Understanding the link between sexual selection, sexual conflict and aging using crickets as a model

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A R T I C L E   I N F O

A B S T R A C T

Aging evolved because the strength of natural selection declines over the lifetime of most organisms. Weak natural selection late in life allows the accumulation of deleterious mutations and may favor alleles that have positive effects on fitness early in life, but costly pleiotropic effects expressed later on. While this decline in natural selection is central to longstanding evolutionary explanations for aging, a role for sexual selection and sexual conflict in the evolution of lifespan and aging has only been identified recently. Testing how sexual selection and sexual conflict affect lifespan and aging is challenging as it requires quantifying male age-dependent reproductive success. This is difficult in the invertebrate model organisms traditionally used in aging research. Research using crickets (Orthoptera: Gryllidae), where reproductive investment can be easily measured in both sexes, has offered exciting and novel insights into how sexual selection and sexual conflict affect the evolution of aging, both in the laboratory and in the wild. Here we discuss how sexual selection and sexual conflict can be integrated alongside evolutionary and mechanistic theories of aging using crickets as a model. We then highlight the potential for research using crickets to further advance our understanding of lifespan and aging.

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1. Introduction

From a demographic perspective, aging is a decline in fertility and rise in mortality risk over time (Baudisch and Vaupel, 2012). Evolutionary explanations for aging rely on the observation that natural selection grows weaker over an organism's lifetime (Haldane, 1942; Hamilton, 1966). This decline in natural selection allows the accumulation of mutations with costly, late-acting effects on fitness (Mutation Accumulation — Medawar, 1952), favors alleles with positive fitness effects early in life, even if they have negative pleiotropic effects expressed later (Antagonistic Pleiotropy — Williams, 1957) and promotes age-associated declines in somatic maintenance (Disposable Soma — Kirkwood, 1977). Natural selection is clearly central to evolutionary explanations for aging, however, we are only beginning to understand how sexual selection and sexual conflict affect the aging process.

Sexual selection occurs because one sex, usually females, invests more heavily in producing offspring than the other sex; fundamentally, males make many, tiny sperm while females produce fewer, large eggs (Trivers, 1972). Because males invest minimally in each offspring they can allocate extra resources towards attracting females (Trivers, 1972). Females then choose from among competing males on the basis of traits that signal the direct material benefits a male may offer at mating (e.g. parental care) or indirect genetic benefits that improve offspring viability (Zahavi, 1975) or attractiveness (Fisher, 1930). This promotes the evolution of traits that help males win intersexual contests (e.g. antlers) and attract females (e.g. bright plumage). Males that invest more heavily in these traits typically gain greater reproductive success. By influencing the nature and the scheduling of reproductive investment, sexual selection can affect the evolution of aging and lifespan (Bonduriansky et al., 2008), particularly in species where sexual selection is intense (e.g. polygamous species). For example, while females often show a steady rate of reproduction, males may increase their reproductive success by investing intensively in reproductive effort early in life, even if this comes at the expense of reduced lifespan (e.g. due to injury or predation) (Kokko, 1998; Vinogradov, 1998). This "live fast, die young" strategy may promote the evolution of shorter lives in males and possibly faster or earlier aging (Bonduriansky et al., 2008). Alternatively, sexual selection may lead to improved reproductive success as males age, for example if older males produce more attractive sexual signals (e.g. learn more complex songs). In this case, males should experience selection for increased lifespan and possibly, slower or later aging (Graves, 2007). Sexual selection can also favor longer lives in males if female choice for high quality males also selects for alleles with positive, pleiotropic effects on lifespan and aging (Bonduriansky et al., 2008; Promislow, 2003). If sexual selection

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promotes sex-specific schedules of reproductive success and in turn, intersexual differences in lifespan and aging, it may lead to sexual conflict over these traits (Bonduriansky et al., 2008; Promislow, 2003).

Sexual conflict occurs when there is sexually antagonistic selection over alleles at one locus (*intralocus conflict*) or different loci (*interlocus conflict*) (Arnqvist and Rowe, 2005). Interlocus sexual conflict arises when each sex has a different optimal outcome in male–female interactions and evolves different traits to bias the outcome of these exchanges. The resultant antagonistic co-evolution can result in an "arms race", whereby adaptations in one sex are harmful for the other (Arnqvist and Rowe, 2005). This may reduce lifespan in one or both sexes (Bonduriansky et al., 2008). A classic example of this is traumatic insemination in bed bugs (*Cimex lectularius*), where a male inseminates a female by piercing her abdominal wall with his genitalia (Stutt and Siva-Jothy, 2001). This improves a male's probability of fertilizing ova but reduces female lifespan and reproductive success (Stutt and Siva-Jothy, 2001). Alternatively, intralocus sexual conflict (IASC) occurs when one trait has a common genetic basis in either sex but sex-specific optima (Bonduriansky and Chenoweth, 2009). This leads to a "tug-of-war" over shared alleles (Rice and Chippindale, 2001), which can constrain trait evolution in either sex and prevent one or both sexes from reaching their phenotypic optimum (Bonduriansky and Chenoweth, 2009). This could improve lifespan in one sex, while reducing it in the other (Bonduriansky et al., 2008). For example, in the Indian mealmoth (*Plodia interpunctella*) selection on lifespan is opposing in the sexes (positive in males and negative in females) but there is a positive genetic correlation for this shared trait across the sexes (Lewis et al., 2011). Females appear to be winning the IASC over this trait as males are displaced further from their optimal lifespan (Lewis et al., 2011). It is unclear how sexual conflict affects aging parameters (e.g. aging rates and/or baseline mortality) to achieve these effects on lifespan (Bonduriansky et al., 2008).

Clearly, there is an established body of theory predicting how sexual selection and sexual conflict should affect the evolution of aging and lifespan. Testing these theories requires measuring age-dependent reproductive effort and/or success. It is possible to collect such data in many species of insects, fish, birds and mammals, for example by using competitive mating assays. However, quantifying reproductive success in many species is often labor intensive and requires continuous monitoring by a researcher. Crickets share the strengths of all invertebrate models of aging in that they are small, easy to maintain and relatively short lived. Most cricket species also express a sexually selected trait (calling to attract females) that can be easily measured using high through-put and automated methods (Fig. 1) and used as a measure of reproductive success in the laboratory and in the wild. This means that sexually selected traits and female choice can be easily measured in large numbers of animals, making crickets a powerful model to integrate sexual selection, sexual conflict and aging.

