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# The hidden ageing costs of sperm competition

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34 **Abstract**

35 Ageing and sexual selection are intimately linked. There is by now compelling evidence from  
36 studies performed across diverse organisms that males allocating resources to mating  
37 competition incur substantial physiological costs, ultimately increasing ageing. However,  
38 although insightful, we argue here that to date these studies cover only part of the relationship  
39 linking sexual selection and ageing. Crucially, allocation to traits important in post-copulatory  
40 sexual selection, i.e. sperm competition, has been largely ignored. As we demonstrate, such  
41 allocation could potentially explain much diversity in male and female ageing patterns  
42 observed both within and among species. We first review how allocation to sperm  
43 competition traits such as sperm and seminal fluid production depends on the quality of  
44 resources available to males and can be associated with a wide range of deleterious effects  
45 affecting both somatic tissues and the germline, and thus modulate ageing in both survival  
46 and reproductive terms. We further hypothesize that common biological features such as  
47 plasticity, prudent sperm allocation and seasonality of ejaculate traits might have evolved as  
48 counter-adaptations to limit the ageing costs of sperm competition. Finally, we discuss the  
49 implications of these emerging ageing costs of sperm competition for current research on the  
50 evolutionary ecology of ageing.

51

52

53

## 54 INTRODUCTION

55 The ageing process is generally defined as a progressive decline in the age-specific  
56 contribution to fitness (Partridge & Barton 1993; Kowald & Kirkwood 2015; Gaillard &  
57 Lemaître 2020), which occurs due to a decrease in fertility and / or survival rates with  
58 advancing age (also called reproductive and actuarial senescence, respectively). Age-specific  
59 decreases in reproductive performance or survival are widespread in the animal kingdom  
60 (Nussey *et al.* 2013; Jones *et al.* 2014), governed by myriad physiological processes (López-  
61 Otín *et al.* 2013; Kennedy *et al.* 2014) and potentially largely uncoupled from each other  
62 (Gaillard & Lemaître 2017).

63 The trade-off between growth and reproductive effort early in life, and ageing in terms  
64 of reproduction and survivorship constitutes a major cornerstone of our current understanding  
65 of the evolution of ageing (Lemaître *et al.* 2015; Flatt & Partridge 2018). Based on the  
66 declining force of natural selection with increasing age (Medawar 1952), Williams (1957)  
67 proposed the *antagonistic pleiotropy* theory of ageing, positing that an allele with a positive  
68 effect on fitness during early adulthood will be selected even if this same allele is responsible  
69 for a decline in reproductive efficiency or survival prospects later in life (Williams 1957;  
70 Gaillard & Lemaître 2017; Austad & Hoffman 2018). One physiological mechanism by  
71 which the evolutionary trade-off between reproductive effort in early life and ageing can  
72 occur is a resource-based allocation trade-off, that constitutes the core of the *disposable soma*  
73 theory of ageing (Kirkwood 1977). This theory postulates that individuals have to allocate the  
74 limited resources they acquire to growth, reproduction and somatic maintenance (Kirkwood &  
75 Rose 1991). This means that substantial allocation to growth during early life leaves fewer  
76 resources to devote to reproduction or somatic maintenance mechanisms (e.g. protein  
77 clearance, Vilchez *et al.* 2014), which is then ultimately responsible for an earlier and/or  
78 faster rate of ageing (Kirkwood & Rose 1991; Kirkwood 2017). Another specific  
79 physiological pathway, the so-called *developmental* theory of ageing (Maklakov & Chapman  
80 2019) offers an alternative mechanism underlying the genetic trade-off envisioned by  
81 Williams (1957). According to that theory, physiological processes that allow fast growth and  
82 intense reproduction early in life have long-lasting effects that generate pathologies at old  
83 ages through cellular hyperfunction (Gems & Partridge 2013). Decades of research performed  
84 under both laboratory and wild conditions support the existence of a trade-off between  
85 reproduction and ageing (Flatt & Promislow 2007; Lemaître *et al.* 2015; Austad & Hoffman  
86 2018).

87           A striking feature of the many studies investigating the ageing consequences of a  
88 strong allocation to reproduction is their overwhelming focus on females (Lemaître *et al.*  
89 2015). For instance, a first compilation of studies testing for such early- vs. late-life trade-offs  
90 in wild populations of vertebrates revealed that 85.3 % of the single-sex studies were focused  
91 on females (Lemaître *et al.* 2015). There are several causes of this bias, including the central  
92 role of females in population dynamics, the higher energetic costs of gamete production for  
93 females compared to males (Hayward & Gillooly 2011), the obvious physiological costs  
94 associated with maternal care (e.g. lactation in harbour seal, *Phoca vitulina*, Bowen *et al.*  
95 1992), and the additional need for genetic analyses (and associated uncertainty) when it  
96 comes to assigning paternity rather than maternity. Even in laboratory settings where  
97 paternity can be assigned more easily, most studies still largely focused on females (but see  
98 below). Yet, the recent evidence that the intensity of ageing in both survival (e.g. Lemaître *et al.*  
99 *et al.* 2020) and reproduction (e.g. Brengdahl *et al.* 2018) can differ widely between males and  
100 females across species strongly emphasizes that we need to investigate how both natural and  
101 sexual selection interact to shape male ageing patterns. Such studies could reveal new insights  
102 about the evolutionary roots of the sex-specific decline in physiological performance and  
103 health issues at late ages (Marais *et al.* 2018).

104           So far, all attempts to reconcile male life history strategies within the early- vs. late-  
105 life trade-off framework offered by the evolutionary theory of ageing have put forward the  
106 predominant role of sexual selection (Vinogradov 1998; Promislow 2003; Bonduriansky *et al.*  
107 2008; Hooper *et al.* 2018). Basically, these studies rely on the traditional ‘sex role’ paradigm  
108 in evolutionary ecology (Bateman 1948; Trivers 1972), with males competing for gaining  
109 access to mating opportunities while females are the choosier sex (Dewsbury 2005; Janicke *et al.*  
110 *et al.* 2016). Evidence that sexual selection favours conspicuous behaviours and extravagant  
111 sexual traits is widespread in nature (Andersson 1994). Moreover, male reproductive effort is  
112 known to be associated with some physiological correlates of ageing (e.g. a decrease in anti-  
113 oxidant defences, Alonso-Alvarez *et al.* 2004, an impaired immune response, Peters *et al.*  
114 2004, or a stronger rate of telomere attrition, Giraudeau *et al.* 2016). Although the exact  
115 physiological pathways linking sexual selection to the degradation of the ‘organismal somatic  
116 state’ are likely to be complex and probably involve a complex role of androgens (Brooks &  
117 Garratt 2017; Metcalf *et al.* 2020), several empirical studies have evidenced an ageing cost of  
118 male allocation to sexual competition (see Table 1). Most of these studies have expressed this  
119 survival cost in terms of lifespan reduction, which may not directly translate into an ageing

120 cost in the strict sense (Péron *et al.* 2019). However, a few studies have also considered  
121 possible consequences in terms of ageing *per se*. For instance, in the wild, male red deer  
122 (*Cervus elaphus*) that allocate strongly to reproductive effort by displaying rutting behaviour  
123 during an extended period of the breeding season or by controlling large harems suffer from a  
124 stronger rate of reproductive ageing, measured through competitive abilities (Lemaître *et al.*  
125 2014).

126 Is sperm competition a neglected cause of ageing? Earlier studies have provided  
127 important insights into how sexual selection influences lifespan and impacts age-specific  
128 reproduction and survival. However, in this perspective article, we argue that studies seeking  
129 to decipher the ageing costs of male allocation to sexual competition need to fully embrace its  
130 complexity. Specifically, male allocation to sexual competition can be divided into two  
131 consecutive episodes: competition over mating (i.e. pre-copulatory competition) and  
132 competition over fertilization (i.e. post-copulatory competition) (Parker 1998; Andersson &  
133 Simmons 2006; Simmons *et al.* 2017). So far, the physiological and ageing consequences of  
134 male allocation to post-copulatory competition have been extensively studied in females (see  
135 Box 1 for a synthesis), but remain almost totally overlooked in males, which prevents us from  
136 drawing any firm conclusion on how male reproductive allocation influences fitness-related  
137 traits in late life.

138 We thus aim to highlight the untapped potential of sperm competition studies for  
139 better understanding the ageing process. As we show, there are multiple ways in which  
140 allocation to sperm competition could alter physiological pathways ultimately linked to  
141 ageing in reproduction and survivorship (Figure 1). Although other components of the male  
142 reproductive phenotype linked to sperm competition success might be considered in the future  
143 (e.g. genital morphology; behavioural adaptations), we deliberately focus here on ejaculate-  
144 related adaptations to post-copulatory competition (both sperm and non-sperm components)  
145 as these seem likely to be most strongly associated with long-term ageing costs. After  
146 considering the various potential costs, conceptually as well as through a critical appraisal of  
147 the limited empirical evidence published so far, we further argue that plasticity in many of  
148 these traits can best be understood in the light of the evolutionary theory of ageing. Finally,  
149 we provide a roadmap for future studies aimed at deciphering the hidden ageing costs of  
150 sperm competition.

151

152 **AGEING COSTS OF SPERM COMPETITION**

153           **(a) Sperm quantity and quality**

154 Female multiple mating is widespread in nature (Birkhead & Møller 1998). As a  
155 consequence, sperm competition (i.e. when sperm from two or more males compete to  
156 fertilize a set of ova, Parker 1970) is found in the vast majority of species (Birkhead & Møller  
157 1998). Across species, males can improve their fertilization success through several (non-  
158 mutually exclusive) pathways. The most studied pathway is undoubtedly through producing  
159 more sperm, as sperm competition game models generally predict that a higher number of  
160 sperm within ejaculates provide a fertilization advantage over competitors (reviewed in  
161 Pizzari & Parker 2009; Parker 2016). In line with these predictions, it has been repeatedly  
162 observed that the production of larger ejaculates is indeed often associated with a higher  
163 fertilization success (e.g. Gage & Morrow 2003; Boschetto *et al.* 2011). Unsurprisingly,  
164 sexual selection has thus promoted the evolution of larger testes (Parker 2016) as well as a  
165 higher proportion of sperm-producing tissue within it (e.g. Lüpold *et al.* 2009) and a faster  
166 rate of spermatogenesis (Ramm & Stockley 2010), under intense levels of sperm competition  
167 (e.g. in promiscuous species). Indeed, the selective pressure of sperm competition likely  
168 shapes multiple aspects of spermatogenesis affecting sperm production rate, from the number  
169 and activity of spermatogonial stem cells, the degree and architecture of their expansion and  
170 their post-meiotic differentiation into highly specialised sperm cells (Ramm *et al.* 2014;  
171 Ramm & Schärer 2014).

172           An increase in the number of sperm allocated per ejaculate is only one of the multiple  
173 pathways boosting fertilization success. Several features of the sperm cell itself have evolved  
174 in response to intense levels of sperm competition (Pizzari & Parker 2009; Fitzpatrick &  
175 Lüpold 2014). Among these characteristics, the positive influence of sperm motility (i.e.  
176 proportion of motile sperm within an ejaculate) and of average within-ejaculate sperm  
177 velocity on male fertilizing ability has been repeatedly documented (Snook 2005; Pizzari &  
178 Parker 2009). These effects are explained by the fact that faster sperm will often reach  
179 female's gametes quicker than slower sperm (see for example Gage *et al.* 2004; Gasparini *et al.*  
180 *al.* 2010 for evidence in external and internal fertilizers, respectively). Comparative analyses  
181 performed across various taxa have revealed that sperm swimming velocity increases with  
182 sperm size (e.g. Fitzpatrick *et al.* 2009 in fishes; Tourmente *et al.* 2011 in mammals),  
183 highlighting that various structural aspects of sperm – especially flagellum or midpiece  
184 length/volume – modulate sperm velocity (Cardullo & Baltz 1991; Pizzari & Parker 2009). In  
185 primates, males from species where females mate with multiple partners display midpieces  
186 with a larger volume (Anderson & Dixson 2002). As larger midpieces are associated with a

187 greater mitochondrial loading supporting sperm motion (Gu *et al.* 2019), this increased  
188 midpiece volume appears to be adaptive when females mate with several males within a given  
189 breeding attempt.

190 In the next sections, we consider the various pathways through which allocation to  
191 these sperm traits imposes costs on males that likely result in accelerated ageing in  
192 reproduction or survivorship.

193  
194 *Energetic costs of sperm production.* One tenet of our current understanding of the evolution  
195 of ageing relies on the energetically-demanding aspect of reproductive allocation (Kirkwood  
196 2017), which is typically the case when it comes to producing an ejaculate and to growing and  
197 maintaining an efficient reproductive machinery (Kenagy & Trombulak 1986). Although  
198 earlier studies assumed that sperm were particularly cheap to produce (see Dewsbury 2005),  
199 the influence of resource availability on sperm production has been demonstrated in a wide  
200 spectrum of organisms. For instance, in fallow deer (*Dama dama*), a species in which females  
201 mate with several males during a given reproductive attempt (Briefer *et al.* 2013), yearling  
202 males with a diet supplemented with protein and amino acids have larger testes, exhibit  
203 Sertoli cells – which play a key nutritional function during spermatogenesis – with higher  
204 workload capacities, higher concentrations of sperm within the epididymis and sperm with a  
205 longer midpiece than do non-supplemented yearling males (Ros-Santaella *et al.* 2019). This  
206 positive effect of an enriched diet on sperm quantity and/or quality has also been repeatedly  
207 found in agronomy research (e.g. Zhao *et al.* 2017) and in invertebrates. In cockroaches  
208 (*Nauphoeta cinerea*), for example, the number of sperm found in the spermatophore delivered  
209 to females (but not sperm viability) increases with the intake of both proteins and  
210 carbohydrates (Bunning *et al.* 2015). The same relationships are observed in the Argentine ant  
211 (*Linepithema humile*), where a protein restriction in the diet during the larval stage (i.e. when  
212 the whole stock of sperm is produced) impairs sperm production but does not decrease sperm  
213 viability (Dávila & Aron 2017). In this social insect, a stronger allocation of the decreased  
214 quantity of resources to sperm quality (i.e. sperm viability) might be adaptive as sperm can be  
215 stored for several years before fertilization in the female spermathecae. Overall, the  
216 production of high-quality ejaculates largely depends on male condition and the quantity of  
217 resources that individuals can allocate to the post-copulatory traits (Perry & Rowe 2010),  
218 although the condition-dependent nature of ejaculate traits likely vary across species (see  
219 Macartney *et al.* 2019 for a meta-analysis).



