

THE EVOLUTIONARY ECOLOGY OF SENESCENCE

Sexual selection, sexual conflict and the evolution of ageing and life span

R. Bonduriansky*, A. Maklakov, F. Zajitschek and R. Brooks

*Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney NSW 2052, Australia***Summary**

1. Classic evolutionary models interpret ageing as a cost of reproduction, but evolutionary research has thus far largely neglected the conceptual links between the evolution of ageing and a key mode of selection on male and female reproductive strategies – sexual selection and sexual conflict.
2. We synthesize ideas and evidence linking sex and ageing, and make the case that a focus on this fascinating problem will ultimately lead to a more complete understanding of both the evolution of ageing and the evolution of sexual strategies.
3. The primary and secondary differentiation of male and female reproductive strategies is expected to produce sex-specific optima for traits that affect longevity and ageing rate, often favouring a ‘live fast, die young’ strategy in males, relative to females, although numerous exceptions to this pattern are observed and sex-differences in ageing rate, in particular, remain poorly understood.
4. Conversely, environmental factors that influence life expectancy or ageing rate can thereby determine the magnitude or even sign of sexual selection.
5. Sexual conflict is expected to displace the sexes from their sex-specific life-history optima through sexually antagonistic interactions, as well as sex-specific selection on loci expressed in both sexes.
6. Despite the availability of interesting and testable hypotheses linking sexual selection and ageing, relevant empirical studies are remarkably sparse, and the complex relation between sex, mortality rate and ageing remains poorly understood.

Key-words: phenotypic plasticity, life history evolution, senescence, aging**Introduction**

Natural selection cannot eliminate ageing because selection on genes expressed late in life is weak, permitting the accumulation of late-acting deleterious mutations and, in particular, genes that enhance early-life reproductive performance while contributing to somatic deterioration. Natural selection thus shapes the life history so as to achieve an optimal compromise between reproductive rate and somatic maintenance, under the constraints imposed by external environment and phylogenetic history.

Theoretical inquiry on the evolution of ageing and life span – as in so many other classic problems in evolutionary biology – has sought to identify life-history optima that maximize population growth rate, while largely ignoring within-population variation and the dynamics of sexual selection and conflict. The primary and secondary differentiation of male and female reproductive traits typically yields sex-specific optima

for life-history traits, including investment in longevity and somatic maintenance. A long-standing idea is that males are often selected to pursue a ‘live fast, die young’ reproductive strategy characterized by higher mortality rate and more rapid ageing in males than females (Vinogradov 1998; Carranza & Pérez-Barbería 2007). However, our understanding of the costs of reproduction has recently been revolutionized by the recognition of pervasive sexual conflict over the outcome of male–female interactions, and evolution of loci affecting reproductive traits (Parker 1979; Lande 1980; Rice 1984; Arnqvist & Rowe 2005). Sexual conflict has the potential to displace the sexes from their sex-specific optima for life span and ageing rate (Promislow 2003). From the genomic point of view, two modes of conflict are commonly recognized (Arnqvist & Rowe 2005), depending on whether sexually antagonistic co-evolution is observed within a locus (intralocus conflict), or between loci (interlocus conflict). Interlocus sexual conflict frequently intensifies the direct costs of reproduction for both sexes through the (co)evolution of sexually antagonistic traits that mediate male–female interactions. Although less well understood, intralocus sexual conflict is expected to

*Correspondence author. E-mail: r.bonduriansky@unsw.edu.au

generate substantial costs through sex-specific selection on loci expressed in both sexes, resulting in an evolutionary tug-of-war over the expression of sexually homologous traits.

Despite recognition of the fundamental importance of sexual selection and sexual conflict in shaping reproductive strategies, and continued interest in the evolution of ageing, evolutionary research has largely neglected the need for detailed exploration of the links between sex and ageing (but see Svensson & Sheldon 1998; Promislow 2003; Tuljapurkar, Puleston & Gurven 2007; Graves 2007). Here, we review and synthesize key ideas and empirical studies linking these disparate areas of research, and argue that our understanding of ageing and life span will be revolutionized by a recognition of the central role of sexual selection and sexual conflict in the evolution of life histories. In 'sexual selection and life-history evolution', we examine the consequences of sexual selection for the evolution of male life history, and for sexual dimorphism in mortality trajectories. We also consider the possibility that variation in ageing and life span can mediate effects of environment on sexual selection. In 'sexual conflict in relation to life span and ageing', we focus on the potential for sexually antagonistic co-evolution to influence life span and ageing in both sexes. In 'conclusions and future directions', we highlight the current dearth of empirical studies and gaps in theoretical understanding bearing on these questions, and offer suggestions for future work.

Sexual selection and life-history evolution

EFFECTS OF SEXUAL SELECTION ON LIFE SPAN AND AGEING

In this section, we make the case that male reproductive strategies are typically associated with elevated mortality risks and weaker selection for long life span relative to females, resulting in 'live fast, die young' male life histories. Although males' elevated mortality rate may also be expected to weaken selection on somatic maintenance and thus drive the evolution of accelerated ageing, current evidence offers little support for this prediction.