In this article, we start by summarizing sexual selection research in crickets in general and then discuss how studies have used crickets to integrate sexual selection, sexual conflict and evolutionary theories of aging in the laboratory and the field. We then discuss the mechanisms by which sexual selection and sexual conflict could affect aging and lifespan. To do this, we first consider how sexual selection affects the association between nutrition and aging in either sex. We then discuss the potential for research on crickets to test the effects of sexual selection on cellular processes implicated in aging (e.g. oxidative damage). Finally, we summarize the strengths and weaknesses of crickets as an aging model and highlight potential areas where research on crickets could further improve our understanding of the evolution and mechanistic basis of aging.

2. Sexual selection in crickets

Crickets have diverse life cycles both across and within species. In some populations all developmental stages are present throughout the year, while in others, crickets enter diapause over winter and emerge in spring (Masaki and Walker, 1987). Despite this diversity, male sexual display and female choice behaviors are surprisingly consistent (Zuk and Simmons, 1997). In general, advertisement begins each night when a male produces a call to attract females, typically from sheltered cracks in the ground or burrows. Males often fight to defend these territories (Alexander, 1961) and how well a male fights may reflect his quality or condition (Rantala and Kortet, 2004). Consequently, females prefer dominant males in some species (Kortet and Hedrick, 2005) but not all (Shackleton et al., 2005). From their calling sites, males stridulate their modified forewings to produce a long-range advertisement call (Alexander, 1961) (Fig. 1A) and this energetically expensive display (Kavanagh, 1987) can signal male quality to females (Ryder, 2000). Females orient and move towards the most attractive calls, meaning that how long a male spends calling each night is often the primary determinant of how many females he attracts (Bentsen et al., 2006; Ketola et al., 2007). Once a female has reached a male, she can assess two further sexual signals. The first is a short-range courtship call that a male produces when a female is near and is typically coupled with a courtship display where a male strokes the female with his antennae and presents his posterior for her to mount (Alexander, 1961) (Fig. 1B). The second is the cuticular hydrocarbon (CHC) profile of the male. CHCs cover the exoskeletons of terrestrial arthropods and evolved primarily to protect against water loss (Blomquist and Bagnères, 2010). However, CHCs are also used in mate choice, for example females in some species prefer mates with dissimilar CHC profiles, which reflects genetic dissimilarity and compatibility between partners (Thomas and Simmons, 2011). A combination of these auditory, chemical and behavioral cues helps females choose a mate. However, even after mating, a male's reproductive success is not assured as females often mate multiply and store sperm (Zuk and Simmons, 1997), creating the opportunity for sperm competition (Simmons et al., 2014). Variation in sperm competitive ability or cryptic female choice can bias the outcome of this competition in favor of particular males (Simmons et al., 2014). Males often attempt to improve their fertilization success, most simply by transferring larger volumes of sperm and preventing females from remating through mate guarding and the production of a nuptial gift (Fig. 1C).

Clearly, sexual selection is well understood in many cricket species. This is because it is relatively easy to measure reproductive effort in both males and females; a challenging (if not impossible) task in many invertebrates. Female reproductive effort can be measured by counting eggs (e.g. Head et al., 2005), and male reproductive effort (calling) can be easily measured using acoustic recording devices (Fig. 1D). This allows us to measure male and female reproductive effort across the life course and to integrate measures of aging alongside reproductive trajectories. Crickets can also be kept in large numbers, allowing us to accurately estimate aging parameters (e.g. aging rates or initial mortality rates) from mortality models (e.g. Gompertz, Weibull, Logistic). When we talk about measuring aging from hereon we are referring to these parameter estimates. The synchronous emergence of many cricket species, coupled with their relatively large size, means that we can assay aging, lifespan and female choice (Fig. 1E) in wild crickets, for example by using classic capture-mark-recapture techniques (Zajitschek et al., 2009b) or video monitoring (Rodríguez-Muñoz et al., 2010) (Fig. 1F–G). This is not possible in most invertebrate models used in aging research (e.g. *Drosophila*, *C. elegans*). In the laboratory, crickets can be reared quickly (typically 6–10 weeks) in large numbers, facilitating quantitative genetic studies to test for IASC over lifespan and rates of aging (e.g. Zajitschek et al., 2007). Finally, powerful dietary manipulation methods have been optimized for crickets (Maklakov et al., 2008) allowing tests of sex-specific nutritional constraints on aging and lifespan. Collectively, these features make crickets a powerful invertebrate model for asking how sexual selection and sexual conflict affect the evolution and mechanistic basis of lifespan and aging.
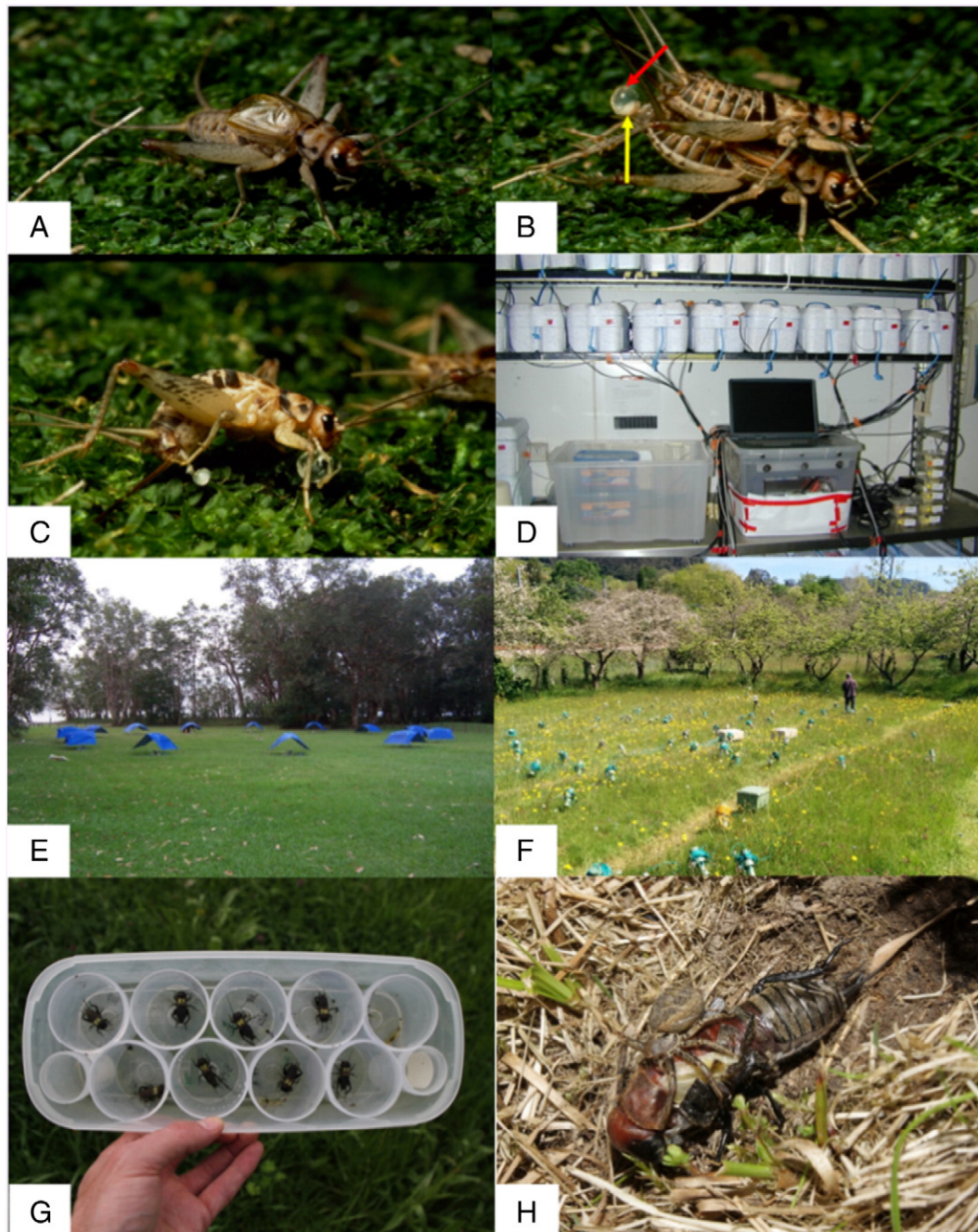
Fig. 1. Mating in decorated crickets (*Gryllodes sigillatus*) (A–C). A male produces an advertisement call to attract a mate (A). At mating, the male transfers a sperm containing ampulla (yellow arrow) and a nuptial gift (the spermatophylax, red arrow) to a female (B). The female eats this gift while sperm transfers from the ampulla to her reproductive tract. The male stands nearby to guard the female during sperm transfer (C). The larger the gift, the more sperm is transferred and the higher a males' probability of paternity (images courtesy of David Funk). Quantifying male calling effort in field crickets (D). To record how much time a male cricket spends calling, males are kept overnight in plastic containers in sound-proof boxes. Microphones in the lid of these containers record songs that are relayed to a computer, which recognizes and stores songs (D). Studying crickets in the wild (E–H). Measuring female choice in a wild population (E). Bentsen et al. (2006) used speakers (underneath blue covers to prevent rain damage) to play one of 300 unique experimental calls, a control call (the average call produced in the study population) or a silent control. Fifty females collected from a nearby field were released nightly at the center of the arena and the number of females caught on a sticky trap under each speaker was used as a measure of the attractiveness of the associated call. Video monitoring of wild cricket populations (F). Cameras in a field in Spain sit beside the burrows of individually labeled *Gryllus campestris* (G) that were monitored 24 h a day for an entire breeding season. This captured a suite of cricket behaviors (e.g. calling, fighting) and mortality (i.e. predation) events (H) (images courtesy of wildcrickets.org).