220           Limitations on resource availability that generally occur in the wild lead to an increase  
221 in the physiological costs of spermatogenesis. This is well illustrated in adders (*Vipera berus*),  
222 where the magnitude of testis growth prior to the reproductive season is positively correlated  
223 with body mass loss (Olsson *et al.* 1997). In this species, the allocation to spermatogenesis  
224 (i.e. post-copulatory traits) accounts for a higher proportion of mass loss than the allocation to  
225 mate searching (i.e. pre-copulatory traits) (Olsson *et al.* 1997), which strongly suggests that  
226 the long-term ageing costs of mass loss generated by repeated reproductive seasons  
227 throughout life might not be trivial. It thus appears that males substantially allocating to  
228 sperm competition might – following the life history of ageing framework (Lemaître *et al.*  
229 2015; Kirkwood 2017) – suffer from strong physiological costs (e.g. immune costs, as  
230 discussed in the next section) that will ultimately lead to a shorter lifespan and/or more  
231 pronounced ageing in fitness components.

232

233 *Immune costs of sperm production.* Pathogen-infected males generally have less efficient  
234 post-copulatory traits than uninfected males, whether pathogens are directly located in the  
235 ejaculate component (e.g. Cunningham & Beagley 2008) or not (e.g. Polak 1998). The  
236 negative association between the allocation to ejaculate-related traits and the performance of  
237 the immune system (or vice-versa) likely accounts for this difference (see Table 2 for a  
238 synthesis). For instance, in Arctic charr (*Salvelinus alpinus*) males, the density of  
239 granulocytes (i.e. white blood cells belonging to the non-specific immune system) is  
240 negatively correlated with the concentration of sperm within semen (Liljedal *et al.* 1999).  
241 Overall, the trade-off between ejaculate quality and immune performance is pervasive, even if  
242 a thorough investigation of the immune repertoire is required because the allocation to  
243 ejaculate-related traits might be negatively related to some immune cells while being  
244 positively associated with others (see Simmons & Roberts 2005 for a case study in crickets,  
245 *Teleogryllus oceanicus*). This decreased activity of the immune system following an increased  
246 sperm production is adaptive because it minimizes the risk of autoimmunity, since antigens at  
247 the surface of sperm cells lead them to be recognized as foreign bodies by the immune cells  
248 (see Skau & Folstad 2005). In line with this functional link, experimental evolution work in  
249 yellow dung flies (*Scathophaga stercoraria*) revealed that males from lines selected under an  
250 elevated sperm competition regime show lower phenoloxydase activity than males from  
251 monandrous lines (Hosken 2001), which makes these males more likely to suffer from an  
252 infection (McKean & Nunney 2001). In addition, the negative association between sperm  
253 production and immunity might be directly reinforced by a resource-based allocation trade-

254 off. This is well-illustrated in crickets (*T. oceanicus*), where the trade-off between  
255 antibacterial activity and sperm viability is only observed in individuals fed with a nutrient-  
256 restricted diet (Simmons 2012).

257         Similar to what has already been reported for the allocation to growth and/or  
258 reproduction in males, or the male allocation to the growth and maintenance of pre-copulatory  
259 traits in males (Folstad & Karter 1992; Rödel *et al.* 2016), a strong allocation to post-  
260 copulatory traits can be highly detrimental for male's immune performance (Table 2). As  
261 immunity constitutes a key physiological function mediating trade-offs among life-history  
262 traits (Sheldon & Verhulst 1996), an elevated allocation to post-copulatory competition  
263 should have long-term consequences in terms of reduced lifespan and increased ageing rates  
264 through the impairment of immune performance throughout life.

265  
266         *Reproductive senescence costs of sperm production.* Similar to what is observed for the  
267 allocation of resources to pre-copulatory traits in early life (Table 1), the long-term fitness  
268 costs of a strong allocation to sperm production could also be expressed in terms of  
269 reproductive ageing. Thus, in *Drosophila melanogaster*, an increased reproductive effort early  
270 in life has a negative impact on subsequent fertility, which is mediated by a pronounced age-  
271 specific decline in sperm numbers (Prowse & Partridge 1997). Similarly, in the domestic fowl  
272 (*Gallus gallus domesticus*), males that produce the highest quality sperm (judged through  
273 sperm velocity) during early life show the steepest decline in sperm quality in late life  
274 (Cornwallis *et al.* 2014). This suggests that males allocating a lot to the production of high-  
275 quality ejaculates during early life might suffer from a stronger decline in reproductive  
276 success at late ages. Evidence that males naturally suffer from a decline in reproductive  
277 success with increasing age is widespread across the tree of life (Johnson & Gemmell 2012;  
278 Lemaître & Gaillard 2017), and the (epi)genetic and physiological mechanisms underlying  
279 this decline are diverse (Evans *et al.* 2019; Fricke & Koppik 2019; Monaghan & Metcalfe  
280 2019). Here we discuss four related aspects that seem especially relevant when sperm  
281 competition occurs.

282         First, the accumulation of mutations on the male germline throughout life (e.g. Velando  
283 *et al.* 2011; Kong *et al.* 2012) might play a key role in causing reproductive ageing  
284 (Monaghan & Metcalfe 2019). In that context, is selection for a higher allocation to sperm  
285 competition responsible for an increased mutation rate? And do elevated mating rates amplify  
286 this mutation load, as males need to replenish their sperm storage quickly to avoid sperm  
287 limitation (Dewsbury 1982; Nakatsuru & Kramer 1982)? There is good evidence that high

288 mating rates impair ejaculate quality in the short-run (e.g. Wedell & Ritchie 2004) but  
289 whether the repeated and/or sustained activation of the spermatogenesis machinery influences  
290 fitness-related traits in late life is much less clear (Vega-Trejo *et al.* 2019), as are the  
291 underlying mechanisms (Fricke & Koppik 2019). The degree to which mutations impact stem,  
292 transit or sperm cells themselves during spermatogenesis will be key to the long-term  
293 consequences of sperm allocation, and this in turn will partly depend on the hierarchical  
294 organisation of cell division within the testis, i.e. on its tissue architecture, which varies  
295 widely among species (see Schärer *et al.* 2008; Ramm & Schärer 2014). But as testicular stem  
296 cell activity increases to support greater sperm production under sperm competition, the  
297 burden of mutation and its manifestation in terms of reproductive ageing is predicted to  
298 increase (Blumenstiel 2007). To date, little work has been done to measure inter- and intra-  
299 specific variation in relevant parameters in response to sperm competition levels, but we  
300 know that in the flatworm *Macrostomum lignano*, an increased stem cell activity and  
301 corresponding faster speed of spermatogenesis support the enhanced sperm production that is  
302 selected when sperm competition occurs (Schärer *et al.* 2004; Giannakara *et al.* 2016).  
303 Moreover, recent evidence in seed beetles, *Callosobruchus maculatus*, suggests that the  
304 higher level of sperm production under sperm competition directly compromises the ability of  
305 the testis to maintain germline integrity, resulting in increased mutation loads being passed to  
306 offspring (Baur & Berger 2020).

307         Second, a plausible route linking sperm production to reproductive ageing is that  
308 increased gonadal activity might have direct detrimental consequences on male reproductive  
309 traits through an increased production of reactive oxygen species (ROS) (Reinhardt 2007;  
310 Monaghan & Metcalfe 2019) - a factor known to influence ageing patterns (Finkel &  
311 Holbrook 2000). Thus, in rats, *Rattus norvegicus*, an increased sexual activity directly leads to  
312 an elevated level of oxidative stress within the testis (Salomon *et al.* 2013). While repeatedly  
313 increased level of oxidative stress might cause impaired testicular function and sperm  
314 fertilization efficiency over time (Aitken & Baker 2006), and thereby increase reproductive  
315 ageing, empirical studies investigating this topic are currently lacking.

316         A third consideration regarding long-term consequences of increased sperm production  
317 concerns the fact that sperm competition has likely selected for the overexpression of genes  
318 promoting cell proliferation, notably in the spermatogonia (Kleene 2005; Lewis *et al.* 2008).  
319 While the expression of such genes might convey an important competitive advantage in  
320 terms of ejaculate size and number, they are likely also to increase the risk of developing  
321 testicular cancer (see Kleene 2005; Lewis *et al.* 2008 for reviews), which could badly impair

322 reproductive success in late life (Huddart *et al.* 2005). So far, these relationships have been  
323 almost solely investigated in *Drosophila spp.* (Hime *et al.* 2007), even though several studies  
324 are now documenting cancers across very diverse species (see Madsen *et al.* 2017;  
325 Albuquerque *et al.* 2018). However, whether selection for enhanced sperm production under  
326 sperm competition is associated with an increased risk of getting cancer (and most  
327 specifically testicular cancer) at both intra- or inter-specific level is yet to be determined  
328 (Lewis *et al.* 2008).

329         Finally, the maintenance of accurate and efficient physiological and cellular processes  
330 throughout life is fundamental to our current understanding of ageing (Kirkwood 2017;  
331 Maklakov & Chapman 2019). In most animals, males have to allocate a substantial quantity  
332 of resources to mechanisms involved in the maintenance of the genome and proteome of the  
333 pool of germline stem cells (Maklakov & Immler 2016), and we expect that these costs should  
334 scale with sperm production capacity. These costs are probably far from negligible, since in  
335 laboratory mice the activity of enzymes repairing DNA is much greater in germ cells than in  
336 somatic cells (Intano *et al.* 2001). Moreover, among somatic cells, the enzymatic activity is  
337 higher in Sertoli cells than in those from other tissues (e.g. liver, brain), highlighting again the  
338 substantial maintenance costs associated with the male reproductive machinery (Intano *et al.*  
339 2001). With increasing age, males suffer from an age-specific decline in germline  
340 maintenance (Maklakov & Immler 2016), which might be responsible for an increased  
341 mutation rate on sperm in old males. However, whether the quantity of resources devoted to  
342 sperm competition limits the allocation to germline maintenance throughout life and  
343 ultimately triggers accelerated reproductive ageing remains to be investigated (but see Baur &  
344 Berger (2020) for a notable case study and Chen *et al.* (2020) for experimental evidence that  
345 preventing allocation to the germline results in an enhanced ability for somatic repair).

346         Overall, although there are several well understood aspects of male reproductive ageing,  
347 the extent to which a strong resource allocation to traits shaping sperm competition in early  
348 life amplifies ageing and thus exacerbates the widely observed decrease of the male gonadal  
349 size and function with increasing age (Lemaître & Gaillard 2017; Fricke & Koppik 2019;  
350 Santiago *et al.* 2019) remains an open question. Answering it is of crucial importance, since  
351 such effects might not only reinforce male reproductive ageing (e.g. through a decrease in  
352 sperm quantity) but could also lead to deleterious consequences more generally for male  
353 condition and health (Bribiescas 2006) – for example, through a decline in testosterone  
354 production over the life course (see Yeap 2009) – which could ultimately impact lifespan and  
355 survival ageing patterns (Bribiescas 2006, see next section). These interactions between

356 ageing in reproduction and survivorship might be even more complex as organisms have to  
357 partition a limited resource pool between germline and somatic maintenance (Figure 1;  
358 Maklakov & Immler 2016) and selection to maintain the integrity of the germline might be  
359 particularly strong (Kirkwood 2005; Maklakov & Immler 2016). Hence, maintaining germline  
360 integrity under sperm competition likely gets harder (as so many more sperm need to be  
361 produced), and this may lead somatic maintenance (see Chen *et al.* 2020 for recent evidence  
362 in vertebrates) and ultimately lifespan to be traded against sperm competition to get  
363 immediate benefits in terms of reproductive output.