Why does theory generally predict weaker selection for long life in males than in females? In most species, the opportunity for and intensity of sexual selection are greater in males because fathers contribute less to each offspring than mothers do. This frees up resources that males can use to compete for additional matings, resulting in higher variance in male fitness than female fitness (Bateman 1948, Trivers 1972). Thus, because of the fundamental divergence in the sex roles originally stemming from anisogamy, females are generally expected to pursue low-risk, low-wear-and-tear strategies with moderate rates of return over extended time periods, whereas males are expected to pursue high-risk, high-wear-and-tear strategies with the potential for a high yield over short time periods (see Vinogradov 1998). Males can benefit by sacrificing longevity for the possibility of enhanced mating success, whereas females cannot gain as much by sacrificing longevity because female fitness is limited by the time

investment and resources-acquisition demands inherent in offspring production. This general prediction becomes less clear-cut, or fails entirely, in relation to species with secondarily convergent sexual strategies, such as monogamous or sex role-reversed animals, as well as in species with age-dependent expression of male secondary sexual traits, where male reproductive rate often increases with age. These considerations suggest that sexual dimorphism in life span and ageing is a complex function of several mating system parameters.

Male reproductive strategies often appear to involve high rates of somatic damage, particularly in highly polygynous species. For example, male-male combat may result in cumulative somatic deterioration. This is particularly true in insects, which are unable to repair damage to their exoskeleton. Since females do not engage in combat, such cumulative damage may result in higher mortality and ageing rates in males, relative to females. Reduced life expectancy may also drive the evolution of more rapid ageing in males (Williams 1957; Hamilton 1966; Kirkwood & Rose 1991; but see Graves 2007). Note, however, that average sex-differences in life span and ageing do not reflect sex-differences in the magnitude of reproductive costs: in most species, each individual has a mother and a father, so the net costs of reproduction must be equal for females and males. Rather, sex-differences in life span and ageing are likely to reflect the nature and scheduling of reproductive effort. Unfortunately, the effects of variation in male sexual strategy and secondary sexual trait expression on life span and ageing remain poorly understood (Kotiaho 2001).

A key element of male reproductive strategy is male-specific hormone secretion. Hormones induce the expression of sexual traits that increase mortality risks and enhance somatic wear-and-tear, thus reducing male life expectancy and probably weakening selection on male life span and somatic maintenance. In vertebrates, testosterone is usually present in higher concentrations in males than in females (Ketterson, Nolan & Sandell 2005), and mediates the development of secondary sexual traits (Ligon *et al.* 1990; Panzica *et al.* 1991; Mougeot *et al.* 2004; Blas *et al.* 2006) and behaviours like territoriality and courtship (Collias, Barfield & Tarvyd 2002; Sakata *et al.* 2003; Day, McBroom & Schlinger 2005; Hume & Wynne-Edwards 2005). Testosterone is also associated with diverse physiological costs, including reduced immunocompetence, increased susceptibility to oxidative stress, and increased basal metabolic rate and energy expenditure (Buchanan *et al.* 2001; Wingfield, Lynn & Soma 2001; Bribiescas 2006; Alonso-Alvarez *et al.* 2007; Cox & John-Alder 2007). Insects lack testosterone, but exhibit male-specific titres of juvenile hormone, insulin-like growth factors, and other hormones that stimulate secondary sexual trait expression (Emlen *et al.* 2006), and affect mortality and ageing (Tatar 2004; Flatt, Tu & Tatar 2005; Keller & Jemielity 2006). Males thus appear to sacrifice viability for enhanced sexual performance, whereas females may benefit by investing more in immunity and longevity (Rolf 2002).

The general prediction of 'live fast, die young' strategies in males is supported by higher mortality rates in males within a broad range of taxa (Comfort 1979; Finch 1990;

Promislow & Harvey 1990; Promislow 1992; Vieira *et al.* 2000). Furthermore, comparative studies on vertebrates support the key role of sexual competition in this pattern. Male mortality rate covaries with sexual size dimorphism, which generally reflects the intensity of male sexual competition (Promislow, Montgomerie & Martin 1992). Likewise, male-biased mortality rates are associated with polygynous mating systems characterized by intense male sexual competition (Clutton-Brock & Isvaran 2007).

However, theoretical considerations suggest that sexual selection need not always promote 'live fast, die young' strategies in males, and empirical studies confirm that mortality rates are not always male-biased (Lints *et al.* 1983; Promislow, Montgomerie & Martin 1992; Fox, Dublin & Pollitt 2003). There are several reasons why males may sometimes be selected for long life.