3. Sexual selection, lifespan and aging in crickets

To test predictions about how sexual selection affects lifespan and aging, we need to know how the reproductive success of each sex changes over time (Bonduriansky et al., 2008; Graves, 2007; Promislow, 2003) and estimate lifespan and aging parameters in both sexes. Ideally, these data would be collected in both the laboratory and the field. The importance of studying aging in both of these environments has been argued repeatedly: in the laboratory we can largely control environmental hazards (e.g. predation, starvation) and replicate experiments but the results we find may not reflect natural populations (Bronikowski and Promislow, 2005). Fortunately, crickets are amenable to being studied in both the laboratory and the wild. In the following sections we summarize what laboratory and field research on crickets has taught us about the effects of sexual selection on lifespan and aging.

3.1. Lessons from laboratory studies

Sexual selection may affect lifespan and aging by changing age-dependent reproductive success in either sex and in turn, the strength of selection against age-associated rises in mortality (Bonduriansky et al., 2008; Graves, 2007; Promislow, 2003). There is good evidence for this in crickets. Laboratory studies have shown that in some species, males show declines in calling effort or quality consistent with reproductive senescence, while other species do not experience these declines or produce better or more energetic calls over time (Table 1). Testing how readily females move towards the calls of males of different ages shows that females can distinguish between males based on age, preferring older males in some species and younger males in others (Table 2). This means that there is enormous scope, at least in the laboratory, for sexual selection to affect the evolution of lifespan and aging.

One of the first studies to explicitly test how sexual selection affects aging used Australian black field crickets (*Teleogryllus commodus*) reared individually from hatching on different diets and measured aging using the two-parameter Gompertz mortality model. This study found sex differences in reproductive schedules: across all dietary treatments, as they aged female fecundity declined while males called more (Zajitschek et al., 2009c). As time spent calling is the primarily determinant of male reproductive success in this species (Bentsen et al., 2006), age-dependent rises in calling effort may mean that older males gain more mates. In agreement with theoretical predictions, these males lived longer lives and aged more slowly than females (Zajitschek et al., 2009c). An almost identical result was found in individually housed decorated crickets (*Gryllodes sigillatus*) from eight highly inbred lines (Archer et al., 2012). In *G. sigillatus*, females experienced fecundity declines while males showed age-dependent rises in calling effort.

Table 1
Changes in male call parameters over time in the laboratory (A) and field (B). This table is based on Verburgt et al. (2011) but has been expanded to include recent literature and only presents data for studies that did not apply dietary manipulation.

Species	Trait and age associated changes			Ref
	Increase	Decrease	No change	
A. Laboratory studies				
Acheta domesticus			Amplitude; frequency; inter-chirp interval; pulses/chirp	[1]
Gryllus assimilis	Amplitude; chirp duration; chirp rate; pulse duration; pulses/chirp; pulse rate; signaling time	Carrier frequency; inter-chirp duration; inter-pulse duration		[2]
G. bimaculatus	Chirp duration; chirp period; inter-chirp interval; inter-syllable interval; pulses/chirp; syllable period	Bandwidth; calling activity dispersion; carrier frequency; daily calling activity; duty cycle; relative amplitude; syllable duration	Peak calling activity	[3]
G. campestris		Carrier frequency; chirp length; syllables/chirp;	Chirp energy; chirp rate; inter-chirp duration	[4]
G. integer			Time spent calling	[5]
G. integer	Time spent calling[a]	Time calling started; time spent calling[a]; mean time calling	Time calling stopped	[6]
G. integer			Pulses/trill	[7]
G. integer			Inter-syllable length; inter-trill interval; missed syllables; peak frequency; syllable rate; syllable length; syllable duty cycle; syllables/trill; trill length; trill duty cycle	[8]
G. integer			Missed syllables/trill; syllable rate	[9]
G. pennsylvanicus			Time spent calling	[5]
G. pennsylvanicus			Chirp duration; inter-chirp duration; syllables/chirp; syllable rate	[10]
G. rubens			Pulse rate	[11]
G. texensis			Pulse rate	[11]
G. veletis			Time spent calling	[5]
G. veletis	Time spent calling; pulses/chirp; chirp duration; inter-chirp duration; pulse duration; inter-pulse duration	Calling effort; song duration; pulse rate; amplitude; carrier frequency		[12]
Oecanthus nigricornis		Pulse duration	Frequency; pulse period	[13]
Teleogryllus africanus			Time spent calling	[5]
T. oceanicus			Song duration; proportion of song that is long chirp. In long chirp: carrier frequency; duration; inter-syllable interval; syllable duration; syllable number; syllable rate. In short chirp: carrier frequency; chirp number; chirp rate; duration; inter-chirp interval; inter-syllable interval; syllable duration.	[14]
B. Field studies				
G. bimaculatus	Coefficient of variation (CV) syllable rate		Chirp duration; chirp interval; chirp rate; fundamental frequency; q3 (tuning at −3 db); syllables/chirp; syllable duration; syllable interval; syllable rate; cv all traits bar syllable rate	[15]
G. campestris			Bouts/min; bout duration; chirp duration; chirp rate; inter-pulse interval; inter-chirp interval; inter-bout interval; pulse duration; pulse rate	[16]
G. integer			Time spent calling	[5]
T. commodus			Effort[b]	[17]