364

365 *Lifespan and survival ageing costs of sperm production.* Despite the accumulation of  
366 evidence that a strong allocation to sperm production can entail acute physiological costs, its  
367 long-term consequences in terms of lifespan or survival ageing have been largely overlooked.  
368 Yet, some studies performed on insects have revealed that high mating rates can shorten male  
369 lifespan (Partridge & Farquhar 1981; Martin & Hosken 2004; Paukku & Kotiaho 2005; Dao  
370 *et al.* 2010; Metzler *et al.* 2016; Jehan *et al.* 2020), which might be due to the down-  
371 regulation of the expression of some specific genes (e.g. metabolic genes) straight after sexual  
372 activity (Branco *et al.* 2017). However, although sperm competition and mating rate are often  
373 related (Parker & Ball 2005), mating rate depends also on the number of receptive females in  
374 the population rather than purely the number of competing males, and so a high mating rate  
375 alone does not constitute the most accurate proxy of a strong resource allocation to sperm  
376 competition (Vahed & Parker 2012). The relative influence of sperm production and mating  
377 rate *per se* on lifespan was disentangled in a pioneering experiment carried out on  
378 *Caenorhabditis elegans* (Van Voorhies 1992). Males (and hermaphrodites) carrying a mutant  
379 *spe-26* gene showed a reduced rate of sperm production but a 65% increased lifespan  
380 compared to wild-type worms, but this gain was not amplified when mutant males were  
381 prevented from mating, suggesting that the long-term fitness costs strictly associated with  
382 sperm production are far from negligible (Van Voorhies 1992). Despite these promising  
383 results, the survival costs of sperm production have remained largely understudied. Yet, in  
384 large milkweed bug (*Oncopeltus fasciatus*), males fed with an ancestral seed diet show a  
385 higher sperm production at the expense of a reduced lifespan (Duxbury *et al.* 2018).  
386 Moreover, in domestic fowl (*Gallus gallus domesticus*), males that produce the highest  
387 quantity of sperm through life show a reduced lifespan (Cornwallis *et al.* 2014) while in the  
388 guppy (*Poecilia reticulata*), the opposite pattern occurs (Gasparini *et al.* 2019).

389 We thus emphasize that studies at the interplay of sexual selection and ageing should  
390 now seek to accurately quantify these long-term survival costs (Figure 1), which would  
391 strongly contribute to understanding the diversity of life history strategies observed across the  
392 tree of life. Importantly, such studies should investigate whether the survival costs of an  
393 increased allocation to sperm competition is mediated by an acceleration of ageing rather than  
394 an immediate rise of the risk of death (Partridge & Andrews 1985). The phylogenetically-  
395 controlled comparison of male actuarial senescence patterns across species displaying  
396 contrasted mating systems or - more accurately - a high variation in the rate of multiple  
397 paternity (e.g. Soulsbury 2010 in mammals) would provide complementary insights on the  
398 role played by sperm competition in shaping lifespan and actuarial senescence patterns in  
399 males. In addition, analyses performed at the population level will enable tests of whether  
400 these long-term survival costs are a consequence of an earlier age at the onset of ageing, an  
401 increased rate of ageing, or both (Péron *et al.* 2019).

402

#### 403 **(b) Seminal fluid**

404 Male fertilization success is also modulated by the non-sperm components of the ejaculate  
405 (Perry *et al.* 2013), with comparative (e.g. Ramm *et al.* 2005) and experimental (e.g.  
406 Simmons *et al.* 2020) data pointing towards the importance of increased allocation to seminal  
407 fluid under heightened levels of sperm competition. Interestingly, the female ageing cost of  
408 repeated exposure to male seminal fluid content has been studied extensively (see box 1). By  
409 contrast, whether the selection acting on the production of complex seminal fluid is associated  
410 with long-term ageing costs in males has largely been overlooked.

411 Multiple lines of evidence suggest that seminal fluid production is energetically costly  
412 (see also Table 2). Metabolic labelling studies in mice indicate that seminal fluid-producing  
413 tissues exhibit high rates of protein turnover (Claydon *et al.* 2012). In some taxa, seminal  
414 fluid allocation can reach extreme proportions. This is well illustrated in several species of  
415 bushcrickets where a single water- and protein-rich spermatophore transferred to a female can  
416 represent as much as 40% of male body mass (Vahed 2006), but also in butterflies where the  
417 production of the sphragis (i.e. an external plug secreted by the male accessory glands and  
418 fixed to the female abdomen to impair further the access to the female genitalia) by males can  
419 constitute up to 20% of the male body mass (Carvalho *et al.* 2017). In line with these  
420 observations, a recent meta-analysis highlighted that the production of seminal fluid show a  
421 higher degree of condition-dependence than sperm production *per se* (Macartney *et al.* 2019).  
422 Moreover, studies of accessory gland size in *Drosophila*, bedbugs and snails all suggest that

423 seminal fluid production may limit male mating rate (De Boer *et al.* 1997; Bangham *et al.*  
424 2002; Reinhardt *et al.* 2011), implying that replenishment of seminal fluid protein reserves  
425 after mating is a non-trivial cost to males. Finally, while the male competitive advantage of  
426 producing large amounts of seminal fluid as well as the deleterious consequences for females  
427 (see Box 1) have been well described in the literature (e.g. Wigby *et al.* 2009), the potential  
428 toxic effects and associated ageing consequences to their repeated storage in male's gonad are  
429 yet to be investigated.

430         Because males usually produce both sperm and seminal fluid simultaneously,  
431 however, it is difficult to tease apart the relative costs of these two ejaculate components. This  
432 difficulty is circumvented in red-sided garter snakes, *Thamnophis sirtalis parietalis*, in which  
433 spermatogenesis and seminal fluid (copulatory plug) production occurs at different times of  
434 the year. Whilst sperm are produced in the late summer and then stored over-winter, seminal  
435 fluid production does not occur until the onset of the mating (and fasting) season in spring.  
436 Friesen and colleagues (2015) took advantage of these biological features to establish that the  
437 elevated metabolic rate associated with plug production are considerable, comparable even to  
438 those incurred by pregnant females. They further showed that these costs are especially  
439 pronounced in small males and, importantly, were able to quantify the energetic costs of  
440 producing a single copulatory plug (up to 18% of the daily energy expenditure). Their  
441 estimate reinforces earlier evidence of substantial mating costs based on the heightened blood  
442 lactate levels observed in mating vs. only courting males (Shine *et al.* 2004). These high  
443 energetic costs mean males can only deposit 1-2 plugs per day (Friesen *et al.* 2013) and again  
444 clearly challenge the traditional idea that seminal fluid production is a trivial expense to  
445 males. Whether the substantial costs of seminal fluid production translate into increased  
446 ageing is currently unclear, due simply to a paucity of relevant data. However, Koppik and  
447 colleagues (2018) recently discovered that, at old ages, sexually active male *D. melanogaster*  
448 display shorter mating, resulting in a lower number of eggs laid by females than following  
449 mating with virgin males. However, this pattern might be more likely due to a decrease in  
450 sperm number rather than in the quantity of seminal fluid proteins delivered to females, when  
451 sexually active males are reaching old ages (see Sepil *et al.* 2020).

452

## 453 **MITIGATION OF THE AGEING COSTS OF SPERM COMPETITION IN THE** 454 **WILD**

455 The evidence compiled above suggests that a strong allocation to traits associated with an  
456 advantage when sperm competition occurs may be associated with some underestimated

457 fitness costs, such as a shortened lifespan or increased ageing. One might thus expect that  
458 counter-adaptations have evolved to buffer the cascade of physiological costs and their fitness  
459 consequences. We discuss below some of these possible adaptations and evaluate how much  
460 they can mitigate fitness costs.

461

#### 462 (a) Phenotypic plasticity in ejaculate production

463 Within species, sperm competition levels can fluctuate considerably across reproductive  
464 seasons and among populations. One way to minimize the various physiological costs  
465 potentially associated with elevated ejaculate expenditure would be to adjust ejaculate quality  
466 and quantity to the level of sperm competition. Such fine-scale adjustments require the  
467 evolution of phenotypic plasticity in the male reproductive machinery. Experimental  
468 manipulations of the social environment faced during the developmental period reveal that  
469 such plasticity might be common. For instance, in house mice (*Mus musculus*) males that  
470 were repeatedly in contact with the odour of multiple unrelated (i.e. rival) males had an  
471 elevated sperm production rate compared to males that were in contact to the odour of only a  
472 single competitor (Ramm & Stockley 2009). A similar experimental design revealed that in  
473 bank voles (*Myodes glareolus*), males who developed under environmental conditions  
474 mimicking high levels of sperm competition developed larger seminal vesicles (but similar  
475 testis mass) than males who developed under environmental conditions mimicking low levels  
476 of sperm competition (Lemaitre *et al.* 2011). Overall, this suggests that the allocation to post-  
477 copulatory traits is modulated in response to (social) environmental conditions, a  
478 characteristic that is widely shared across animal species for various sperm and non-sperm  
479 ejaculate traits (e.g. Immler *et al.* 2010 in birds; Stockley & Seal 2001; Simmons &  
480 Lovegrove 2017; Sloan *et al.* 2018 in insects; Nakadera *et al.* 2019 in snails; Janicke *et al.*  
481 2013; Giannakara *et al.* 2016; Ramm *et al.* 2019 in flatworms; Tan *et al.* 2004 in leeches and  
482 Crean & Marshall 2008 in a broadcast spawning ascidian). Such fine-tuning to match the  
483 prevailing demand – or in other words, minimizing the expenditure where possible – may thus  
484 be one of the means through which males can limit the substantial physiological costs  
485 associated with the high metabolic demand of spermatogenesis and seminal fluid production.  
486 In line with this prediction, an experiment performed in *D. melanogaster* has revealed that  
487 males reared with rivals produced more offspring during early life (in non-competitive trials)  
488 but paid a long-term survival cost with a median lifespan reduced by 19% (Bretman *et al.*  
489 2013), which suggests that curtailing ejaculate production in absence of competitors might  
490 limit long-term ageing costs.



491

492 **(b) Context-dependent sperm allocation**

493 In addition to fine-tuning how many resources to expend on ejaculate production, a further  
494 level of male allocation likely occurs with respect to how many sperm and/or how much  
495 seminal fluid is transferred in each individual ejaculate. Thus, whilst traditionally assumed to  
496 be cheap, it has now been recognised for some time that males should prudently allocate  
497 ejaculate components according to relevant cues of sperm competition at the time of mating  
498 (see Wedell *et al.* 2002; Cameron *et al.* 2007; Parker & Pizzari 2010; Perry *et al.* 2013 for  
499 reviews). For example, it typically pays to allocate more sperm per ejaculate under conditions  
500 of high sperm competition risk (e.g. delBarco-Trillo & Ferkin 2004), to allocate fewer per  
501 ejaculate at high sperm competition intensity (e.g. Pilastro *et al.* 2002), to adjust the proteins  
502 compounds of the seminal fluid according to the degree of sperm competition (Hopkins *et al.*  
503 2019) and to modulate ejaculate size depending on own social status (e.g. Bartlett *et al.* 2017)  
504 or to the male mating order and female reproductive status (Thomas & Simmons 2007).  
505 Whilst these responses can be understood in terms of maximising fitness returns given a  
506 certain gamete number (or seminal fluid amount) available to allocate, they ultimately stem  
507 from the fact that the ejaculate supply is limited – one reason for which being that producing  
508 both sperm and non-sperm ejaculate components likely imposes substantial costs, many of  
509 which may ultimately increase the intensity of ageing.

510

511 **(c) Sperm production seasonality**

512 Besides using cues from their social environment to fine-tune sperm production and  
513 allocation, males of many taxa also show clear seasonal variation in traits such as testis size  
514 and sperm in storage, with peak production or availability often timed to coincide with a  
515 specific breeding season (reviewed in Ramm & Schärer 2014). In male fallow deer, for  
516 example, there is a three-fold increase in testis volume from its minimum to its peak just  
517 before the annual rut (Gosch & Fischer 1989; for a broader survey across mammals, see  
518 Setchell & Breed 2006). Even more marked variation is reported in other taxa with highly  
519 seasonal reproductive seasons such as the annual variation observed in male (and female)  
520 gonado-somatic index in many broadcast spawners (see Parker *et al.* 2018 and references  
521 therein) and some fishes (e.g. Turner 1919). As discussed by Ramm and Schärer (2014), such  
522 seasonal variation can be accompanied by specific features of spermatogenesis, such as the  
523 long branch lengths (many rounds of mitotic division) observed for example in cichlids,  
524 meaning thousands of spermatids are produced per primary spermatogonium, supporting the

525 delivery of a large number of sperm at a specific time of the year (Fishelson 2003). These and  
526 other features emphasize the expensive nature of spermatogenesis. Moreover, as we have  
527 seen, the fact that sperm production sometimes occurs asynchronously with the breeding  
528 season – when energetic demand from other traits such as mate searching, pre-copulatory  
529 competition and courtship also peaks - is probably also indicative of its high costs (Olsson *et*  
530 *al.* 1997). However, we cannot rule out that in some species, such uncoupling might be a  
531 constraint associated with prolonged periods of torpor (Gustafson 1979).

532 Overall, we expect that the ‘savings’ to be made from seasonal fluctuation in ejaculate  
533 production will be highly species-specific and depend on its particular reproductive ecology,  
534 but that matching supply and demand in this manner is a widespread mechanism to minimise  
535 the energetic and other costs outlined above, all of which would otherwise ultimately  
536 feedback on accelerated survival and/or reproductive ageing.

537

## 538 **ROADMAP FOR FUTURE RESEARCH**

539 Overall, studies that seek to quantify the long-term ageing cost of a strong allocation to sperm  
540 competition and to decipher the underlying physiological pathways are thus badly required.  
541 Such studies would undeniably enhance our knowledge in two main areas of evolutionary  
542 ecology, namely sexual selection and ageing. We propose below a few potential avenues for  
543 future research.