First, selection on male condition and performance may favour genes with positive pleiotropic effects on longevity and somatic maintenance (Abrams 1993; Williams & Day 2003; Bronikowski & Promislow 2005). For example, although an increase in the abundance of predators (and concomitant reduction in life expectancy) is generally assumed to permit the evolution of accelerated ageing, the opposite effect has been observed for some indices of ageing in guppies (Reznick *et al.* 2004). This may occur because predators select on diverse aspects of whole-organism performance in their prey (Bronikowski & Promislow 2005). Likewise, sexual competition imposes strong selection on male condition and whole-organism performance (Lailvaux & Irschick 2006), potentially favouring alleles with positive pleiotropic effects on life span and somatic maintenance.

Second, in species with age-dependent expression of secondary sexual traits, sexual selection may favour males that can survive and maintain their soma long enough to attain a large body size, large weapons or signals, or high social rank (Clutton-Brock 1982, 1988; Clinton & Le Boeuf 1993; Kokko *et al.* 1999). For example, selection on social status may account for the high mating success of older men in traditional human societies (Tuljapurkar *et al.* 2007). Indeed, Graves (2007) points out that selection may favour slower ageing in males than in females, despite male-biased mortality rates, if male mating success tends to increase with age (also see Partridge & Barton 1996). Theory suggests that signalers may sometimes be selected to increase signal magnitude with age (see Kokko 1997), resulting in selection for enhanced somatic maintenance.

Third, in species with secondarily convergent sex roles, such as monogamous species (see Promislow 2003), or sex role-reversed species where females compete for matings and males invest heavily in offspring, males may adopt a female-like 'live slow, die old' strategy. This idea is supported by comparative studies showing that the degree of male bias in mortality rate covaries with indices of sexual selection strength on males (Promislow, Montgomerie & Martin 1992; Clutton-Brock & Isvaran 2007). Direct comparison of species with reversed vs. conventional sex roles would provide an additional, powerful test of the ideas discussed here.

Promislow (2003) suggested that longer life span may be expected to evolve in cooperatively breeding birds because helpers at the nest appear to reduce the costs of sexual conflict. There are several other reasons why complex sociality may promote long life (Blumstein & Møller 2008). Nonetheless, a large comparative analysis found no evidence of an association between complex sociality and extended life span (Blumstein & Møller 2008).

Variation in life span and ageing among males also appears to reflect variation in reproductive investment. Evidence from a variety of organisms, and from both sexes, shows that elevated reproductive rate is associated with reduced life span and, in some cases, accelerated ageing (Rose & Charlesworth 1981; Ernesting & Isaaks 1991; Kirkwood & Rose 1991; Service 1993; Tatar, Carey & Vaupel 1993; Kotiaho 2001; Hunt *et al.* 2004). Such costs can be interpreted in light of the disposable soma model (Kirkwood 1977; Kirkwood & Rose 1991; Kirkwood & Austad 2000), which suggests that ageing occurs because resources allocated to reproductive traits are unavailable for investment in somatic repair. Consequently, individuals or populations that invest more in sexual traits may be expected to exhibit shorter life span and faster ageing. Several studies on insects have reported reduced longevity in males that invest more heavily in reproduction or secondary sexual trait expression (Partridge & Farquhar 1981; Alcock 1996; Cordts & Partridge 1996; Clutton-Brock & Langley 1997; Prowse & Partridge 1997; Hunt *et al.* 2004; Bonduriansky & Brassil 2005), although reproduction sometimes imposes only immediate costs (Partridge & Andrews 1985). However, such studies do not distinguish between the effects of elevated resource allocation to sexual functions, and other reproductive costs such as increased wear-and-tear caused by more intense sexual competition.

Whereas accounting for variation in life span poses considerable challenges, understanding variation in ageing rate is likely to prove even more difficult. Although theory generally predicts that higher mortality rate will drive the evolution of more rapid ageing (Williams 1957; Hamilton 1966), the available evidence does not yield any clear pattern of sexual dimorphism in ageing, nor any simple relation between life span and ageing. For example, in the fly *Telostylinus angusticollis*, Kawasaki *et al.* (2008) observed both higher initial mortality rate and more rapid ageing in males than in females in the wild, and in most laboratory assays. In wild field crickets, *Teleogryllus commodus*, Zajitschek *et al.* (2008) also observed a higher initial mortality rate in males, but found little evidence of sexually dimorphic ageing rates. In seed beetles, Fox *et al.* (2003) found lower initial mortality rate but faster ageing in males than in females of *Callosobruchus maculatus*, but higher initial mortality in males and no sex-difference in ageing rate in *Stator limbatus*. Promislow & Haselkorn (2002) found every combination of sexual dimorphism in life span, initial mortality rate and ageing rate among five species of *Drosophila*. In a seabird, females aged more rapidly than males (Reed *et al.* 2008). In humans, women exhibit lower mortality rates than men in most populations (Hamilton & Mestler 1969; Kinsella & Gist 1998; Stindl 2004; Terioknin *et al.* 2004; Kruger & Nesse 2006), and men are more susceptible to many