References: [1] (Gray, 1997); [2] (Bertram and Rook, 2011); [3] (Verburgt et al., 2011); [4] (Jacot et al., 2007); [5] (Cade and Wyatt, 1984); [6] (Bertram, 2000); [7] (Gray and Cade, 1999); [8] (Martin et al., 2000); [9] (Souroukis et al., 1992); [10] (Ciceran et al., 1994); [11] (Walker, 2000); [12] (Fitzsimmons and Bertram, 2011); [13] (Brown et al., 1996); [14] (Walker and Cade, 2003); [15] (Simmons and Zuk, 1992); [16] (Simmons, 1995); [17] (Zajitschek et al., 2009a).
  [a] Time spent calling peaked in mid-life.
  [b] No effect of age on calling effort was found when individuals that did not call were excluded from analysis.

Table 2
The association between male age and how readily females orient towards their call (A) and the likelihood that a male will gain a mating in either the laboratory (B) or in the wild (C). The terms "young" and "old" are comparative and so the exact age of young or old males differs across studies. The high reproductive success of old males in the field relative to the laboratory may reflect that older males are often bigger and so may gain more reproductive success by outcompeting their rivals in a natural setting. This means that older males may be either more attractive to females or have greater success in male–male competition. Laboratory tests can be used to distinguish between these possibilities, for example by measuring copulation latency to assay male attractiveness in different male age cohorts.

Species	Lab/field	Age class with greatest success	Ref
A. Female response to call			
Ephippiger ephippiger	Lab	Young	[1]
Gryllus bimaculatus	Lab	Young	[2]
G. pennsylvanicus	Semi-natural	Old	[3]
G. veletis	Semi-natural	Old	[3]
Oecanthus nigricornis	Lab	None	[4]
Poecilimon schmidti	Lab	None	[5]
B. Mating trials			
G. integer	Lab	None	[6]
G. pennsylvanicus	Lab	Young/old[a]	[7]
C. Comparison of male age in mating versus solitary males			
G. bimaculatus	Field	Old	[8]
G. campestris	Field	Old	[9]
G. pennsylvanicus	Field	Old	[10]
G. veletis	Field	Old	[10]

References: [1] (Ritchie et al., 1995); [2] (Verburgt et al., 2011); [3] (Zuk, 1987b); [4] (Brown et al., 1996); [5] (Hartley and Stephen, 1989); [6] (Proctor, 1994); [7] (Judge, 2010); [8] (Simmons and Zuk, 1992); [9] (Simmons, 1995); [10] (Zuk, 1988).

[a] Female preference for male age was affected by mating experience; virgin females preferred particular male age/size combinations (old/large and young/small) while females reared in mixed-sex populations preferred older males.

Accordingly, males lived longer and aged more slowly than females, although in this species males experienced greater baseline mortality. Clearly, sexual selection can drive differences in aging and lifespan in the direction predicted by current theory. It remains unclear on the basis of these studies however, if sexual selection drives the evolution of sex differences in lifespan and aging in natural populations.

3.2. Lessons from field studies

While it is important to study aging in the field, it is challenging. Traditionally, to assess the relationship between age and reproductive success, cricket studies have compared the ages of paired (i.e. mating) and unpaired males (Table 2) by counting the growth rings in the hind tibia of captured males in these categories. Growth rings are daily growth layers present in the cuticle that enable crickets from the wild to be aged, much like fish scales or otoliths (Neville, 1963). However, this approach has limitations. First, it is unlikely that the correlation between pairing status and reproductive success will be particularly strong. In most cricket species, females are highly polyandrous, store the sperm of multiple males and the post-mating hatching success of eggs is highly variable (e.g. Tregenza and Wedell, 2002). These factors could weaken the relationship between pairing success and reproductive success and obscure any relationship between age and fitness. Second, although the number of growth rings is equivalent to the number of days post-eclosion until the cricket is 25–30 days old, cuticle growth is complete after this point and no further rings are added (Zuk, 1987a). Consequently, crickets older than 25–30 days cannot be reliably aged using this technique. Finally, comparing growth rings in paired and solitary crickets only captures a snap-shot of the age structure of a study population. Age structure will change across the season so this snap-shot will depend heavily on when a population is sampled. While this is information is useful, it is better to collect longitudinal data on age-dependent reproductive success and lifespan in individual animals (Nussey et al., 2008).

To this end, Zajitschek et al. (2009a) monitored survival daily in 79 male and 134 female Australian field crickets (*T. commodus*) in semi-natural field enclosures (labeling method similar to Fig. 1G). In these enclosures both sexes experienced declines in reproductive effort over time, although these began earlier and were more pronounced in females than males. Females also aged faster than males. However, unlike in laboratory studies of this species, males experienced consistently higher baseline mortality and died earlier than females (Zajitschek et al., 2009a). Living in a semi-natural environment clearly imposed severe costs on males, reducing their ability to invest in reproduction and elevating their mortality. This effect was even more pronounced when aging was assayed in wild crickets (Zajitschek et al., 2009b). Here, adult crickets were individually labeled and survival was monitored using capture-mark-recapture techniques (recapture probabilities 32.1% — males, 46.7% — females). Once again, male baseline mortality was so high that females lived longer than males. That is, the sex differences in lifespan observed in the laboratory were reversed when animals were studied in the field. This may be because males calling in the wild experience higher predation (Fig. 1H) or parasitism (Zuk and Kolluru, 1998) or simply because the high metabolic costs of calling (Kavanagh, 1987) reduced male survival in a resource limited environment. This high risk of mortality in the field may mean that selection on male condition is particularly strong. This, in turn, may favor the evolution of high quality, long lived males. These effects on aging and lifespan of condition dependent mortality risk may be visible in favorable environments (i.e. the laboratory) but not in the field. Whatever the underlying cause, the direct costs of sexual display reduced the benefits of sexual selection for lifespan and aging in males in the wild.