544

### 545 **(a) Do production plasticity, resource allocation and seasonality limit male** 546 **ageing?**

547 Whilst at some level it is clear that any reduction in ejaculate demand must ultimately be less  
548 costly than the alternative, few studies have to date sought to use either intra- or interspecific  
549 variation in, for example, the incidence of sperm competition or length of the breeding season  
550 to better understand the nature and magnitude of these costs, or to quantify their impact on  
551 ageing of fitness components. Comparative work in this area is likely to be highly  
552 informative, and one of the most promising of all would be experimental approaches that seek  
553 to modify one or more of these axes and then measure the ageing consequences. Potentially  
554 useful approaches here might include experimental evolution to test for the correlated  
555 evolution of ageing effects in lines selected for higher or lower allocation toward sperm  
556 competition traits or under different intensity of sexual conflict. Recent experiments  
557 performed in *D. melanogaster* have revealed that males from monogamous lines (i.e. without  
558 sperm competition) reduce their allocation to various post-copulatory traits. For instance, they

559 show a lower expression of genes coding for seminal fluid proteins compared to males from  
560 polygamous lines (Hollis *et al.* 2019). Investigating whether these males also display a  
561 delayed and/or reduced reproductive and/or survival senescence patterns compared to males  
562 evolving under competitive conditions would be very informative to assess whether natural  
563 and sexual selection have fine-tuned the allocation to post-copulatory traits to limit its  
564 detrimental ageing consequences.

565 Where experimentally feasible, the direct manipulation of relevant physiological  
566 pathways involved in ejaculate production using gene knockdown or gene-editing techniques  
567 would also be insightful. By thereby manipulating the capacity for plasticity or allocation, one  
568 could more precisely identify the mechanisms involved in both short- and long-term fitness  
569 consequences. Precisely such an approach was recently adopted to test for a trade-off between  
570 germline and somatic maintenance in the zebrafish *Danio rerio* (Chen *et al.* 2020). Un-  
571 manipulated and germline-free knockdown individuals were exposed to sublethal low-dose  
572 ionizing radiation, revealing that somatic recovery occurred much faster in the germline-free  
573 individuals that were prevented from allocating to reproduction (Chen *et al.* 2020). These  
574 results thus support the idea that germline maintenance is costly. As we emphasized above,  
575 these costs likely scale with sperm competition level. Finally, experimental manipulations of  
576 the quantity of resources available in the environment would also provide relevant insights.  
577 As emphasized above, the allocation to ejaculate production increases with resource  
578 availability (Zhao *et al.* 2017; Ros-Santaella *et al.* 2019). Therefore, for a given level of  
579 sperm competition perceived in the environment, we can predict that males should their  
580 increase their allocation to post-copulatory competition, at no or very limited costs in terms of  
581 ageing.

582

583 **(b) Ageing consequences of allocation to both pre- and post-copulatory traits in a**  
584 **trade-off world**

585 As pointed out in the Introduction, male allocation to sexual competition is a complex process  
586 encompassing both a pre- and post-copulatory phase (Parker 1998). While we have  
587 demonstrated in this perspective article that allocation to post-copulatory competition is likely  
588 to be associated with long-term ageing costs, substantial evidence that the competition for  
589 gaining mating opportunities also shortens lifespan and accelerates ageing in terms of both  
590 reproduction and survival has accumulated (e.g. Bonduriansky *et al.* 2008; Table 1). The  
591 physiological pathways involved in mediating the relationships between the allocation to pre-  
592 or post-copulatory competition on the one hand and those linking them to ageing on the other

593 are also likely to strongly overlap. For instance, in three-spined sticklebacks (*Gasterosteus*  
594 *aculeatus*), males with an increased carotenoid-based red coloration on their cheeks and  
595 throats show the strongest levels of oxidative DNA damage in both sperm and somatic tissues  
596 (Kim & Velando 2020), which highlights that a resource-based allocation trade-off between  
597 sexual selection and somatic maintenance mediates the long-term ageing costs of both pre-  
598 and post-copulatory sexual competition. Interestingly, as allocation to both primary (e.g.  
599 sperm-producing tissue within the testes) and secondary (e.g. ornaments and armaments)  
600 sexually-selected traits relies on the quantity of resources available in the environment, males  
601 cannot maximize both aspects of allocation to sexual competition simultaneously (Parker  
602 1998; Parker *et al.* 2013). Evidence for trade-offs between pre- and post-copulatory traits are  
603 widespread in nature, at both inter- and intra-specific levels (see Simmons *et al.* 2017 for a  
604 review). For instance, across pinnipeds, the relative testes mass and the degree of sexual size  
605 dimorphism are negatively correlated (Fitzpatrick *et al.* 2012). Overall, the resource-  
606 allocation strategy towards pre- and post-copulatory competition is likely fine-tuned by the  
607 fitness payoff of favoring one set of sexual traits at the expense of the other, which is likely to  
608 result from complex interactions between species- or population-specific traits (e.g. mating  
609 system, mating tactic) (Simmons *et al.* 2017) and environmental characteristics determining  
610 the nature and degree of sexual competition (Vahed & Parker 2012). In practice, it is  
611 particularly difficult to predict what aspects of sexual competition will predominantly drive  
612 the physiological costs of sexual selection (e.g. Olsson *et al.* 1997 in the case of adders),  
613 especially since the relative allocation to each sexual trait might change over the male's life  
614 course (Lemaître & Gaillard 2017). Nevertheless, any thorough investigation of the ageing  
615 costs of sexual selection should consider the cumulative costs associated with both aspects of  
616 a male's allocation to sexual competition, which is lacking to date.

617

### 618 **(c) Contribution to the sex differences in lifespan and ageing across species**

619 In most species, males and females differ in lifespan and ageing patterns (Austad 2011;  
620 Austad & Fischer 2016; Marais *et al.* 2018). While some factors (e.g. sex chromosomes)  
621 provide relevant explanations for the average direction in sex differences in lifespan across  
622 species (Xirocostas *et al.* 2020), the evolutionary roots of the large magnitude of sex  
623 differences in lifespan and ageing patterns observed across species remain poorly understood  
624 (see Lemaître *et al.* 2020 in mammals). So far, most comparative analyses that seek to explain  
625 this diversity have focused on the role of sexual selection (e.g. Clutton-Brock & Isvaran  
626 2007), with the expectation that sex differences in lifespan and ageing rates should increase in

627 species where males devote a substantial amount of resources to pre-copulatory competition  
628 (generally measured through the degree of sexual size dimorphism, see Tidière *et al.* 2015).  
629 However, these results remain largely equivocal and current evidence that the allocation to  
630 pre-copulatory competition influences the evolution of sex differences in lifespan and ageing  
631 in wild populations is limited at best (Lemaître *et al.* 2020). Here, we argue that comparative  
632 analyses should carefully consider the long-term costs associated with post-copulatory  
633 competition, which might also contribute to shaping the magnitude of sex differences in  
634 lifespan and ageing patterns. Species displaying high levels of sperm competition should  
635 allocate a much higher quantity of resources towards germline maintenance, at the expense of  
636 somatic maintenance (Maklakov & Immler 2016). So far, these long-term costs have only  
637 been considered in an analysis focused on large herbivores and in this study, species-specific  
638 allocation to post-copulatory competition - measured by the relative testes mass - did not  
639 influence the degree of sexual size dimorphism in lifespan (Lemaître & Gaillard 2013a).  
640 However, the mean allocation to testis size is weak and shows little variation among large  
641 herbivores compared to other taxa (Gomendio *et al.* 2011), and similar analyses need to be  
642 performed using a broader taxonomic range. Moreover, such studies should fully embrace the  
643 multi-dimensional nature of allocation to post-copulatory competition by considering not just  
644 relative testes mass but also several other costly sperm features (e.g. size, velocity) and the  
645 level of allocation to the seminal fluid component of the ejaculate. In addition, such inter-  
646 specific studies should control for the basal metabolic rate, as species displaying a high mass-  
647 specific metabolic rate can more easily allocate to high quality ejaculates (e.g. through the  
648 production of particularly long sperm, see Gomendio *et al.* 2011). Lastly, such comparative  
649 analyses should include the socio-ecological context. As shown above, the environmental  
650 conditions that affect the amount of available food resources, the habitat heterogeneity that  
651 influences spatial distribution of both sexes and the level of sexual segregation, and the  
652 population size and structure that define the operational sex ratio and female group size  
653 distribution should all determine the male investment corresponding to a given allocation to  
654 traits that shape the intensity of post-copulatory competition, and thereby fine-tune this  
655 allocation (Figure 1).

656         Species-specific differences in the level of sperm competition could also shape diverse  
657 patterns of reproductive ageing in males (and thus various patterns of sex differences in  
658 reproductive ageing). Interestingly, a comparative analysis performed across 18 species of  
659 rodents maintained in lab conditions revealed a positive relationship between levels of sperm  
660 competition and DNA fragmentation among sperm (delBarco-Trillo *et al.* 2016), which

661 suggests that inter-specific differences in the level of sperm competition can explain between-  
662 species differences in sperm integrity. Whether these differences are exacerbated with  
663 increasing age and occur in the wild is unknown but this clearly deserves attention. Recently,  
664 delBarco-Trillo and colleagues (2018) compared different post-copulatory traits (e.g. relative  
665 testes mass, various sperm features) between a small sample of young and old males for three  
666 species of rodents, all belonging to the genus *Mus* and displaying contrasting levels of sperm  
667 competition. While this transversal study did not reveal any clear difference in the age-  
668 specific changes in post-copulatory traits among these three species, it clearly set out a  
669 promising framework for future longitudinal studies comparing the age-specific decline in  
670 post-copulatory traits over the life course of individuals and across a wider range of species.  
671 The study of male reproductive ageing is currently attracting significant attention in  
672 evolutionary ecology (Lemaître & Gaillard 2017; Fricke & Koppik 2019; Monaghan &  
673 Metcalfe 2019) and such approaches would be particularly relevant to understand the  
674 evolutionary roots of male reproductive ageing.

675

676

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686

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## 688 **REFERENCES**

689

- 690 Aitken, R.J. & Baker, M.A. (2006). Oxidative stress, sperm survival and fertility control.  
691 *Molecular and cellular endocrinology*, 250, 66–69.
- 692 Albuquerque, T.A., Drummond do Val, L., Doherty, A. & de Magalhães, J.P. (2018). From  
693 humans to hydra: patterns of cancer across the tree of life. *Biological Reviews*, 93,  
694 1715–1734.
- 695 Alonso-Alvarez, C., Bertrand, S., Devevey, G., Prost, J., Faivre, B. & Sorci, G. (2004).  
696 Increased susceptibility to oxidative stress as a proximate cost of reproduction. *Ecology*

697 *Letters*, 7, 363–368.

698 Anderson, M.J. & Dixson, A.F. (2002). Sperm competition: motility and the midpiece in  
699 primates. *Nature*, 416, 496.

700 Andersson, M. & Simmons, L.W. (2006). Sexual selection and mate choice. *Trends in*  
701 *ecology & evolution*, 21, 296–302.

702 Andersson, M.B. (1994). *Sexual selection*. Princeton University Press.

703 Arnqvist, G. & Rowe, L. (2005). *Sexual conflict*. Princeton University Press.

704 Austad, S.N. (2011). Sex differences in longevity and aging. In: *The Handbook of the Biology*  
705 *of Aging*. Academic Press, San Diego, pp. 479–496.

706 Austad, S.N. & Fischer, K.E. (2016). Sex differences in lifespan. *Cell metabolism*, 23, 1022–  
707 1033.

708 Austad, S.N. & Hoffman, J.M. (2018). Is Antagonistic Pleiotropy Ubiquitous in Aging  
709 Biology? *Evolution, Medicine, and Public Health*, 1, 287–294.

710 Avila, F.W., Ram, K.R., Qazi, M.C.B. & Wolfner, M.F. (2010). Sex peptide is required for  
711 the efficient release of stored sperm in mated *Drosophila* females. *Genetics*, 186, 595–  
712 600.

713 Bangham, J., Chapman, T. & Partridge, L. (2002). Effects of body size, accessory gland and  
714 testis size on pre-and postcopulatory success in *Drosophila melanogaster*. *Animal*  
715 *Behaviour*, 64, 915–921.

716 Bartlett, M.J., Steeves, T.E., Gemmill, N.J. & Rosengrave, P.C. (2017). Sperm competition  
717 risk drives rapid ejaculate adjustments mediated by seminal fluid. *Elife*, 6, e28811.

718 Bateman, A.J. (1948). Intra-sexual selection in *Drosophila*. *Heredity*, 2, 349–368.

719 Baur, J. & Berger, D. (2020). Experimental evidence for effects of sexual selection on  
720 condition-dependent mutation rates. *Nature Ecology & Evolution*, 1–8.

721 Birkhead, T.R. & Møller, A.P. (1998). *Sperm competition and sexual selection*. Elsevier.

722 Blumenstiel, J.P. (2007). Sperm competition can drive a male-biased mutation rate. *Journal of*  
723 *theoretical biology*, 249, 624–632.

724 Bonduriansky, R., Maklakov, A., Zajitschek, F. & Brooks, R. (2008). Sexual selection, sexual  
725 conflict and the evolution of ageing and life span. *Functional ecology*, 22, 443–453.

726 Boschetto, C., Gasparini, C. & Pilastro, A. (2011). Sperm number and velocity affect sperm  
727 competition success in the guppy (*Poecilia reticulata*). *Behavioral Ecology and*  
728 *Sociobiology*, 65, 813–821.

729 Bowen, W.D., Oftedal, O.T. & Boness, D.J. (1992). Mass and energy transfer during lactation  
730 in a small phocid, the harbor seal (*Phoca vitulina*). *Physiological Zoology*, 65, 844–866.

731 Branco, A.T., Schilling, L., Silkaitis, K., Dowling, D.K. & Lemos, B. (2017). Reproductive  
732 activity triggers accelerated male mortality and decreases lifespan: genetic and gene  
733 expression determinants in *Drosophila*. *Heredity*, 118, 221–228.

734 Brengdahl, M., Kimber, C.M., Maguire-Baxter, J., Malacrinò, A. & Friberg, U. (2018).  
735 Genetic quality affects the rate of male and female reproductive aging differently in  
736 *Drosophila melanogaster*. *The American Naturalist*, 192, 761–772.