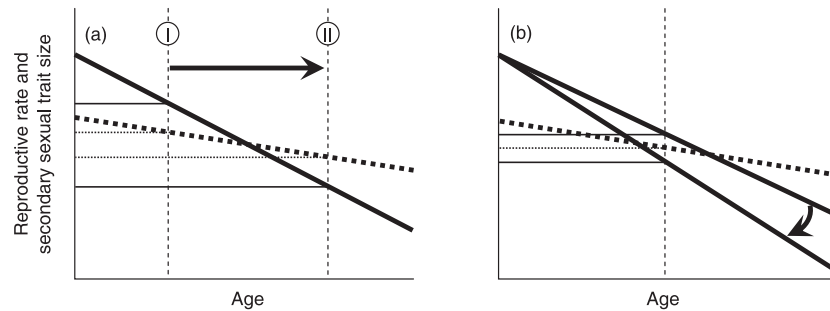


Fig. 1. Theory suggests that ageing can mediate effects of environment on sexual selection when phenotypes vary in lifespan or ageing rate. (a) Environmental variation in extrinsic mortality risk: if life expectancy is brief (denoted by vertical line I), then individuals that invest more heavily in reproduction in early life (solid line) will achieve higher life-time fitness than individuals that invest less in reproduction (dotted line), and the traits mediating variation in reproductive rate will be under positive sexual selection. If extrinsic mortality rate is reduced (arrow), extending life expectancy from vertical line I to II, then individuals with a lower investment in reproduction will achieve higher life-time fitness. (b) Environmental effects on the expression of ageing: In this example, an environmental change has resulted in accelerated ageing (arrow) in individuals that exhibit a high reproductive rate through large investment in a secondary sexual trait (solid lines), but no appreciable effect on individuals that exhibit a lower reproductive rate as a result of less investment in a secondary sexual trait (dotted line). Prior to the environmental change, at the life expectancy indicated by the vertical line, high-investing individuals achieved higher life-time fitness and sexual selection on the secondary sexual trait was positive; after the change, the sign of sexual selection is reversed. Age-specific fitness functions are represented as straight lines for simplicity, but similar results emerge with more complex life histories.

'diseases of ageing' (Kinsella & Gist 1998). However, the onset of ageing appears to be later in men than in women (Graves, Strand & Lindsay 2006). It remains unclear how sex-specific mortality relates to sexual dimorphism in ageing rate, or why this relation varies among taxa.

EFFECTS OF LIFE SPAN AND AGEING ON SEXUAL SELECTION

A phenotype's net (i.e. life time) fitness depends on its early-life reproductive rate, pattern of change in reproductive rate with age (ageing), and life span. As the preceding section suggests, phenotypes are likely to vary in life span and ageing rate, and this variation may reflect secondary sexual trait expression. Below, we show that variation in life span and ageing can therefore modulate the magnitude or even the sign of sexual selection.

We begin with an empirical example. In a wild population of the antler fly, *Protophila litigata*, male mating rate is an increasing function of male body size (Bonduriansky & Brooks 1998; Bonduriansky & Brooks 1999), but males suffer reductions in both survival and mating rate with age (Bonduriansky & Brassil 2002). Moreover, the rate of reproductive ageing increases with male body size (Bonduriansky & Brassil 2005), reflecting either the physiological costs of large body size, or large males' propensity to engage in more intense or frequent combat (Bonduriansky & Brooks 1999). Because the net (life time) advantage of large body size is diminished by the tendency for large males to deteriorate more rapidly with age, the covariation between male body size and ageing rate is manifested in a reduction in the gradient of net sexual selection on male body size (Bonduriansky *et al.* 2005). In other words, if large males could maintain their mating rate advantage over small males as they aged, net sexual selection on male body size would have been stronger.

Reproductive rate need not always covary positively with ageing rate, however. If high-condition individuals can achieve both higher reproductive rate and better somatic maintenance, then their relative advantage will increase with age, strengthening net sexual selection on their secondary sexual traits. This may occur if variation in condition is sufficient to overwhelm allocation trade-offs (Van Noordwijk & Dejong 1986; Stearns 1989a,b; Houle 1991, also see Nussey *et al.* in this volume).

The antler fly example illustrates a general principle: phenotypic variation in life span and ageing can affect sexual selection. This example also suggests how such effects could be modulated by ambient conditions. Life expectancy is a function of extrinsic (background) mortality rate. If extrinsic mortality is reduced and life expectancy correspondingly extended, then the relative net fitness of phenotypes that age more rapidly will be reduced (Fig. 1a). Conversely, if extrinsic mortality rate increases, phenotypes that age more rapidly will perform relatively better over the life time. These are basic predictions of life-history theory (Williams 1957; Hamilton 1966), but they have interesting implications for sexual selection. If phenotypes that age more rapidly are those that invest more in secondary sexual traits (as in the antler fly example and in the model shown in Fig. 1), then, all else being equal, reduced mortality will weaken or even reverse sexual selection, because such phenotypes will have reduced net fitness, relative to phenotypes that invest less in secondary sexual traits. Conversely, elevated mortality will tend to enhance the relative fitness of phenotypes that invest more in secondary sexual traits, strengthening sexual selection. Some of the variation among populations in the strength and direction of sexual selection may thus reflect variation in extrinsic mortality.