Clearly, to fully understand the costs of living in the wild requires more detailed monitoring than conventional capture-mark-recapture methods can provide. This can be achieved in crickets, for example, Rodríguez-Muñoz et al. (2010) used 64 motion-sensitive, infrared-equipped video cameras to monitor occupied burrows of *Gryllus campestris* for 24 h a day across a breeding season (Fig. 1F–H). This revealed which crickets mated, how often, how long individuals lived and in many cases, how they died (e.g. predation). Coupling this information with genotyping of all adults at 11 microsatellite loci, the authors estimated the lifetime reproductive success of all focal crickets. While expensive, this method shows how life-history data can be collected in wild crickets to a level of detail typically reserved for larger vertebrate systems. Using this method to monitor reproductive trajectories and to quantify aging parameters would help fully appreciate how sex differences in lifespan and aging have evolved in the field.

4. Sexual conflict and aging in crickets

There is support for both inter- and intra-locus sexual conflict affecting the evolution of aging and lifespan in crickets. Interlocus sexual conflict occurs at different loci, when males and females would each prefer different outcomes in a particular male–female interaction. This can have pronounced effects on male and female lifespan. For example, males may attempt to manipulate female fecundity to increase investment in their own offspring. Males can do this by transferring accessory substances (Avila et al., 2011) or resources such as amino acids (Vahed, 1998) in their ejaculate that elevate or trigger female fecundity. The direct damage caused by these seminal substances or the increased investment in egg laying can reduce female lifespan. There is clear support for this in crickets, females that mate multiply often experience improved fecundity but reduced lifespan (Table 3). Females in some species may have evolved ways of overcoming these mating costs and live longer after mating multiple times (Table 3). Irrespective of whether mating improves or reduces female lifespan, the mechanisms by which this is achieved are poorly understood (but see Fedorka and Zuk, 2005).

Sexual conflict may also be fought over a single locus and there is the potential for this in crickets where male and females schedule their reproductive effort differently over time, leading to sex differences in aging and lifespan. This suggests that the sexes are under contrasting

Table 3
The effect of multiple mating on female lifespan (LS), fecundity (Fec), the proportion of her eggs that hatch (Hatch) and survive to maturity (Surv). Treatments usually take the form "total number of mating events:number of mates" (e.g. 10:1). Burpee and Sakaluk (1993) did not quantify mating number but paired females with a single male for either 15 days post eclosion (Limited) or for their entire lifespan (Continuous). Responses to each treatment are described as the effect of multiple mating relative to the control: NA — trait not assayed, ↑ — trait value increased, ↓ — trait value decreased, X — no effect of treatment.

Species	Treatment (no. matings:no. mates)		Fitness effects				Ref
	Multiple mating	Control	LS	Fec	Hatch	Surv	
Allonemobius socius	4:1	1:1	X	↑	X	X	[1]
	4:4	1:1	↓	X	↑	X	
	4:1	1:1	↓	↑	NA	NA	[2]
	4:4	1:1	↓	↑	NA	NA	
Gryllus lineaticeps	3:1	1:1	↑	X	NA	NA	[3]
	3:3	1:1	↑	↑	NA	NA	
Gryllodes sigillatus	3:1	1:1	X	NA	X	X	[4][a]
	3:3	1:1	X	NA	X	↑	
	5:1	1:1	X	NA	X	X	
	5:5	1:1	X	NA	X	↑	
	Limited	Virgin	↓	NA	NA	NA	[5][b]
	Continuous	Virgin	X	NA	NA	NA	
	Continuous	Limited	↑	↑	NA	NA	
Gryllus vocalis	10:1	5:1	X	↑	X	NA	[6]
	15:1	5:1	X	↑	X	NA	
Gryllus veletis	Limited	Virgin	↓	NA	NA	NA	[5][b]
	Continuous	Virgin	X	NA	NA	NA	
	Continuous	Limited	↑	↑	NA	NA	

References: [1] (Fedorka and Mousseau, 2002); [2] (Fedorka and Zuk, 2005); [3] (Wagner et al., 2001). [4] (Ivy and Sakaluk, 2005); [5] (Burpee and Sakaluk, 1993), [6] (Gershman, 2010). Note that for *G. lineaticeps* lifetime fecundity, rather than daily fecundity, differed across treatment groups.

[a] This study conducted principal component analysis (PCA) and so PCA values have been associated with the most appropriate fitness trait.

[b] In this study, diet was manipulated but we present data for animals fed ad libitum.

patterns of selection over these traits, which may lead to IASC if reproductive effort, aging and/or lifespan are affected by shared alleles in either sex. There is some evidence that this may be the case for lifespan in *T. commodus*. Artificially selecting on male lifespan led to changes in longevity in both sexes; these correlated responses indicate that a shared suite of genes affect lifespan in males and females (Hunt et al., 2006). However, selecting on male lifespan also led to changes in age-dependent calling effort (Hunt et al., 2006) and females may have responded to this by altering their own schedules of reproduction. Changing fertility schedules, rather than selection on shared alleles, may have led to changes in female lifespan following selection on male survival (Zajitschek et al., 2007). Therefore, while this experimental evolution experiment suggests the potential for IASC over lifespan, to test for it formally requires quantifying intersexual genetic correlations (r_{mf}) for this trait.

r_{mf} estimates the extent to which a trait can evolve independently in either sex (Bonduriansky and Chenoweth, 2009). A negative r_{mf} for fitness indicates that the evolution of improved fitness in one sex is associated with reduced fitness in the other and so provides support for IASC (Bonduriansky and Chenoweth, 2009). For specific traits there is good evidence for IASC when there is sexually antagonistic selection on that trait and a strong and positive r_{mf} (Lewis et al., 2011). There would be additional support for IASC over lifespan and reproduction if there are differences in the strength or sign of genetic correlations between these traits in either sex, indicating sex-specific resolution of any trade-offs. Using these predictions as a framework, Zajitschek et al. (2007) tested for IASC over aging and reproductive schedules in *T. commodus*. In agreement with Hunt et al. (2006), the strength of the genetic correlations between reproductive effort and lifespan differed in the sexes. However, a strong positive r_{mf} for lifetime reproductive effort (a proxy for fitness) indicated the absence of sexual conflict and

a weak r_{mf} for lifespan suggested that this trait is free to evolve independently in either sex. Overall, this study provided little support for there being strong, current IASC over lifespan in *T. commodus*. However, in decorated crickets (*G. sigillatus*), the strength of the genetic correlation between early-life reproductive effort and the rate of aging also differs in either sex, illustrating the potential for IASC. Additionally, despite clear sex differences in schedules of reproductive effort, lifespan and aging, indicative of contrasting patterns of selection, these traits exhibited strong positive r_{mf}. This suggests that these life-history traits are not free to evolve independently in either sex and that there is the potential for IASC (Archer et al., 2012).