737 Bretman, A. & Fricke, C. (2019). Exposure to males, but not receipt of sex peptide,  
738 accelerates functional ageing in female fruit flies. *Functional Ecology*, 33, 1459–1468.

739 Bretman, A., Westmancoat, J.D., Gage, M.J. & Chapman, T. (2013). Costs and benefits of  
740 lifetime exposure to mating rivals in male *Drosophila melanogaster*. *Evolution*, 67,  
741 2413–2422.

742 Bribiescas, R.G. (2006). On the evolution, life history, and proximate mechanisms of human  
743 male reproductive senescence. *Evolutionary Anthropology: Issues, News, and Reviews:*  
744 *Issues, News, and Reviews*, 15, 132–141.

745 Briefer, E.F., Farrell, M.E., Hayden, T.J. & McElligott, A.G. (2013). Fallow deer polyandry is  
746 related to fertilization insurance. *Behavioral ecology and sociobiology*, 67, 657–665.

- 747 Brooks, R.C. & Garratt, M.G. (2017). Life history evolution, reproduction, and the origins of  
748 sex-dependent aging and longevity. *Annals of the New York Academy of Sciences*, 1389,  
749 92–107.
- 750 Bunning, H., Rapkin, J., Belcher, L., Archer, C.R., Jensen, K. & Hunt, J. (2015). Protein and  
751 carbohydrate intake influence sperm number and fertility in male cockroaches, but not  
752 sperm viability. *Proceedings of the Royal Society of London B: Biological Sciences*,  
753 282, 20142144.
- 754 Cameron, E., Day, T. & Rowe, L. (2007). Sperm competition and the evolution of ejaculate  
755 composition. *The American Naturalist*, 169, E158–E172.
- 756 Cardullo, R.A. & Baltz, J.M. (1991). Metabolic regulation in mammalian sperm:  
757 mitochondrial volume determines sperm length and flagellar beat frequency. *Cell*  
758 *motility and the cytoskeleton*, 19, 180–188.
- 759 Carvalho, A.P.S., Orr, A.G. & Kawahara, A.Y. (2017). A review of the occurrence and  
760 diversity of the sphragis in butterflies (Lepidoptera, Papilionoidea). *ZooKeys*, 41.
- 761 Chapman, T., Bangham, J., Vinti, G., Seifried, B., Lung, O., Wolfner, M.F., *et al.* (2003). The  
762 sex peptide of *Drosophila melanogaster*: female post-mating responses analyzed by  
763 using RNA interference. *Proceedings of the National Academy of Sciences*, 100, 9923–  
764 9928.
- 765 Chapman, T., Liddle, L.F., Kalb, J.M., Wolfner, M.F. & Partridge, L. (1995). Cost of mating  
766 in *Drosophila melanogaster* females is mediated by male accessory gland products.  
767 *Nature*, 373, 241–244.
- 768 Chen, H., Jolly, C., Bublys, K., Marcu, D. & Immler, S. (2020). Trade-off between somatic  
769 and germline repair in a vertebrate supports the expensive germ line hypothesis.  
770 *Proceedings of the National Academy of Sciences*.
- 771 Claydon, A.J., Ramm, S.A., Pennington, A., Hurst, J.L., Stockley, P. & Beynon, R. (2012).  
772 Heterogenous turnover of sperm and seminal vesicle proteins in the mouse revealed by  
773 dynamic metabolic labeling. *Molecular & Cellular Proteomics*, 11, 1-13.
- 774 Clutton-Brock, T. & Langley, P. (1997). Persistent courtship reduces male and female  
775 longevity in captive tsetse flies *Glossina morsitans morsitans* Westwood (Diptera:  
776 Glossinidae). *Behavioral Ecology*, 8, 392–395.
- 777 Clutton-Brock, T.H. & Isvaran, K. (2007). Sex differences in ageing in natural populations of  
778 vertebrates. *Proceedings of the Royal Society of London B: Biological Sciences*, 274,  
779 3097–3104.
- 780 Cordts, R. & Partridge, L. (1996). Courtship reduces longevity of male *Drosophila*  
781 *melanogaster*. *Animal Behaviour*, 52, 269–278.
- 782 Cornwallis, C.K., Dean, R. & Pizzari, T. (2014). Sex-specific patterns of aging in sexual  
783 ornaments and gametes. *The American Naturalist*, 184, E66–E78.
- 784 Crean, A.J. & Marshall, D.J. (2008). Gamete plasticity in a broadcast spawning marine  
785 invertebrate. *Proceedings of the National Academy of Sciences*, 105, 13508–13513.
- 786 Crudgington, H.S. & Siva-Jothy, M.T. (2000). Genital damage, kicking and early death.  
787 *Nature*, 407, 855–856.
- 788 Cunningham, K.A. & Beagley, K.W. (2008). Male genital tract chlamydial infection:  
789 implications for pathology and infertility. *Biology of reproduction*, 79, 180–189.
- 790 Dao, A., Kassogue, Y., Adamou, A., Diallo, M., Yaro, A.S., Traore, S.F., *et al.* (2010).  
791 Reproduction-longevity trade-off in *Anopheles gambiae* (Diptera: Culicidae). *Journal of*  
792 *medical entomology*, 47, 769–777.
- 793 Dávila, F. & Aron, S. (2017). Protein restriction affects sperm number but not sperm viability  
794 in male ants. *Journal of Insect Physiology*, 100, 71–76.
- 795 De Boer, P., Jansen, R.F., Koene, J.M. & Ter Maat, A. (1997). Nervous control of male  
796 sexual drive in the hermaphroditic snail *Lymnaea stagnalis*. *Journal of Experimental*



797 *Biology*, 200, 941–951.

798 Dewsbury, D.A. (1982). Ejaculate cost and male choice. *The American Naturalist*, 119, 601–

799 610.

800 Dewsbury, D.A. (2005). The Darwin-Bateman paradigm in historical context. *Integrative and*

801 *Comparative Biology*, 45, 831–837.

802 Duxbury, A.E., Weathersby, B., Sanchez, Z. & Moore, P.J. (2018). A study of the transit

803 amplification divisions during spermatogenesis in *Oncopeltus fasciatus* to assess

804 plasticity in sperm numbers or sperm viability under different diets. *Ecology and*

805 *evolution*, 8, 10460–10469.

806 Eberhard, W.G. (1985). *Sexual selection and animal genitalia*. Harvard University Press

807 Cambridge, MA.

808 Edward, D.A. & Chapman, T. (2011). Mechanisms underlying costs of reproduction.

809 Evans, J., Wilson, A., Pilastro, A. & Garcia-Gonzalez, F. (2019). Ejaculate-mediated paternal

810 effects: evidence, mechanisms and evolutionary implications. *Reproduction*, 157, R109–

811 R126.

812 Finkel, T. & Holbrook, N.J. (2000). Oxidants, oxidative stress and the biology of ageing.

813 *Nature*, 408, 239.

814 Fishelson, L. (2003). Comparison of testes structure, spermatogenesis, and

815 spermatocytogenesis in young, aging, and hybrid cichlid fish (Cichlidae, Teleostei).

816 *Journal of Morphology*, 256, 285–300.

817 Fitzpatrick, J.L., Almbro, M., Gonzalez-Voyer, A., Kolm, N. & Simmons, L.W. (2012). Male

818 contest competition and the coevolution of weaponry and testes in pinnipeds. *Evolution:*

819 *International Journal of Organic Evolution*, 66, 3595–3604.

820 Fitzpatrick, J.L. & Lüpold, S. (2014). Sexual selection and the evolution of sperm quality.

821 *Molecular Human Reproduction*, 20, 1180–1189.

822 Fitzpatrick, J.L., Montgomerie, R., Desjardins, J.K., Stiver, K.A., Kolm, N. & Balshine, S.

823 (2009). Female promiscuity promotes the evolution of faster sperm in cichlid fishes.

824 *Proceedings of the National Academy of Sciences*, 106, 1128–1132.

825 Flatt, T. & Partridge, L. (2018). Horizons in the evolution of aging. *BMC Biol.*, 16, 93.

826 Flatt, T. & Promislow, D.E. (2007). Still pondering an age-old question. *Science*, 318, 1255–

827 1256.

828 Folstad, I. & Karter, A.J. (1992). Parasites, bright males, and the immunocompetence

829 handicap. *The American Naturalist*, 139, 603–622.

830 Franceschi, C., Bonafè, M., Valensin, S., Olivieri, F., De Luca, M., Ottaviani, E., *et al.*

831 (2000). Inflamm-aging. An evolutionary perspective on immunosenescence. *Annals of*

832 *the New York Academy of Sciences*, 908, 244.

833 Fricke, C. & Koppik, M. (2019). Male reproductive ageing—a tale of the whole ejaculate.

834 *Reproduction*, 158, R219–R229.

835 Friesen, C.R., Powers, D.R., Copenhaver, P.E. & Mason, R.T. (2015). Size dependence in

836 non-sperm ejaculate production is reflected in daily energy expenditure and resting

837 metabolic rate. *Journal of Experimental Biology*, 218, 1410–1418.

838 Friesen, C.R., Shine, R., Krohmer, R.W. & Mason, R.T. (2013). Not just a chastity belt: the

839 functional significance of mating plugs in garter snakes, revisited. *Biological Journal of*

840 *the Linnean Society*, 109, 893–907.

841 Gage, M.J., Macfarlane, C.P., Yeates, S., Ward, R.G., Searle, J.B. & Parker, G.A. (2004).

842 Spermatozoal traits and sperm competition in Atlantic salmon: relative sperm velocity is

843 the primary determinant of fertilization success. *Current Biology*, 14, 44–47.

844 Gage, M.J. & Morrow, E.H. (2003). Experimental evidence for the evolution of numerous,

845 tiny sperm via sperm competition. *Current Biology*, 13, 754–757.

846 Gaillard, J.-M. & Lemaître, J.-F. (2017). The Williams’ legacy: A critical reappraisal of his

847 nine predictions about the evolution of senescence. *Evolution*, 71, 2768–2785.

848 Gaillard, J.-M. & Lemaître, J.-F. (2020). An integrative view of senescence in nature.

849 *Functional Ecology*, 34, 4–16.

850 Gasparini, C., Devigili, A. & Pilastro, A. (2019). Sexual selection and ageing: interplay

851 between pre- and post-copulatory traits senescence in the guppy. *Proceedings of the*

852 *Royal Society B*, 286, 20182873.

853 Gasparini, C., Simmons, L.W., Beveridge, M. & Evans, J.P. (2010). Sperm swimming

854 velocity predicts competitive fertilization success in the green swordtail *Xiphophorus*

855 *helleri*. *PloS one*, 5.

856 Gems, D. & Partridge, L. (2013). Genetics of longevity in model organisms: debates and

857 paradigm shifts. *Annual Review of Physiology*, 75, 621–644.

858 Giannakara, A., Schärer, L. & Ramm, S.A. (2016). Sperm competition-induced plasticity in

859 the speed of spermatogenesis. *BMC Evolutionary Biology*, 16, 60.

860 Giraudeau, M., Friesen, C.R., Sudyka, J., Rollings, N., Whittington, C.M., Wilson, M.R., *et*

861 *al.* (2016). Ageing and the cost of maintaining coloration in the Australian painted

862 dragon. *Biology Letters*, 12, 20160077.

863 Gomendio, M., Tourmente, M. & Roldan, E.R. (2011). Why mammalian lineages respond

864 differently to sexual selection: metabolic rate constrains the evolution of sperm size.

865 *Proceedings of the Royal Society of London B: Biological Sciences*, 278, 3135–3141.

866 Gosch, B. & Fischer, K. (1989). Seasonal changes of testis volume and sperm quality in adult

867 fallow deer (*Dama dama*) and their relationship to the antler cycle. *Reproduction*, 85,

868 7–17.

869 Gu, N.-H., Zhao, W.-L., Wang, G.-S. & Sun, F. (2019). Comparative analysis of mammalian

870 sperm ultrastructure reveals relationships between sperm morphology, mitochondrial

871 functions and motility. *Reproductive Biology and Endocrinology*, 17, 66.

872 Gustafson, A.W. (1979). Male reproductive patterns in hibernating bats. *Reproduction*, 56,

873 317–331.

874 Hayward, A. & Gillooly, J.F. (2011). The cost of sex: quantifying energetic investment in

875 gamete production by males and females. *PLoS One*, 6, e16557.

876 Hime, G.R., Loveland, K.L. & Abud, H.E. (2007). Drosophila spermatogenesis: insights into

877 testicular cancer. *International journal of andrology*, 30, 265–274.

878 Hollis, B., Koppik, M., Wensing, K.U., Ruhmann, H., Genzoni, E., Erkosar, B., *et al.* (2019).

879 Sexual conflict drives male manipulation of female postmating responses in *Drosophila*

880 *melanogaster*. *Proceedings of the National Academy of Sciences*, 116, 8437–8444.

881 Hooper, A.K., Lehtonen, J., Schwanz, L.E. & Bonduriansky, R. (2018). Sexual competition

882 and the evolution of condition-dependent ageing. *Evolution Letters*, 2, 37–48.

883 Hopkins, B.R., Sepil, I., Thézénas, M.-L., Craig, J.F., Miller, T., Charles, P.D., *et al.* (2019).

884 Divergent allocation of sperm and the seminal proteome along a competition gradient in

885 *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences*, 116,

886 17925–17933.

887 Hosken, D.J. (2001). Sex and death: microevolutionary trade-offs between reproductive and

888 immune investment in dung flies. *Current Biology*, 11, R379–R380.