Moreover, environment can affect the expression of both actuarial and reproductive ageing. Ageing is an extremely plastic trait, influenced by diet (Medawar 1946; Tu & Tatar 2003), temperature (Tatar, Chien & Priest 2001), substrate

(Shook & Johnson 1999; Van Voorhies, Fuchs & Thomas 2005), population density (Mysterud *et al.* 2001) and even sensory stimuli (Nakamura *et al.* 1999; Libert *et al.* 2007). If environmental effects on the expression of ageing covary with secondary sexual trait expression, then such environmental effects will modulate sexual selection (Fig. 1b).

One potentially important environmental variable is crowding, which can reflect population density or resource distribution. The effect of a change in crowding on life span or ageing may covary with secondary sexual trait expression if, for example, such phenotypic variation is associated with discrete or continuous variation in mating tactics, or the costs of agonistic interactions. Another key environmental parameter is diet. Dietary restriction appears to induce a sharp decline in reproductive allocation and/or the biochemical damage associated with reproduction (see Shanley & Kirkwood 2000; Partridge, Gems & Withers 2005; Masoro 2006; Piper & Partridge 2007; Lee 2008). Diet will affect sexual selection if different phenotypic variants respond differently to diet, and if these effects covary with secondary sexual trait expression.

Sexual conflict in relation to life span and ageing

Contrasting reproductive strategies may often result in sex-specific optima for life-history traits. In this section, we discuss how a fundamental property of sexual co-evolution – sexual conflict – may displace both sexes from their sex-specific optima for life span and ageing.

INTERLOCUS SEXUAL CONFLICT

Sexual conflict occurs when the genetic interests of males and females diverge (Parker 1979; Holland & Rice 1998; Arnqvist *et al.* 2005). Such conflict can result in arms races where adaptations in one sex are harmful for the other sex (Rice 1996b; Arnqvist & Rowe 2002; Chapman *et al.* 2003; Martin & Hosken 2003). This co-evolution is now recognized as one of the key evolutionary processes shaping life histories.

Male sexual traits can affect female life span and ageing rate (Svensson & Sheldon 1998; Maklakov, Kremer & Arnqvist 2005; Promislow 2003). Such effects can be direct, via physical damage or interference with foraging, or indirect, via manipulation of female reproductive schedules. For example, females of various insect species suffer from toxic male ejaculates (Das *et al.* 1980; Chapman *et al.* 1995), physical injuries incurred from spiky male genitalia (Crudginton & Siva-Jothy 2000; Rönn, Katvala & Arnqvist 2007), or other forms of ‘traumatic insemination’ (Stutt & Siva-Jothy 2001; Tataric, Cassis & Hochuli 2006; Kamimura 2007). Such male traits may evolve in response to sperm competition. On the other hand, males in polyandrous species can increase female short-term reproductive rate at the expense of female future reproduction (Chapman *et al.* 2001). If increased investment in early reproduction translates into elevated mortality late in life (Sgro & Partridge 1999), such male adaptations can reduce female life expectancy and contribute to female ageing.

Because female-specific selection typically favours lower mating rate than male-specific selection, females are expected to oppose harmful male adaptations with counter-adaptations that may, in turn, lead to elevated mortality or accelerated resource depletion and somatic deterioration in males. Putative female counter-adaptations include aggressive behaviour towards potential mates, sometimes involving sexual cannibalism (Birkhead, Lee & Young 1988; Elgar & Fahey 1996), release of anti-aphrodisiacs (Andersson, Borg-Karlson & Wiklund 2004), ejaculate dumping (Snook & Hosken 2004; Wagner, Helfenstein & Danchin 2004), and ejaculate ingestion (Bonduriansky, Wheeler & Rowe 2005). A common form of female resistance to mating – male-female struggles before and/or during copulation (Parker & Thompson 1980; Rowe *et al.* 1994; Bonduriansky 2003) – results in elevated energy expenditure and predation risk for both sexes (Rowe 1994; Watson, Arnqvist & Stallmann 1998), and may contribute to somatic deterioration.

By increasing mortality rate, sexually antagonistic traits and interactions may weaken selection against alleles with deleterious late-life effects and, thus, promote the evolution of rapid ageing (Promislow 2003). In general, more intense interlocus sexual conflict should therefore result in shorter life span and more rapid ageing for one or both sexes (Promislow 2003). This prediction is supported by the finding that experimentally imposed monandry leads to the evolution of males that cause reduced direct harm to females (Holland & Rice 1999; Martin & Hosken 2003), although effects on female ageing remain unclear. Note, however, that Promislow’s prediction may be negated or even reversed – sexually antagonistic co-evolution may have no net effect, or even result in slower ageing – if sexually antagonistic interactions impose strong selection on somatic condition and vigour (see ‘Effects of sexual selection on life span and ageing’!