There is clearly scope for IASC over aging, lifespan and reproduction in crickets and there is preliminary evidence both for (Archer et al., 2012) and against (Zajitschek et al., 2007) this conflict being realized. However, more work is needed to robustly test for IASC in these systems. This is because the sex-specific life-history schedules seen in Australian black field crickets and decorated crickets do not show conclusively that there is sexually antagonistic selection on these traits. We need formal confirmation of contrasting patterns of selection on reproduction, lifespan and aging to estimate the potential for IASC to drive the evolution of these traits. Additionally, r_{mf} make assumptions that may not be met (e.g. all genetic variance is additive and equal in either sex), and genetic correlations are often environment specific and hard to interpret (Bonduriansky and Chenoweth, 2009). Finally, the strength and even the existence of IASC may vary between populations and environments (Delph et al., 2011). To unambiguously test for IASC over aging and lifespan, and to estimate its prevalence and strength, future studies should estimate sex-specific fitness surfaces for these traits (Lewis et al., 2011), in different ecological contexts.

5. Sexual selection, diet and demography

Sexual selection can clearly shape strategies of age-dependent investment in reproduction and in turn, affect the evolution of aging and lifespan. However, to really understand sexual selection effects on aging, it is important that we understand the mechanistic basis of these sex differences. One mechanism by which sexual selection could shape differences in aging and lifespan across the sexes, is via an interaction with diet.

Diet influences reproduction and lifespan in a range of species. Strikingly, individuals fed moderately restricted diets often live longer than fully fed animals (Nakagawa et al., 2012; Simons et al., 2013). Evolutionary explanations for responses to this manipulation (called Dietary Restriction — DR) rely on the observation that while DR increases lifespan, it often reduces reproductive effort. This leads to the prediction that when food is limited, resources are allocated away from reproductive effort (because the survival prospects of offspring are poor) and towards somatic maintenance promoting a longer life (Harrison and Archer, 1989; Holliday, 1989; Phelan and Austad, 1989; Shanley and Kirkwood, 2000). This idea helps explain why females often show a stronger response to DR (Nakagawa et al., 2012): the energetic demands of reproduction are usually higher in females than in males, meaning that the trade-off between lifespan and fecundity in females is more pronounced. By affecting the costs of reproduction in either sex, sexual selection can mean that responses to dietary manipulation differ in males and females. This idea has been tested in crickets.

Lyn et al. (2011) achieved DR in house crickets (*Acheta domesticus*) by feeding animals intermittently or by diluting their diets with indigestible cellulose. Each treatment had sex-specific effects on survivorship but the greatest lifespan extension in the adult phase (1.77-fold) was seen in females. This loosely supports the idea that the trade-off between lifespan and reproduction is stronger in females than in males. This may not be the case where sexual selection favors intense investment in male sexual advertisement. For example, Hunt et al. (2004) manipulated the protein content of diets fed to *T. commodus* from hatching until death. Females fed high-protein diets lived longer

lives than females fed low protein foods. In males the opposite was true; males fed high protein foods died earlier because they called more intensely early in life. In *Gryllus pennsylvanicus*, diet also affected age-dependent strategies of calling effort, in this case crickets fed high quality diets could call significantly more later in life (Judge et al., 2008). By altering age-dependent strategies of reproduction in males, diet may be one mechanism that helps drive sex differences in aging.

These studies are informative but oversimplify the association between diet, sexual selection, aging and lifespan. In many species, the amount and blend of nutrients that individuals eat affects the expression of fitness determining traits (Simpson and Raubenheimer, 2012). For example, female *Drosophila melanogaster* live longest when they eat a 1:16 ratio of protein (P) to carbohydrate (C) but maximize egg production when they eat a 1:2 P:C ratio (Jensen et al., in press). If different traits are best expressed in animals that eat precise combinations of different nutrients, dietary optima are likely to vary across the sexes. This is because maximizing fitness clearly requires investing in very different traits in either sex (e.g. reproduction versus lifespan) and these traits may have distinct dietary optima. The Geometric Framework of Nutrition (GF) (Simpson and Raubenheimer, 2012), has been used to test this idea in crickets.

The GF involves feeding individual animals diets that differ in their ratio and amount of key nutrients but are otherwise identical (Fig. 2A). In crickets, these nutrients are usually protein and carbohydrate. Nutrient intake and traits of interest (e.g. reproduction) are then accurately measured. Response surface methodologies (Lande and Arnold, 1983) can quantify the linear and nonlinear effects of nutrient intake on each trait and three-dimensional surfaces (known as nutritional landscapes — Fig. 2B) can be constructed to visualize these effects. The GF is most powerful when precise holidic (i.e. chemically defined) diets are used, which is challenging in *C. elegans* that feed on bacteria. Furthermore, the GF requires precise measures of individual food intake which is difficult (but not impossible) in *Drosophila* (Deshpande et al., 2014; Piper et al., 2014). Omnivorous crickets that survive well on artificial, holidic diets provided in powdered form do not have these limitations and so are an emerging model for testing how sexual selection affects dietary optima across the sexes.

The first study to use the GF to ask how sexual selection affects dietary optima for lifespan and reproduction across the sexes used the Australian black field cricket (*T. commodus*) (Maklakov et al., 2008). Using 24 powdered, holidic diets varying in their total amount (protein (P) + carbohydrate (C) = 12% to 84%) and ratio (P:C = 5:1 to 1:8) of protein to carbohydrate Maklakov et al. (2008) measured nutrient intake and reproductive effort across the lives of 228 male and 213 female crickets. They found that lifespan was maximized in both sexes when consuming a high carbohydrate, low protein diet (Maklakov et al., 2008). This intake also allowed males to maximize their time spent calling, presumably because eating high carbohydrate diets fuelled the energetic costs of calling. Females however, required greater intake of protein (1:1 P:C) to maximize egg laying. These sex-specific dietary optima for reproduction mean that females in this species face a trade-off between reproductive effort and survival but males do not. When crickets were allowed to choose between alternate diets, both sexes preferentially consumed a 1:3 P:C ratio, this intake falls between sex-specific peaks for reproduction and is particularly costly for female lifetime reproductive success. This suggests that female nutrient regulation may be constrained and indicates the potential for IASC over dietary intake (Maklakov et al., 2008). However, this study did not quantify the genetic correlations between these traits that are needed to formally show IASC.