889 Huddart, R.A., Norman, A., Moynihan, C., Horwich, A., Parker, C., Nicholls, E., *et al.*

890 (2005). Fertility, gonadal and sexual function in survivors of testicular cancer. *British*

891 *Journal of Cancer*, 93, 200–207.

892 Hunt, J., Brooks, R., Jennions, M.D., Smith, M.J., Bentsen, C.L. & Bussiere, L.F. (2004).

893 High-quality male field crickets invest heavily in sexual display but die young. *Nature*,

894 432, 1024.

895 Immler, S., Pryke, S.R., Birkhead, T.R. & Griffith, S.C. (2010). Pronounced within-individual

896 plasticity in sperm morphometry across social environments. *Evolution: International*

897 *Journal of Organic Evolution*, 64, 1634–1643.

898 Intano, G.W., McMahan, C.A., Walter, R.B., McCarrey, J.R. & Walter, C.A. (2001). Mixed  
899 spermatogenic germ cell nuclear extracts exhibit high base excision repair activity.  
900 *Nucleic acids research*, 29, 1366–1372.

901 Janicke, T., Häderer, I.K., Lajeunesse, M.J. & Anthes, N. (2016). Darwinian sex roles  
902 confirmed across the animal kingdom. *Science advances*, 2, e1500983.

903 Janicke, T., Marie-Orleach, L., De Mulder, K., Berezikov, E., Ladurner, P., Vizoso, D.B., *et al.*  
904 (2013). Sex allocation adjustment to mating group size in a simultaneous  
905 hermaphrodite. *Evolution*, 67, 3233–3242.

906 Jehan, C., Chogne, M., Rigaud, T. & Moret, Y. (2020). Sex-specific patterns of senescence in  
907 artificial insect populations varying in sex-ratio to manipulate reproductive effort. *BMC*  
908 *evolutionary biology*, 20, 18.

909 Jennions, M.D. & Petrie, M. (2000). Why do females mate multiply? A review of the genetic  
910 benefits. *Biological Reviews*, 75, 21–64.

911 Johnson, S.L. & Gemmill, N.J. (2012). Are old males still good males and can females tell  
912 the difference? Do hidden advantages of mating with old males off-set costs related to  
913 fertility, or are we missing something else? *Bioessays*, 34, 609–619.

914 Jones, O.R., Scheuerlein, A., Salguero-Gómez, R., Camarda, C.G., Schaible, R., Casper, B.B.,  
915 *et al.* (2014). Diversity of ageing across the tree of life. *Nature*, 505, 169.

916 Kenagy, G.J. & Trombulak, S.C. (1986). Size and function of mammalian testes in relation to  
917 body size. *Journal of Mammalogy*, 67, 1–22.

918 Kennedy, B.K., Berger, S.L., Brunet, A., Campisi, J., Cuervo, A.M., Epel, E.S., *et al.* (2014).  
919 Geroscience: linking aging to chronic disease. *Cell*, 159, 709–713.

920 Kerr, A.M., Gershman, S.N. & Sakaluk, S.K. (2010). Experimentally induced spermatophore  
921 production and immune responses reveal a trade-off in crickets. *Behavioral Ecology*,  
922 21, 647–654.

923 Kim, S.-Y. & Velando, A. (2020). Attractive male sticklebacks carry more oxidative DNA  
924 damage in the soma and germline. *Journal of evolutionary biology*, 33, 121–126.

925 Kirkwood, T.B. (1977). Evolution of ageing. *Nature*, 270, 301.

926 Kirkwood, T.B. (2005). Understanding the odd science of aging. *Cell*, 120, 437–447.

927 Kirkwood, T.B. (2017). The Disposable Soma Theory. In: *The evolution of senescence in the*  
928 *tree of life*. p. 23.

929 Kirkwood, T.B. & Rose, M.R. (1991). Evolution of senescence: late survival sacrificed for  
930 reproduction. *Phil. Trans. R. Soc. Lond. B*, 332, 15–24.

931 Kleene, K.C. (2005). Sexual selection, genetic conflict, selfish genes, and the atypical patterns  
932 of gene expression in spermatogenic cells. *Developmental biology*, 277, 16–26.

933 Kong, A., Frigge, M.L., Masson, G., Besenbacher, S., Sulem, P., Magnusson, G., *et al.*  
934 (2012). Rate of de novo mutations and the importance of father's age to disease risk.  
935 *Nature*, 488, 471.

936 Kowald, A. & Kirkwood, T.B. (2015). Evolutionary significance of ageing in the wild.  
937 *Experimental gerontology*, 71, 89–94.

938 Lemaître, J.-F., Berger, V., Bonenfant, C., Douhard, M., Gamelon, M., Plard, F., *et al.* (2015).  
939 Early-late life trade-offs and the evolution of ageing in the wild. *Proc. R. Soc. B*. 282,  
940 20150209.

941 Lemaître, J.-F., Cheynel, L., Douhard, F., Bourgoïn, G., Débias, F., Ferté, H., *et al.* (2018).  
942 The influence of early-life allocation to antlers on male performance during adulthood:  
943 Evidence from contrasted populations of a large herbivore. *Journal of Animal Ecology*,  
944 87, 921–932.

945 Lemaître, J.-F. & Gaillard, J.-M. (2013a). Male survival patterns do not depend on male  
946 allocation to sexual competition in large herbivores. *Behavioral Ecology*, 24, 421–428.

- 947 Lemaître, J.-F. & Gaillard, J.-M. (2013b). Polyandry Has No Detectable Mortality Cost in  
948 Female Mammals. *PLoS ONE*, 8, e66670.
- 949 Lemaître, J.-F. & Gaillard, J.-M. (2017). Reproductive senescence: new perspectives in the  
950 wild: Reproductive senescence in the wild. *Biological Reviews*, 92, 2182–2199.
- 951 Lemaître, J.-F., Gaillard, J.-M., Pemberton, J.M., Clutton-Brock, T.H. & Nussey, D.H.  
952 (2014). Early life expenditure in sexual competition is associated with increased  
953 reproductive senescence in male red deer. *Proceedings of the Royal Society of London*  
954 *B: Biological Sciences*, 281, 20140792.
- 955 Lemaitre, J.-F., Ramm, S.A., Hurst, J.L. & Stockley, P. (2011). Social cues of sperm  
956 competition influence accessory reproductive gland size in a promiscuous mammal.  
957 *Proceedings of the Royal Society B: Biological Sciences*, 278, 1171–1176.
- 958 Lemaître, J.-F., Ronget, V., Tidière, M., Allainé, D., Berger, V., Cohas, A., *et al.* (2020). Sex  
959 differences in adult lifespan and aging rates of mortality across wild mammals.  
960 *Proceedings of the National Academy of Sciences*, 117, 8546–8553.
- 961 Lewis, Z., Price, T.A.R. & Wedell, N. (2008). Sperm competition, immunity, selfish genes  
962 and cancer. *Cellular and molecular life sciences*, 65, 3241.
- 963 Liljedal, S., Folstad, I. & Skarstein, F. (1999). Secondary sex traits, parasites, immunity and  
964 ejaculate quality in the Arctic charr. *Proceedings of the Royal Society of London. Series*  
965 *B: Biological Sciences*, 266, 1893–1898.
- 966 López-Otín, C., Blasco, M.A., Partridge, L., Serrano, M. & Kroemer, G. (2013). The  
967 Hallmarks of Aging. *Cell*, 153, 1194–1217.
- 968 Lüpold, S., Linz, G.M., Rivers, J.W., Westneat, D.F. & Birkhead, T.R. (2009). Sperm  
969 competition selects beyond relative testes size in birds. *Evolution*, 63, 391–402.
- 970 Macartney, E.L., Crean, A.J., Nakagawa, S. & Bonduriansky, R. (2019). Effects of nutrient  
971 limitation on sperm and seminal fluid: a systematic review and meta-analysis.  
972 *Biological Reviews*, 94, 1722–1739.
- 973 Madsen, T., Arnal, A., Vittecoq, M., Bernex, F., Abadie, J., Labrut, S., *et al.* (2017). Cancer  
974 prevalence and etiology in wild and captive animals. In: *Ecology and evolution of*  
975 *cancer*. Elsevier, pp. 11–46.
- 976 Maklakov, A.A. & Chapman, T. (2019). Evolution of ageing as a tangle of trade-offs: energy  
977 versus function. *Proceedings of the Royal Society B*, 286, 20191604.
- 978 Maklakov, A.A. & Immler, S. (2016). The expensive germline and the evolution of ageing.  
979 *Current Biology*, 26, R577–R586.
- 980 Marais, G., Gaillard, J.-M., Vieira, C., Plotton, I., Sanlaville, D., Gueyffier, F., *et al.* (2018).  
981 Sex-specific differences in aging and longevity: can sex chromosomes play a role?  
982 *Biology of Sex Differences*, 9, 33.
- 983 Martin, O.Y. & Hosken, D.J. (2004). Copulation reduces male but not female longevity in  
984 *Saltella sphondylii* (Diptera: Sepsidae). *Journal of Evolutionary Biology*, 17, 357–362.
- 985 McKean, K.A. & Nunney, L. (2001). Increased sexual activity reduces male immune function  
986 in *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences*, 98,  
987 7904–7909.
- 988 McNamara, K.B., Van Lieshout, E., Jones, T.M. & Simmons, L.W. (2013). Age-dependent  
989 trade-offs between immunity and male, but not female, reproduction. *Journal of Animal*  
990 *Ecology*, 82, 235–244.
- 991 Medawar, P.B. (1952). *An unsolved problem of biology*. College.
- 992 Metcalf, C.J.E., Roth, O. & Graham, A.L. (2020). Why leveraging sex differences in immune  
993 tradeoffs may illuminate the evolution of senescence. *Functional Ecology*, 34, 129–140.
- 994 Metzler, S., Heinze, J. & Schrempf, A. (2016). Mating and longevity in ant males. *Ecology*  
995 *and Evolution*, 6, 8903–8906.
- 996 Monaghan, P. & Metcalfe, N.B. (2019). The deteriorating soma and the indispensable

- 997 germline: gamete senescence and offspring fitness. *Proc. R. Soc. Lond. B*, 286,  
998 20192187.
- 999 Nakadera, Y., Giannakara, A. & Ramm, S.A. (2019). Plastic expression of seminal fluid  
1000 protein genes in a simultaneously hermaphroditic snail. *Behavioral Ecology*, 30, 904–  
1001 913.
- 1002 Nakatsuru, K. & Kramer, D.L. (1982). Is sperm cheap? Limited male fertility and female  
1003 choice in the lemon tetra (Pisces, Characidae). *Science*, 216, 753–755.
- 1004 Nunn, C.L., Gittleman, J.L. & Antonovics, J. (2000). Promiscuity and the primate immune  
1005 system. *Science*, 290, 1168–1170.
- 1006 Nussey, D.H., Froy, H., Lemaitre, J.-F., Gaillard, J.-M. & Austad, S.N. (2013). Senescence in  
1007 natural populations of animals: widespread evidence and its implications for bio-  
1008 gerontology. *Ageing research reviews*, 12, 214–225.
- 1009 Olsson, M., Madsen, T. & Shine, R. (1997). Is sperm really so cheap? Costs of reproduction  
1010 in male adders, *Vipera berus*. *Proceedings of the Royal Society of London B: Biological*  
1011 *Sciences*, 264, 455–459.
- 1012 Orr, T.J. & Brennan, P.L. (2016). All features great and small—the potential roles of the  
1013 baculum and penile spines in mammals. *Integrative and comparative biology*, 56, 635–  
1014 643.
- 1015 Papadopoulos, N.T., Liedo, P., Müller, H.-G., Wang, J.-L., Molleman, F. & Carey, J.R.  
1016 (2010). Cost of reproduction in male medflies: the primacy of sexual courting in  
1017 extreme longevity reduction. *Journal of Insect Physiology*, 56, 283–287.
- 1018 Parker, G.A. (1970). Sperm competition and its evolutionary consequences in the insects.  
1019 *Biological Reviews*, 45, 525–567.
- 1020 Parker, G.A. (1998). Sperm competition and the evolution of ejaculates: towards a theory  
1021 base. *Sperm competition and sexual selection*, 3–54.
- 1022 Parker, G.A. (2016). The evolution of expenditure on testes. *Journal of Zoology*, 298, 3–19.
- 1023 Parker, G.A. & Ball, M.A. (2005). Sperm competition, mating rate and the evolution of testis  
1024 and ejaculate sizes: a population model. *Biology Letters*, 1, 235–238.
- 1025 Parker, G.A., Lessells, C.M. & Simmons, L.W. (2013). Sperm competition games: a general  
1026 model for precopulatory male–male competition. *Evolution*, 67, 95–109.
- 1027 Parker, G.A. & Pizzari, T. (2010). Sperm competition and ejaculate economics. *Biological*  
1028 *Reviews*, 85, 897–934.
- 1029 Parker, G.A., Ramm, S.A., Lehtonen, J. & Henshaw, J.M. (2018). The evolution of gonad  
1030 expenditure and gonadosomatic index (GSI) in male and female broadcast-spawning  
1031 invertebrates. *Biological Reviews*, 93, 693–753.
- 1032 Partridge, L. & Andrews, R. (1985). The effect of reproductive activity on the longevity of  
1033 male *Drosophila melanogaster* is not caused by an acceleration of ageing. *Journal of*  
1034 *Insect Physiology*, 31, 393–395.
- 1035 Partridge, L. & Barton, N.H. (1993). Optimally, mutation and the evolution of ageing. *Nature*,  
1036 362, 305.
- 1037 Partridge, L. & Farquhar, M. (1981). Sexual activity reduces lifespan of male fruitflies.  
1038 *Nature*, 294, 580–582.
- 1039 Paukku, S. & Kotiaho, J.S. (2005). Cost of reproduction in *Callosobruchus maculatus*: effects  
1040 of mating on male longevity and the effect of male mating status on female longevity.  
1041 *Journal of Insect Physiology*, 51, 1220–1226.
- 1042 Péron, G., Lemaître, J.-F., Ronget, V., Tidière, M. & Gaillard, J.-M. (2019). Variation in  
1043 actuarial senescence does not reflect life span variation across mammals. *PLoS biology*,  
1044 17, e3000432.
- 1045 Perry, J.C. & Rowe, L. (2010). Condition-dependent ejaculate size and composition in a  
1046 ladybird beetle. *Proceedings of the Royal Society B: Biological Sciences*, 277, 3639–

1047 3647.

