P., & Tregenza, T. (2019). Slower senescence in a wild insect population in years with a more female-biased sex ratio. *Proceedings of the Royal Society B: Biological Sciences*, 286(1900), 20190286. <https://doi.org/10.1098/rspb.2019.0286>.
- Rodríguez-Muñoz, R., Boonekamp, J. J., Liu, X. P., Skicko, I., Fisher, D. N., Hopwood, P., et al. (2019). Testing the effect of early-life reproductive effort on age-related decline in a wild insect. *Evolution*, 73, 317–328. <https://doi.org/10.1111/evo.13679>.
- Rodríguez-Muñoz, R., Boonekamp, J. J., Liu, X. P., Skicko, I., Haugland Pedersen, S., Fisher, D. N., et al. (2019). Comparing individual and population measures of senescence across 10 years in a wild insect population. *Evolution*, 73, 293–302. <https://doi.org/10.1111/evo.13674>.
- Rodríguez-Muñoz, R., Hopwood, P., Fisher, D., Skicko, I., Tucker, R., Woodcock, K., et al. (2019). Older males attract more females but get fewer matings in a wild field cricket. *Animal Behaviour*, 153, 1–14. <https://doi.org/10.1016/j.anbehav.2019.04.011>.
- Rodríguez-Muñoz, R., Bretman, A., Slate, J., Walling, C. A., & Tregenza, T. (2010). Natural and sexual selection in a wild insect population. *Science*, 328(5983), 1269–1272. <https://doi.org/10.1126/science.1188102>.
- Rodríguez-Muñoz, R., Bretman, A., & Tregenza, T. (2011). Guarding males protect females from predation in a wild insect. *Current Biology*, 21(20), 1716–1719. <https://doi.org/10.1016/j.cub.2011.08.053>.
- Rose, M. R. (1991). *Evolutionary biology of aging*. New York, NY: Oxford University Press.
- Shefferson, R. P., Jones, O. R., & Salguero-Gómez, R. (2017). *The evolution of senescence in the tree of life*. Cambridge, U.K.: Cambridge University Press.
- Sparkman, A. M., Blois, M., Adams, J., Waits, L., Miller, D. A. W., & Murray, D. L. (2016). Evidence for sex-specific reproductive senescence in monogamous cooperatively breeding red wolves. *Behavioral Ecology and Sociobiology*, 71(1), 6. <https://doi.org/10.1007/s00265-016-2241-9>.
- Trivers, R. L. (1871–1971). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 1871–1971). Chicago, IL: Aldine-Atherton, 136–172.
- Van de Pol, M., & Wright, J. (2009). A simple method for distinguishing within-versus between-subject effects using mixed models. *Animal Behaviour*, 77(3), 753–758.
- Vaupel, J. W., Manton, K. G., & Stallard, E. (1979). The impact of heterogeneity in individual frailty on the dynamics of mortality. *Demography*, 16(3), 439–454. <https://doi.org/10.2307/2061224>.
- Vinogradov, A. E. (1998). Male reproductive strategy and decreased longevity. *Acta Biotheoretica*, 46(2), 157–160. <https://doi.org/10.1023/a:1001181921303>.
- Vrenozi, B., Uchman, A., & Muceku, B. (2015). First data on the burrows of *Gryllus campestris* Linnaeus, 1758 from dajti mountain, Albania. In *13th International Ichnofabric Workshop, Ichnofabric Studies Linking Past, Present, and Future, Kochi, Japan*.
- Williams, G. C. (1957). Pleiotropy, natural selection, and the evolution of senescence. *Evolution*, 11, 398–411.
- Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist*, 100(916), 687–690.
- Zajitschek, F., Bonduriansky, R., Zajitschek, S. R. K., & Brooks, R. C. (2009). Sexual dimorphism in life history: Age, survival, and reproduction in male and female field crickets *Teleogryllus commodus* under seminatural conditions. *American Naturalist*, 173(6), 792–802. <https://doi.org/10.1086/598486>.
- Zajitschek, F., Brassil, C. E., Bonduriansky, R., & Brooks, R. C. (2009). Sex effects on life span and senescence in the wild when dates of birth and death are unknown. *Ecology*, 90(6), 1698–1707. Retrieved from <http://www.jstor.org/stable/25592671>.
- Zajitschek, F., Zajitschek, S., & Bonduriansky, R. (2019). Senescence in wild insects: Key questions and challenges. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.13399>.