CASE STUDIES OF SEXUALLY ANTAGONISTIC CO-EVOLUTION

For sexual co-evolution to contribute to the evolution of ageing, evolutionary change in genes expressed in one sex should affect senescence in the other sex. Recent experimental studies with seed beetles *Acanthoscelides obtectus* support this hypothesis and suggest that males in populations maintained under different life-history schedules evolve to affect female mortality rates differently (Maklakov *et al.* 2005). Furthermore, age-specific change in female sexually selected traits was found to be related to life-history evolution (Maklakov *et al.* 2005). However, direct support for Promislow’s (2003) prediction that higher levels of sexual conflict should result in the evolution of more rapid ageing is currently lacking. Maklakov, Fricke & Arnqvist (2007) subjected another seed beetle, *C. maculatus*, to either true random monogamy or polygamy. In theory, such an approach permits investigation of the evolution of age-specific mortality rates when the potential for both ‘good genes’ and antagonistic co-evolution is removed. Virgin females from polygamous populations exhibited reduced life span compared to those from monogamous

populations, as predicted by the sexual conflict theory. However, while re-mating rates were slightly higher in polygamous populations, there was little evidence that monandrous males evolved to be more benign towards females (Fricke & Arnqvist 2007). Notably, differences in female life span between distinct selection regimes seemed to reflect differences in background mortality rather than ageing. We need more experimental studies that assess the effects of both pre- and post-copulatory sexual selection on ageing, under levels of sexual conflict reflecting the recent evolutionary history of the study organisms.

INTRALOCUS SEXUAL CONFLICT

The evolution of optimal sexual dimorphism is constrained by the fact that most genes are expressed and subject to divergent (i.e. sex-specific) selection in both sexes. The result is *intralocus sexual conflict*, whereby evolution of a locus towards the sex-specific optimum is impeded by selection on the same locus in the opposite sex (Rice & Chippindale 2001; Arnqvist *et al.* 2005). Several genetic mechanisms can potentially ameliorate intralocus sexual conflict, including *sex-limitation* (Rhen 2000), *sex-linkage* (Bull 1983; Rice 1984; Rice 1996a), and *genomic imprinting* (Day & Bonduriansky 2004; Bonduriansky & Rowe 2005). Evidence for intralocus sexual conflict comes from breeding experiments in the laboratory (Fedorka & Mousseau 2004), cytogenetic cloning of haploid chromosome sets in *Drosophila melanogaster* (Chippindale, Gibson & Rice 2001; Pischedda & Chippindale 2006), studies of pedigreed wild vertebrate populations (Foerster *et al.* 2007), and experimental evolution where selection on one sex is removed (Prasad *et al.* 2007). These studies suggest that intralocus sexual conflict is widespread, and imposes an appreciable genetic load on populations.

Sexual selection and sexual conflict generate sex-dependent selection on life span and ageing, as well as the nature, amount and scheduling of reproductive effort. However, the possibility that life span and ageing mediate intralocus sexual conflict has received little attention from theorists or empiricists. The potential importance of intralocus sexual conflict is illustrated by the work of Tuljapurkar *et al.* (2007), who characterized differences between men and women in several societies in the age-dependence of reproductive success. They suggested that the substantial reproductive success of older men in 'traditional' societies may have favoured autosomal alleles that promote long life and slow ageing, and argued that expression of such male-benefit alleles in both sexes may explain women's long post-menopausal life spans. This example would represent a case of intralocus sexual conflict if it could be shown that female investment in post-menopausal longevity results in reduced fecundity, and such costs are not balanced by inclusive-fitness benefits (e.g. via grand-maternal care). If we are to understand the extent of intralocus sexual conflict over life span and ageing, we need estimates of realized mortality and ageing rates in both sexes, and sex-specific optima for investment in longevity and somatic maintenance.

In addition to understanding sex-differences in selection

and in patterns of ageing, we need a firm understanding of the genetic basis of ageing and related traits in both sexes. Strong positive intersexual genetic correlations would suggest genetic constraints on the potential for male and female life span and ageing to be optimized independently. Few if any comparable estimates of the genetic basis of ageing *per se* in males and females exist (but see Spencer *et al.* 2003). However, an accumulating body of evidence suggests that the genetic architecture of life span differs markedly between the sexes (Nuzhdin *et al.* 1997; Spencer *et al.* 2003; Fox *et al.* 2006; Tower 2006; Zajitschek *et al.* 2007). The only study to test explicitly for intralocus sexual conflict over ageing-related traits (Zajitschek *et al.* 2007) found a low intersexual genetic correlation for longevity (compared with other traits), suggesting little contemporary potential for intralocus sexual conflict. Studies that estimate genetic parameters for both reproductive and actuarial ageing are a high priority.