1048 Perry, J.C., Sirot, L. & Wigby, S. (2013). The seminal symphony: how to compose an  
1049 ejaculate. *Trends in Ecology & Evolution*, 28, 414–422.

1050 Peters, A., Delhey, K., Denk, A.G. & Kempenaers, B. (2004). Trade-offs between immune  
1051 investment and sexual signaling in male mallards. *The American Naturalist*, 164, 51–59.

1052 Pilastro, A., Scaggiante, M. & Rasotto, M.B. (2002). Individual adjustment of sperm  
1053 expenditure accords with sperm competition theory. *Proceedings of the National  
1054 Academy of Sciences*, 99, 9913–9915.

1055 Pizzari, T. & Parker, G.A. (2009). Sperm competition and sperm phenotype. In: *Sperm  
1056 biology*. Elsevier, pp. 207–245.

1057 Poiani, A. (2006). Complexity of seminal fluid: a review. *Behavioral Ecology and  
1058 Sociobiology*, 60, 289–310.

1059 Polak, M. (1998). Effects of ectoparasitism on host condition in the *Drosophila-Macrocheles*  
1060 system. *Ecology*, 79, 1807.

1061 Preston, B.T., Jalme, M.S., Hingrat, Y., Lacroix, F. & Sorci, G. (2011). Sexually extravagant  
1062 males age more rapidly. *Ecology Letters*, 14, 1017–1024.

1063 Promislow, D. (2003). Mate choice, sexual conflict, and evolution of senescence. *Behavior  
1064 genetics*, 33, 191–201.

1065 Prowse, N. & Partridge, L. (1997). The effects of reproduction on longevity and fertility in  
1066 male *Drosophila melanogaster*. *Journal of Insect Physiology*, 43, 501–512.

1067 Radhakrishnan, P. & Fedorka, K.M. (2012). Immune activation decreases sperm viability in  
1068 both sexes and influences female sperm storage. *Proceedings of the Royal Society B:  
1069 Biological Sciences*, 279, 3577–3583.

1070 Ramm, S.A., Lengerer, B., Arbore, R., Pjeta, R., Wunderer, J., Giannakara, A., *et al.* (2019).  
1071 Sex allocation plasticity on a transcriptome scale: Socially sensitive gene expression in  
1072 a simultaneous hermaphrodite. *Molecular ecology*, 28, 2321–2341.

1073 Ramm, S.A., Parker, G.A. & Stockley, P. (2005). Sperm competition and the evolution of  
1074 male reproductive anatomy in rodents. *Proceedings of the Royal Society of London B:  
1075 Biological Sciences*, 272, 949–955.

1076 Ramm, S.A. & Schärer, L. (2014). The evolutionary ecology of testicular function: size isn't  
1077 everything. *Biological Reviews*, 89, 874–888.

1078 Ramm, S.A., Schärer, L., Ehmcke, J. & Wistuba, J. (2014). Sperm competition and the  
1079 evolution of spermatogenesis. *Molecular Human Reproduction*, 20, 1169–1179.

1080 Ramm, S.A. & Stockley, P. (2009). Adaptive plasticity of mammalian sperm production in  
1081 response to social experience. *Proceedings of the Royal Society B: Biological Sciences*,  
1082 276, 745–751.

1083 Ramm, S.A. & Stockley, P. (2010). Sperm competition and sperm length influence the rate of  
1084 mammalian spermatogenesis. *Biology Letters*, 6, 219–221.

1085 Reinhardt, K. (2007). Evolutionary consequences of sperm cell aging. *The Quarterly review  
1086 of biology*, 82, 375–393.

1087 Reinhardt, K., Naylor, R. & Siva-Jothy, M.T. (2011). Male mating rate is constrained by  
1088 seminal fluid availability in bedbugs, *Cimex lectularius*. *PloS one*, 6.

1089 Richard, M., Massot, M., Clobert, J. & Meylan, S. (2012). Litter quality and inflammatory  
1090 response are dependent on mating strategy in a reptile. *Oecologia*, 170, 39–46.

1091 Rödel, H.G., Zapka, M., Stefanski, V. & Holst, D. von. (2016). Reproductive effort alters  
1092 immune parameters measured post-partum in European rabbits under semi-natural  
1093 conditions. *Functional Ecology*, 30, 1800–1809.

1094 Rodríguez-Muñoz, R., Boonekamp, J.J., Liu, X.P., Skicko, I., Fisher, D.N., Hopwood, P., *et  
1095 al.* (2019). Testing the effect of early-life reproductive effort on age-related decline in a  
1096 wild insect. *Evolution*, 73, 317–328.

- 1097 Rolff, J. & Siva-Jothy, M.T. (2002). Copulation corrupts immunity: a mechanism for a cost of  
1098 mating in insects. *Proceedings of the National Academy of Sciences*, 99, 9916–9918.
- 1099 Ros-Santaella, J.L., Kotrba, R. & Pintus, E. (2019). High-energy diet enhances spermatogenic  
1100 function and increases sperm midpiece length in fallow deer (*Dama dama*) yearlings.  
1101 *Royal Society open science*, 6, 181972.
- 1102 Salomon, T.B. & Benfato, M.S. (2018). Sexual activity affects the redox profile along the  
1103 aging process in male rats. *Biogerontology*, 19, 13–21.
- 1104 Salomon, T.B., Hackenhaar, F.S., Almeida, A.C., Schüller, A.K., Alabarse, P.V.G.,  
1105 Ehrenbrink, G., *et al.* (2013). Oxidative stress in testis of animals during aging with and  
1106 without reproductive activity. *Experimental gerontology*, 48, 940–946.
- 1107 Santiago, J., Silva, J.V., Alves, M.G., Oliveira, P.F. & Fardilha, M. (2019). Testicular aging:  
1108 an overview of ultrastructural, cellular, and molecular alterations. *The Journals of*  
1109 *Gerontology: Series A*, 74, 860–871.
- 1110 Schärer, L., Da Lage, J.-L. & Joly, D. (2008). Evolution of testicular architecture in the  
1111 *Drosophilidae*: a role for sperm length. *BMC evolutionary biology*, 8, 143.
- 1112 Schärer, L., Ladurner, P. & Rieger, R.M. (2004). Bigger testes do work more: experimental  
1113 evidence that testis size reflects testicular cell proliferation activity in the marine  
1114 invertebrate, the free-living flatworm *Macrostomum* sp. *Behavioral Ecology and*  
1115 *Sociobiology*, 56, 420–425.
- 1116 Sella, G. & Lorenzi, M.C. (2003). Increased sperm allocation delays body growth in a  
1117 protandrous simultaneous hermaphrodite. *Biological Journal of the Linnean Society*, 78,  
1118 149–154.
- 1119 Sepil, I., Hopkins, B.R., Dean, R., Bath, E., Friedman, S., Swanson, B., *et al.* (2020). Male  
1120 reproductive aging arises via multifaceted mating-dependent sperm and seminal  
1121 proteome declines, but is postponable in *Drosophila*. *PNAS*.
- 1122 Setchell, B. & Breed, W. (2006). Anatomy, vasculature, and innervation of the male  
1123 reproductive tract. Elsevier.
- 1124 Sheldon, B.C. (1993). Sexually transmitted disease in birds: occurrence and evolutionary  
1125 significance. *Philosophical Transactions of the Royal Society of London. Series B:*  
1126 *Biological Sciences*, 339, 491–497.
- 1127 Sheldon, B.C. & Verhulst, S. (1996). Ecological immunology: costly parasite defences and  
1128 trade-offs in evolutionary ecology. *Trends in ecology & evolution*, 11, 317–321.
- 1129 Shine, R., Phillips, B., Langkilde, T., Lutterschmidt, D.I., Wayne, H. & Mason, R.T. (2004).  
1130 Mechanisms and consequences of sexual conflict in garter snakes (*Thamnophis sirtalis*,  
1131 *Colubridae*). *Behavioral Ecology*, 15, 654–660.
- 1132 Simmons, L.W. (2012). Resource allocation trade-off between sperm quality and immunity in  
1133 the field cricket, *Teleogryllus oceanicus*. *Behavioral Ecology*, 23, 168–173.
- 1134 Simmons, L.W. & Lovegrove, M. (2017). Socially cued seminal fluid gene expression  
1135 mediates responses in ejaculate quality to sperm competition risk. *Proceedings of the*  
1136 *Royal Society B: Biological Sciences*, 284, 20171486.
- 1137 Simmons, L.W., Lüpold, S. & Fitzpatrick, J.L. (2017). Evolutionary trade-off between  
1138 secondary sexual traits and ejaculates. *Trends in ecology & evolution*.
- 1139 Simmons, L.W. & Roberts, B. (2005). Bacterial immunity traded for sperm viability in male  
1140 crickets. *Science*, 309, 2031–2031.
- 1141 Simmons, L.W., Sloan, N.S. & Firman, R.C. (2020). Sexual Selection Shapes Seminal  
1142 Vesicle Secretion Gene Expression in House Mice. *Molecular Biology and Evolution*,  
1143 37, 1114–1117.
- 1144 Skau, P.A. & Folstad, I. (2005). Does immunity regulate ejaculate quality and fertility in  
1145 humans? *Behavioral Ecology*, 16, 410–416.
- 1146 Sloan, N.S., Lovegrove, M. & Simmons, L.W. (2018). Social manipulation of sperm

1147 competition intensity reduces seminal fluid gene expression. *Biology letters*, 14,  
1148 20170659.

1149 Snook, R.R. (2005). Sperm in competition: not playing by the numbers. *Trends in ecology &*  
1150 *evolution*, 20, 46–53.

1151 Soulsbury, C.D. (2010). Genetic patterns of paternity and testes size in mammals. *PLoS One*,  
1152 5, e9581.

1153 South, S.H., Steiner, D. & Arnqvist, G. (2009). Male mating costs in a polygynous mosquito  
1154 with ornaments expressed in both sexes. *Proceedings of the Royal Society B: Biological*  
1155 *Sciences*, 276, 3671–3678.

1156 Stockley, P. (1997). Sexual conflict resulting from adaptations to sperm competition. *Trends*  
1157 *in Ecology & Evolution*, 12, 154–159.

1158 Stockley, P. & Seal, N.J. (2001). Plasticity in reproductive effort of male dung flies  
1159 (*Scatophaga stercoraria*) as a response to larval density. *Functional Ecology*, 96–102.

1160 Stürup, M., Baer, B. & Boomsma, J.J. (2014). Short independent lives and selection for  
1161 maximal sperm survival make investment in immune defences unprofitable for leaf-  
1162 cutting ant males. *Behavioral ecology and sociobiology*, 68, 947–955.

1163 Tan, G.N., Govedich, F.R. & Burd, M. (2004). Social group size, potential sperm competition  
1164 and reproductive investment in a hermaphroditic leech, *Helobdella papillornata*  
1165 (Euhirudinea: Glossiphoniidae). *Journal of evolutionary biology*, 17, 574–580.

1166 Thomas, M.L. & Simmons, L.W. (2007). Male crickets adjust the viability of their sperm in  
1167 response to female mating status. *The American Naturalist*, 170, 190–195.

1168 Thomsen, R., Soltis, J., Matsubara, M., Matsubayashi, K., Onuma, M. & Takenaka, O.  
1169 (2006). How costly are ejaculates for Japanese macaques? *Primates*, 47, 272–274.

1170 Thrall, P.H., Antonovics, J. & Bever, J.D. (1997). Sexual transmission of disease and host  
1171 mating systems: within-season reproductive success. *The American Naturalist*, 149,  
1172 485–506.

1173 Tidière, M., Gaillard, J.-M., Müller, D.W., Lackey, L.B., Gimenez, O., Clauss, M., *et al.*  
1174 (2015). Does sexual selection shape sex differences in longevity and senescence  
1175 patterns across vertebrates? A review and new insights from captive ruminants.  
1176 *Evolution*, 69, 3123–3140.

1177 Tourmente, M., Gomendio, M. & Roldan, E.R. (2011). Sperm competition and the evolution  
1178 of sperm design in mammals. *BMC Evolutionary Biology*, 11, 12.

1179 delBarco-Trillo, J. & Ferkin, M.H. (2004). Male mammals respond to a risk of sperm  
1180 competition conveyed by odours of conspecific males. *Nature*, 431, 446.

1181 delBarco-Trillo, J., García-Álvarez, O., Soler, A.J., Tourmente, M., Garde, J.J. & Roldan,  
1182 E.R.S. (2016). A cost for high levels of sperm competition in rodents: increased sperm  
1183 DNA fragmentation. *Proc Biol Sci*, 283.