Harrison et al. (2014) used the GF to see how diet affects aging and reproduction in both sexes of the field cricket *Gryllus veletis*. In this case, diets varied in their ratio (3:1 to 1:8 P:C) and amount (14, 45 or 76% indigestible cellulose) of protein and carbohydrate and also in their phosphorous (Ph) content (0.45, 1.45, 2.45% Ph by mass). While Ph did not influence any of the life-history traits studied, both protein
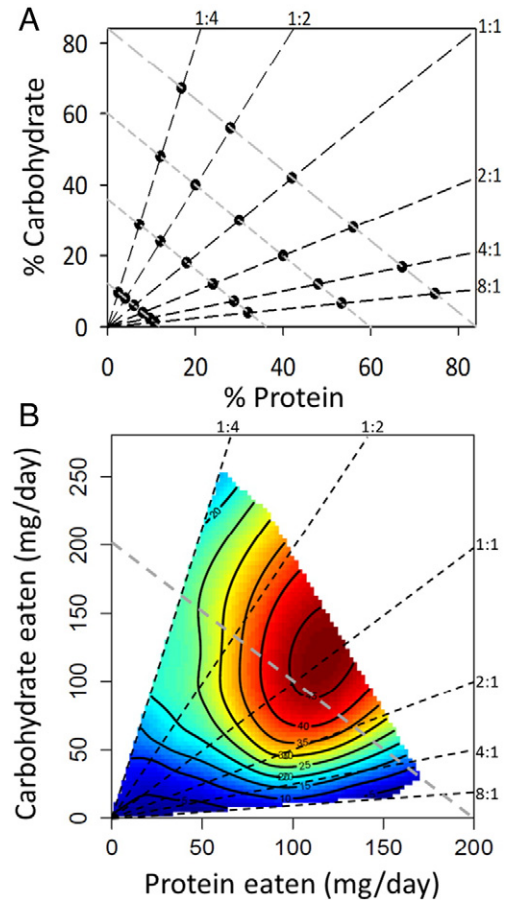
Fig. 2. An example of a nutritional landscape examining the effects of protein (P) and carbohydrate (C) consumption on lifespan. (A) To characterize the nutritional landscape, individuals are provided with a single diet from within a geometric array of *n* diets (in our example there are 24 possible diets indicated by black circles). Diets in this array are arranged along nutritional rails (black dashed lines) that have a fixed P:C ratio and are spaced according to total nutritional content (in our example, the total nutritional content of diets on each rail is 12%, 36%, 60% and 84%). Diets on different nutritional rails are matched for total nutritional content and can be connected by isocaloric lines (i.e. lines of equal caloric intake, gray dashed lines). As each individual receives a single diet, they can only feed along a given nutritional rail. (B) To examine the effect of P and C intake on lifespan, the consumption of diet is accurately measured across the lifetime of each individual and this is converted into daily intake of nutrients (as individuals have different lifespans). Response surface analysis can then be used to determine the linear and nonlinear effects of nutrient intake on lifespan and a thin-plate spline can be used to construct a nutritional landscape to help visualize these relationships. In the nutritional landscape provided, red areas show regions of higher lifespan, whereas blue areas show regions of lower lifespan. In this example, lifespan is maximized at a high intake of both P and C at a P:C ratio of 1:1.

and carbohydrate had pronounced and sex-specific effects on life-history strategies. Male calling effort was greatest in individuals fed nutrient rich diets (e.g. high P + C), while lifespan was best in individuals fed a 1:3 P:C ratio. Therefore, males could eat a single diet to maximize expression of both traits but in females, optimal egg laying required more protein than the diet best for survival. To resolve this trade-off, females compromised and ate an intermediate P:C ratio that allowed moderate expression of both traits (Harrison et al., 2014). These studies show that the ratio and amount of nutrients eaten mediates trade-offs between lifespan and reproduction and that sexual selection drives differences in the magnitude of these trade-offs across the sexes.

The GF has also been used to test how diet affects aging i.e. Gompertz parameters (Zajitschek et al., 2012), functional senescence (Lailvaux et al., 2011) and reproductive schedules (Maklakov et al., 2009; Zajitschek et al., 2012) in *T. commodus*. This work shows that, first, diet has a much stronger effect on how males schedule their

reproductive effort over time than females (Maklakov et al., 2009). This should be taken into account in laboratory studies of sex-specific reproductive trajectories and may also drive inter-population differences in life-histories in wild crickets. Second, diet affects aging parameters (Zajitschek et al., 2012) and the rate at which different traits lose function with age (Lailvaux et al., 2011). However, these effects are complex and depend on a cricket's mating experience and sex (Lailvaux et al., 2011; Zajitschek et al., 2012). This complexity illustrates the challenges associated with testing how sexual selection interacts with diet to affect aging but shows that doing so can help improve our overall understanding of the mechanistic association between sex and death.

6. The mechanistic basis of aging in crickets

Research using crickets has helped validate roles for sexual selection and sexual conflict in the evolution of lifespan and aging. It has also demonstrated how diet mediates sex-differences in the trade-off between lifespan and reproduction. Research has now begun to test the mechanisms responsible for these effects and attention has focused heavily on the role of Reactive Oxygen Species (ROS). ROS are highly reactive and principally produced during energy production in the mitochondria (Finkel and Holbrook, 2000) ROS perform important cellular functions, such as cellular signaling (Veal et al., 2007) but their high reactivity also means that they can damage cellular molecules, such as protein, lipids and DNA. These positive and negative effects mean that ROS levels must be tightly regulated. Antioxidants (AOX), which can neutralize ROS, are central to this regulation: if ROS levels exceed the capacity of circulating AOX defenses, then oxidative damage occurs. If this damage cannot be repaired, then it accumulates. This accumulated damage has been implicated in causing aging (free radical theory — Harman, 1956) and more recently, in mediating the association between lifespan, aging and reproduction (Dowling and Simmons, 2009; Isaksson et al., 2011; Monaghan et al., 2009).