Whereas interlocus sexual conflict is likely to result in reduced life span (and perhaps in accelerated ageing) in one or both sexes, the effects of intralocus sexual conflict on these traits can be either positive or negative. Indeed, intralocus sexual conflict may displace both sexes from their sex-specific optima towards intermediate (less dimorphic) trait values. For example, if males experience weaker positive selection on life span than females as a result of sexual selection, then intralocus sexual conflict may result in an extension of male life span and reduction of female life span, relative to the sex-specific optima (or vice versa: see Tuljapurkar *et al.* 2007). Such effects may occur if selection on life span and ageing is strongly divergent in males and females, and if the intersexual genetic correlation is substantial. It remains unclear how broadly these conditions are met (Zajitschek *et al.* 2007).

NON-MENDELIAN INHERITANCE

Although there are few direct estimates of genetic correlations between male and female expression of ageing-related traits, one possible signature of intralocus sexual conflict is non-Mendelian inheritance of genetic variation for such traits. Strong intralocus sexual conflict is expected to favour the evolution of strategies that bias either the inheritance (Bull 1983; Rice 1984, 1996a) or expression (Rhen 2000; Day & Bonduriansky 2004) of sexually antagonistic fitness traits toward the sex in which they deliver a fitness benefit and away from the other sex. Consistent with this prediction, the sex chromosomes appear to be hotspots of sexually antagonistic variation (Lindholm & Breden 2002; Parisi *et al.* 2003; Fitzpatrick 2004; Tower 2006).

Across taxa, sex-biased mortality rates are often associated with heterogamy (Trivers 1985; Liker & Szekely 2005; Fox *et al.* 2006; Tower 2006), suggesting that the accumulation of sexually antagonistic genes on sex chromosomes relates (perhaps causally) to sex differences in mortality rates and, potentially, ageing. It remains possible, however, that heterogamy and sex-biased gene expression are as much a cause of sex-biased mortality as a consequence of intralocus sexual conflict. Deleterious recessive X- or Z-linked alleles

will be expressed in the heterogametic sex (males in XX/XY systems, females in ZZ/ZW systems) more often than in the homogametic sex, where they are masked from selection by dominance. By similar argument, sex-specific ageing could be a consequence of heterogamy because Y- or W-linked alleles are only expressed in the heterogametic sex, and seldom or never recombine. Alleles that cause ageing (or other deleterious effects) can accumulate on these chromosomes if they also deliver sex-specific benefits, or via hitch-hiking or Muller's ratchet (Rice 1996a; Brooks 2000; Chippindale & Rice 2001).

MITOCHONDRIA AND INTRAGENOMIC CONFLICT

Exclusively maternal inheritance of the mitochondrial genome means that selection cannot produce a response to male-specific selection on the mitochondria, or the interaction between the mitochondrial and nuclear genomes (Zeh & Zeh 2007). In line with this notion, Rand *et al.* (2001) showed that cytoplasmic genomes that are 'good' for females can be 'bad' for males and *vice versa*. The mitochondria are integral to the ageing process not least through association with reactive oxygen species pathways (Ballard & Whitlock 2004). Recent work on *Drosophila* shows that variation in mtDNA can affect ageing (James & Ballard 2003; Maklakov *et al.* 2006). The accumulation of mtDNA mutations that reduce male fitness may be expected to result in accelerated ageing in males, compared to females (Tower 2006) but, contrary to this prediction, some taxa exhibit female-biased mortality rates (Liker & Szekely 2005 and references therein). Further, work on *Drosophila* shows that sex-specific differences in mitochondrial metabolism are associated with sex-specific differences in ageing, but not necessarily with females living longer than males (Ballard *et al.* 2007). Nonetheless, it remains a strong possibility that maternal inheritance of mtDNA could be a major source of intralocus sexual conflict over life-history optimization, a possibility supported by evidence of sexually antagonistic fitness effects of interactions between cytoplasmic and X-linked factors (Rand *et al.* 2001; Rand, Fry & Sheldahl 2006).

Conclusions and future directions

The ideas and evidence reviewed above suggest that, as a general rule-of-thumb, sexual selection results in elevated mortality and weakened selection on life span in males, relative to females. However, this general prediction applies only partially, or not at all, to systems characterized by age-dependent expression of male secondary sexual traits, where long-lived males may be the most successful, or to species with secondarily convergent sex roles, such as monogamous or sex role-reversed species. A further complication might arise if male sexual competition imposes strong selection on condition, favouring genes with positive pleiotropic effects on survival and somatic maintenance. Theory and evidence also suggest that sexual conflict may displace one or both sexes from their sex-specific optima for ageing and life span. Observed variation in life span among males within and across species, and between the sexes, is broadly consistent with

these expectations, although numerous apparent exceptions remain. On the other hand, sex-differences in ageing rate remain poorly understood, perhaps because of the theoretical difficulties inherent in characterizing ageing rate and predicting its evolution (see Williams *et al.* 2006). Variation within and among species in mortality rate, life span and ageing, and in sexual dimorphism for these traits, may thus reflect a complex interplay of numerous mating system parameters, as well as phylogenetic history and ambient conditions.