ROS could underpin trade-offs between lifespan and reproductive effort if AOX are used during reproduction, for example, during sexual display (Pike et al., 2007). In this case AOX could be allocated to either protecting the soma against oxidative damage and improving lifespan or towards greater reproduction (Monaghan et al., 2009). Alternatively, if reproduction increases metabolic rate and this elevates mitochondrial ROS production, reproduction could increase oxidative damage, accelerate aging and reduce lifespan. In support of this, metabolic rate negatively correlates with lifespan in some species, including the decorated cricket *G. sigillatus* (Okada et al., 2011). However, there is no consistent evidence of a positive association between metabolic rate and ROS production (Galtier et al., 2009). If ROS and AOX drive trade-offs between reproduction, lifespan and aging, sexual selection may affect how either sex resolves these trade-offs. Archer et al. (2013) tested this idea in decorated crickets (*G. sigillatus*) and found that females, the shorter lived sex, had greater oxidative damage to proteins. Moreover, levels of damage were negatively genetically correlated with lifespan in both sexes. There was also evidence that ROS production mediated the trade-off between lifespan, aging and reproduction (Archer et al., 2012). In females, high egg production early in life was associated with greater oxidative damage to proteins later on and in turn, this damage was positively correlated with the rate of aging. This suggests that oxidative damage may be a cost of producing eggs that accelerates female aging. While these results provide general support for the free radical theory of aging, oxidative damage did not accumulate with age. This adds to a growing body of evidence suggesting that the free radical theory grossly oversimplifies the association between ROS and aging (Speakman and Selman, 2011).

Other mechanistic theories of aging have not really been tested in crickets but there is increasing potential to ask how sexual selection drives sex differences in cellular processes implicated in aging. For example, telomeres (protective repeats of nucleotide sequences that cap chromosome ends) may help regulate human aging (Aubert and Lansdorp, 2008). Most human cells lack sufficient levels of the enzyme telomerase to maintain telomere length, which means that with each round of replication telomeres grow shorter. If telomeres become too short and chromosome ends are "uncapped", then cell death is triggered. This may contribute towards aging. *C. elegans* are not a strong model for testing how telomere shortening affects aging because somatic cells are post-mitotic (Kenyon, 2005), while *Drosophila* telomeres have different DNA sequences (but are functionally similar) to those of other eukaryotes (Mason et al., 2008). In crickets it is unknown if telomere length affects aging but telomerase activity has been detected (Sasaki and Fujiwara, 2000) and telomeric TTAGG repeats identified (Kojima et al., 2002). This means that we can now start to test how telomere length affects aging and lifespan across the sexes.

The genetic pathways central to aging are also poorly understood in crickets relative to other invertebrate aging models. Developed molecular methods for model species have helped identify genetic pathways that affect lifespan and aging in rodents, *Drosophila* and *C. elegans* (Kimura et al., 1997; Partridge et al., 2011; Selman et al., 2008). Strikingly, genome-wide association studies suggest that some of these pathways (insulin/IGF-1 signaling and telomere maintenance pathways) may also be associated with human lifespan (Deelen et al., 2013). Unfortunately, limited molecular tools (Danley et al., 2007) have restricted the use of crickets in testing the molecular basis of aging. Fortunately, molecular methods for cricket species are being developed at an increasing rate (e.g. Bailey et al., 2013; Danley et al., 2007) and molecular approaches have been used to construct detailed pedigrees in wild cricket populations (Rodríguez-Muñoz et al., 2010) and ask how sexual selection (Bailey et al., 2007a) and dispersal (Bailey et al., 2007b) might drive speciation (Bailey et al., 2005). Further developments of this nature will enable cricket research to increasingly test mechanistic theories of aging and, relative to other invertebrate aging modes, test these theories in light of sexual selection. There is also the potential to extend these molecular tools to help test mechanistic theories in the field; an approach that has not received much attention but is critical to assess the generality of laboratory studies.

7. Strengths, limitations and future directions in cricket aging research

For crickets to be useful in aging research they must share many attributes that make *Drosophila* and *C. elegans* powerful invertebrate models for studying lifespan and aging. Indeed, like fruit flies and nematodes, crickets are typically cheap and easy to rear in large numbers in the laboratory (Lyn et al., 2011), are short lived (Zajitschek et al., 2009c) and functional senescence can be easily assayed (e.g. Lailvaux et al., 2011). However, crickets have additional attributes that are useful in aging research. It is easy to track the development of crickets through their instar stages and to determine sex prior to adulthood (Lyn et al., 2011). Compared to nematodes, the large size of crickets allows molecular or biochemical analyses to be performed on specific tissue types (Bailey et al., 2013). Relative to *Drosophila*, crickets can be more easily studied in the field (e.g. Rodríguez-Muñoz et al., 2010) and dietary intake can be readily manipulated and nutrient intake measured (e.g. Maklakov et al., 2008). Finally, a long history of sexual selection and sexual conflict research on crickets and the ability to easily quantify changes in male and female reproductive effort with age allow powerful tests of how these evolutionary processes affect aging.

Crickets have clear limitations as models for aging research. In *D. melanogaster* and *C. elegans* the genome is sequenced and annotated, each species has extensive RNAi libraries, transgenic strains can be produced relatively easily and stocks with altered gene expression are widely available. This means that the genetic pathways involved in regulating lifespan and aging are comparatively well understood (Rogina, 2011; Tissenbaum, 2015). There is also a better understanding in these species of age-associated changes in physiology (e.g. cardiac function, stress responses) and how different manipulations (e.g.

mild stress, temperature) affect lifespan and aging (Rogina, 2011; Tissenbaum, 2015). However, the development of molecular tools for crickets means that we can begin to unravel the molecular regulation of lifespan and aging in crickets and crucially, integrate this information with sexual selection and sexual conflict theory.

We have only begun to explore how sexual selection and sexual conflict influence the evolution of lifespan and aging in crickets and there is still much scope for future research. Future work could ask if female choice for high quality males or condition dependent male mortality also selects for the evolution of longer male lifespans (see Chen and Maklakov, 2014) and if male mate choice affects the evolution of sex differences in aging and lifespan. While males are not thought to be very choosey about mates, the high costs of producing nuptial gifts in some cricket species can prompt male choice for virgins, which tend to be younger than mated females (Bateman and Ferguson, 2004). If males prefer younger female mates this might affect aging and lifespan across the sexes, as has been suggested for humans (Tuljapurkar et al., 2007). Moreover, the mechanistic basis of how sexual conflict reduces lifespan in either sex is poorly understood. Testing how either sex invests in protecting against cellular damage implicated in aging (e.g. oxidative damage, telomere shortening) versus reproduction would help improve our understanding. Dietary manipulation may help us do this: for example, diet could be used to manipulate lifespan, aging and reproduction in the sexes and see how this affects oxidative damage, telomere length, or molecular signaling pathways that may be involved in aging.

Over the last decade, there has been a growing appreciation that to better understand the evolution of aging we need to integrate evolutionary theories of aging with sexual selection theory (Bonduriansky et al., 2008; Graves, 2007; Promislow, 2003). We hope we have been able to demonstrate that crickets provide a powerful, alternate model to *Drosophila* or nematodes to achieve this and crucially, present many exciting future research opportunities.

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