Despite the complexity of the problem, several broad predictions are possible: (i) Within species, male phenotypes that invest more heavily in sexual competition should generally suffer more rapid ageing, except when mean male reproductive success increases with male age. This prediction applies both to discrete genetic or conditional polymorphisms, and to continuous variation in male phenotype; (ii) among species, those that exhibit more intense sexual selection and interlocus sexual conflict will generally suffer more rapid ageing in one or both sexes. However, the tendency for sexual selection and conflict to increase mortality and ageing rate may be weakened or reversed if male sexual competition selects strongly on whole-organism performance, or if mean male mating success increases with male age (Partridge & Barton 1996; Graves 2007); (iii) where one sex appears to have a relative disadvantage in the sexual arms race, that sex will tend to exhibit a higher mortality rate or faster ageing, relative to the same sex in related species (Promislow 2003); (iv) since the intensity of sexual selection may generally be reflected in morphological sexual dimorphism, variation among species in the degree of dimorphism in morphology may be expected to covary positively with dimorphism in mortality and ageing (Promislow, Montgomerie & Martin 1992; Promislow 2003); and (v) the degree of sexual dimorphism in life span and ageing will be reduced in proportion to the magnitude of the intersexual genetic correlation for these traits (see Zajitschek *et al.* 2007).

Several open-ended questions also arise: (i) how much of the variation among populations in ageing and life span is accounted for by variation in sexual selection and conflict, relative to more conventional factors such as background mortality rate and phylogenetic history?; (ii) what is the relative contribution of 'good genes' sexual selection vs. sexually antagonistic co-evolution to inter-population variation in ageing and life span?; and (iii) how much of the variation among populations in sexual selection gradients reflects the downstream consequences of environmental effects on ageing or life span?

Surprisingly, at this point, very few studies have directly addressed the key hypotheses and assumptions of the sexual conflict theory of ageing and life span. We have evidence that males evolve to affect life span and ageing in females, and that such evolution is contingent upon female life history. Consistent with theory, the evidence also suggests that such evolution always benefits males, but may or may not be beneficial to females. We have no evidence that sexual selection improves survival when sexual conflict is operating. In addition, fascinating indirect evidence suggests that

selection on mtDNA in females may impede the optimization of male life history.

All previous studies that attempted to test for the role of sexual selection in the evolution of ageing manipulated either mating system or life-history schedule. Given the complex nature of the interaction between sexual selection and life history, future experimental studies should aim to control both the mating system and the direction of selection on life-history traits. Such an approach has yielded important insights into the role of sexual selection in evolution and adaptation to different hosts (Fricke & Arnqvist 2007), and is likely to further our understanding of the evolution of life span and ageing.

Artificial selection and experimental evolution represent two powerful means to address the relation between sexual selection, life span and ageing. Traditionally, such studies have been conducted using a handful of model organisms (Chippindale 2006), particularly *Drosophila melanogaster* (Partridge & Barton 1993, but see Tucci *et al.* 1996). However, to assess the generality of our findings, we will need to broaden the taxonomic horizon of ageing research. In addition, comparative studies have been of paramount importance in identifying general patterns of sexual dimorphism in life span and in providing correlative tests of evolutionary hypotheses (Promislow 1992; Promislow, Montgomerie & Martin 1992; Liker & Szekely 2005). One potentially powerful methodology is to combine comparative and experimental techniques in the same research program (Rönn *et al.* 2007).

A further issue is the need to understand the effects of environment on the expression of ageing and life span and, in particular, the implications of studying ageing and sexual selection in the highly artificial environment of the laboratory. As noted above, ageing and life span are highly plastic traits. Likewise, it is clear that estimates of selection gradients, fitness components and quantitative-genetic parameters are highly sensitive to environment, and experimental results, including the outcome of selection experiments, may be strongly influenced by the peculiarities of the laboratory setting (Harshman & Hoffmann 2000; Pigliucci & Kaplan 2006; Kawasaki *et al.* 2008). This has been shown most clearly in studies that use quantitative-genetic breeding designs to estimate genetic correlations in order to test for trade-offs associated with age-dependent antagonistic pleiotropy (Service & Rose 1985; Houle 1991). Moreover, there is strong evidence that wild animals exhibit much higher extrinsic mortality rates, shorter life expectancies and, in some cases, more rapid ageing, than their captive counterparts (Ricklefs 2000; Bonduriansky & Brassil 2002; Bronikowski *et al.* 2002; Kawasaki *et al.* 2008), despite possessing the genetic capacity for long life span and slow ageing (Sgrò & Partridge 2000; Linnen, Tatar & Promislow 2001; Miller *et al.* 2002). Although challenging, research on ageing and sexual selection in wild populations can yield important insights and complement results from conventional laboratory studies.

In addition to addressing these questions empirically, there is a need for further development of theory. Given the complex dynamics of sexual co-evolution (e.g. Gavrilits &

Hayashi 2006), simulation analysis may yield useful insights into the evolution of ageing and life span under sexual conflict, and lead to novel hypotheses. Variation in ageing rate remains especially poorly understood, highlighting the need for further theoretical work to clarify the relation between reproductive strategy, life expectancy and ageing.

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