1184 Trivers, R.L. (1972). *Parental investment and sexual selection.*[W:] B. Campbell (red.)  
1185 *Sexual selection and the descent of man, 1871-1971*. Chicago: Aldine.

1186 Turner, C.L. (1919). *The seasonal cycle in the spermary of the perch*.

1187 Vahed, K. (2006). Larger ejaculate volumes are associated with a lower degree of polyandry  
1188 across bushcricket taxa. *Proceedings of the Royal Society B: Biological Sciences*, 273,  
1189 2387–2394.

1190 Vahed, K. & Parker, D.J. (2012). The evolution of large testes: sperm competition or male  
1191 mating rate? *Ethology*, 118, 107–117.

1192 Van Voorhies, W.A. (1992). Production of sperm reduces nematode lifespan. *Nature*, 360,  
1193 456–458.

1194 Vega-Trejo, R., Fox, R.J., Iglesias-Carrasco, M., Head, M.L. & Jennions, M.D. (2019). The  
1195 effects of male age, sperm age and mating history on ejaculate senescence. *Functional*  
1196 *Ecology*.



- 1197 Velando, A., Noguera, J.C., Drummond, H. & Torres, R. (2011). Senescent males carry  
1198 premutagenic lesions in sperm. *Journal of evolutionary biology*, 24, 693–697.
- 1199 Vilchez, D., Saez, I. & Dillin, A. (2014). The role of protein clearance mechanisms in  
1200 organismal ageing and age-related diseases. *Nature communications*, 5, 5659.
- 1201 Vinogradov, A.E. (1998). Male reproductive strategy and decreased longevity. *Acta*  
1202 *biotheoretica*, 46, 157–160.
- 1203 Voigt, C.C., Michener, R. & Kunz, T.H. (2005). The energetics of trading nuptial gifts for  
1204 copulations in katydids. *Physiological and Biochemical Zoology*, 78, 417–423.
- 1205 Wedell, N. (2010). Variation in male courtship costs in butterflies. *Behavioral ecology and*  
1206 *sociobiology*, 64, 1385–1391.
- 1207 Wedell, N., Gage, M.J.G. & Parker, G.A. (2002). Sperm competition, male prudence and  
1208 sperm-limited females. *Trends in Ecology & Evolution*, 17, 313–320.
- 1209 Wedell, N. & Ritchie, M.G. (2004). Male age, mating status and nuptial gift quality in a  
1210 bushcricket. *Animal Behaviour*, 67, 1059–1065.
- 1211 Wigby, S. & Chapman, T. (2005). Sex peptide causes mating costs in female *Drosophila*  
1212 *melanogaster*. *Current Biology*, 15, 316–321.
- 1213 Wigby, S., Sirot, L.K., Linklater, J.R., Buehner, N., Calboli, F.C., Bretman, A., *et al.* (2009).  
1214 Seminal fluid protein allocation and male reproductive success. *Current Biology*, 19,  
1215 751–757.
- 1216 Williams, G.C. (1957). Pleiotropy, natural selection, and the evolution of senescence.  
1217 *Evolution*, 11, 398–411.
- 1218 Xirocostas, Z.A., Everingham, S.E. & Moles, A.T. (2020). The sex with the reduced sex  
1219 chromosome dies earlier: a comparison across the tree of life. *Biology Letters*, 16,  
1220 20190867.
- 1221 Yasukawa, K. (1987). Breeding and nonbreeding season mortality of territorial male red-  
1222 winged blackbirds (*Agelaius phoeniceus*). *The Auk*, 104, 56–62.
- 1223 Yeap, B.B. (2009). Testosterone and ill-health in aging men. *Nature clinical practice*  
1224 *Endocrinology & metabolism*, 5, 113–121.
- 1225 Zhao, J., Jin, Y., Du, M., Liu, W., Ren, Y., Zhang, C., *et al.* (2017). The effect of dietary  
1226 grape pomace supplementation on epididymal sperm quality and testicular antioxidant  
1227 ability in ram lambs. *Theriogenology*, 97, 50–56.
- 1228

1229

1230 **BOX 1: Sperm competition influences ageing in females**

1231

1232 In contrast to males, the consequences of sperm competition for female lifespan and ageing  
1233 have been well studied. By aiming to answer the question “*why do females mate with multiple*  
1234 *males in most species?*”, behavioural ecologists have provided compelling evidence that  
1235 polyandry (i.e. the female propensity to mate with several males and thus to incite sperm  
1236 competition among males) is associated with both benefits and costs (Jennions & Petrie  
1237 2000). In males, sperm competition has led to the evolution of many behavioural, anatomical  
1238 and physiological adaptations that increase the probability to fertilize a female’s eggs  
1239 (Birkhead & Møller 1998). However, several of these adaptations can have detrimental effects  
1240 on female reproductive success and survival (reviewed in Stockley 1997; Arnqvist & Rowe  
1241 2005), notably in late life. Among these adaptations, the role played by male seminal fluid  
1242 proteins constitutes an iconic example.

1243 Seminal fluid proteins can have various detrimental effects for females (Poiani 2006)  
1244 and those are particularly well studied in the fruit fly, *D. melanogaster*. In this species, the  
1245 repeated exposure to seminal fluid proteins transferred during copulation increases female  
1246 death rate (Chapman *et al.* 1995). More specifically, the decrease in female survival prospects  
1247 appears to be predominantly caused by the sex-peptide (Wigby & Chapman 2005) - a protein  
1248 produced by the male accessory glands - that enhances male reproductive success in a  
1249 competitive context by reducing the degree of female receptivity and increasing sperm storage  
1250 by females (Chapman *et al.* 2003; Avila *et al.* 2010). The female-specific deleterious effects  
1251 of male sex peptide on lifespan and late-life reproductive success are mediated by several  
1252 physiological pathways, notably through a rise in the release of juvenile hormones (Edward &  
1253 Chapman 2011). Strikingly, it has been recently shown that - independently of the transfer of  
1254 sex peptide - both mating and the amount of exposure to males not only decrease female  
1255 survival but also increase the degree of physiological ageing (measured by the age-specific  
1256 decline in climbing activity and starvation resistance) (Bretman & Fricke 2019). These results  
1257 strongly emphasize the complexity of the interactions between mating rates, physiological  
1258 processes and both reproductive and survival ageing in females.

1259 While the production of seminal fluid proteins in response to sperm competition and  
1260 its consequence for female’s ageing are well studied - at least in flies - studying other  
1261 instances of sexual conflict over mating and fertilization might shed interesting light on the  
1262 evolution of demographic ageing in females. This is well illustrated by the very peculiar  
1263 genitalia that have evolved to improve sperm transfer abilities, and more generally,  
1264 fertilization efficiency in many species (Eberhard 1985) and that are already known to  
1265 influence female survival in the short run (e.g. Crudginton & Siva-Jothy 2000). Across  
1266 mammals, the level of polyandry (measured by the species-specific relative testes mass) does  
1267 not seem to increase the female rate of ageing in survivorship (Lemaître & Gaillard 2013b).  
1268 However, keratinized spines found at the surface of the penis of several mammalian species  
1269 (e.g. some primates, rodents and felids) can be responsible for lesions of the female  
1270 reproductive tract (Orr & Brennan 2016), which could ultimately compromise the late-life  
1271 reproductive success of the most polyandrous females.

1272 Finally, high levels of polyandry are associated with a higher risk of contracting  
1273 sexually transmitted diseases (Thrall *et al.* 1997) that can impair reproductive success and  
1274 survival in the long-run (Sheldon 1993). To counteract these adverse effects, polyandrous  
1275 females have evolved immune systems that might mitigate these fitness costs through an  
1276 increased resistance to infections (e.g. Nunn *et al.* 2000 in primates). This is well illustrated in  
1277 lizards (*Zootoca vivipara*) where polyandrous females show a greater ability to mount an  
1278 inflammatory immune response than monandrous females (Richard *et al.* 2012). While a

1279 greater allocation of resources to immune defences in polyandrous females is likely to convey  
1280 fitness benefits at a short-time scale, they might also lead to an overall increased rate of  
1281 ageing through an over-activation of the immune system (e.g. inflammaging) (Franceschi *et*  
1282 *al.* 2000). Yet, how much this and many other consequences of male allocation to sperm  
1283 competition contribute to the observed differences in female ageing at both inter- and intra-  
1284 specific levels is yet to be determined.  
1285

1286 **Table 1: Evidence of long-term lifespan and ageing costs associated to an increased allocation to pre-copulatory competition. Such**  
 1287 **relationships have been assessed across different types of populations (L: laboratory, W: wild populations, SC: semi-captive**  
 1288 **populations).**

1289

Taxon	Common name		Population	Measure of allocation to pre-copulatory competition <sup>1</sup>	Late-life trait impacted	Reference
Insect	Mediterranean fruit fly	<i>Ceratitis capitata</i>	L	Courtship effort	Lifespan	Papadopoulos <i>et al.</i> 2010
Insect	Fruit fly	<i>Drosophila melanogaster</i>	L	Courtship effort	Lifespan	Cordts & Partridge 1996
Insect	Tsetse fly	<i>Glossina morsitans morsitans</i>	L	Courtship effort	Lifespan	Clutton-Brock & Langley 1997
Insect	Field cricket	<i>Gryllus campestris</i>	W	Searching activity	Rate of reproductive senescence <sup>2</sup>	Rodríguez-Muñoz <i>et al.</i> 2019
Insect	Green-veined white	<i>Pieris napi</i>	L	Courtship effort	Lifespan	Wedell 2010
Insect	Mosquito	<i>Sabethes cyaneus</i>	L	Courtship effort	Lifespan	South <i>et al.</i> 2009
Insect	Black field cricket	<i>Teleogryllus commodus</i>	L	Calling effort	Lifespan	Hunt <i>et al.</i> 2004
Bird	Red-winged Blackbird	<i>Agelaius phoeniceus</i>	W	Wing length	Lifespan	Yasukawa 1987
Bird	Houbara bustard	<i>Chlamydotis undulata</i>	SC	Sexual display effort	Rate of reproductive senescence <sup>3</sup>	Preston <i>et al.</i> 2011
Mammal	Red deer	<i>Cervus elaphus</i>	W	Harem size and rutting duration	Rate of reproductive senescence <sup>4</sup>	Lemaître <i>et al.</i> 2014

1290

1291 <sup>1</sup> Articles linking horn length (or horn growth) to lifespan in bovids were deliberately omitted because these studies have been subjected to some controversies, due to the  
 1292 possible confounding effects of trophy hunting (see Lemaître *et al.* 2018 for a compilation of these studies).

1293 <sup>2</sup> Reproductive senescence measured by the age-specific decline in calling activity.

1294 <sup>3</sup> Reproductive senescence measured by the age-specific decline in ejaculate quality.

1295 <sup>4</sup> Reproductive senescence measured by the age-specific decline in harem size.

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1299 **Table 2: Compiled evidence of physiological costs associated to an increased allocation to sperm competition. This table reports the**  
 1300 **relationships that have been established between the allocation to an ejaculate-related trait (e.g. sperm viability) and the impaired**  
 1301 **physiological function (e.g. body growth, immune activity). Such relationships have been assessed across different types of populations**  
 1302 **(L: laboratory, WC/L: wild-caught population brought to the laboratory, W: wild populations).**  
 1303

Taxon	Species	Population	Ejaculate-related trait	Physiological trait	Reference
Polychaeta	<i>Ophryotrocha diadema</i>	L	Sperm allocation and replenishment	Body growth	Sella & Lorenzi 2003
Insect	Fruitfly <i>Drosophila melanogaster</i>	L	Sperm viability	Immune activity	Radhakrishnan & Fedorka 2012
Insect	Cotton bollworm <i>Helicoverpa armigera</i>	L	Sperm allocation	Immune activity	McNamara <i>et al.</i> 2013 <sup>1</sup>
Insect	Field cricket <i>Teleogryllus oceanicus</i>	L	Sperm viability	Lysozyme activity	Simmons & Roberts 2005
Insect	Tropical house cricket <i>Gryllodes sigillatus</i>	WC/L	Spermatophore size and production rate	Immune activity	Kerr <i>et al.</i> 2010
Insect	Gemeine Plumpschrecke <i>Isophya kraussi</i>	WC/L	Spermatophore production	Energy expenditure	Voigt <i>et al.</i> 2005
Insect	Leaf-cutting ant <i>Atta colombica</i>	WC/L	Sperm viability	Immune activity	Stürup <i>et al.</i> 2014
Insect	Leaf-cutting ant <i>Acromyrmex echinator</i>	WC/L	Sperm viability	Immune activity	Stürup <i>et al.</i> 2014
Insect	Mealworm <i>Tenebrio molitor</i>	L	Sexual activity	Immune activity	Rolff & Siva-Jothy 2002 <sup>2</sup>
Mammal	Japanese macaque <i>Macaca fuscata</i>	W & L	Ejaculate production	Basal metabolic rate	Thomsen <i>et al.</i> 2006
Mammal	Wistar rats <i>Rattus norvegicus</i>	L	Sexual activity	Age-specific redox profile	Salomon & Benfato 2018
Mammal	Wistar rats <i>Rattus norvegicus</i>	L	Sexual activity	Oxidative damage in the testes	Salomon <i>et al.</i> 2013 <sup>3</sup>
Fish	Arctic charr <i>Salvelinus alpinus</i>	WC/L	Spermatocrit	Granulocyte density	Liljedal <i>et al.</i> 1999
Fish	Arctic charr <i>Salvelinus alpinus</i>	WC/L	Spermatocrit	Spleen mass	Liljedal <i>et al.</i> 1999
Fish	Arctic charr <i>Salvelinus alpinus</i>	WC/L	Sperm motility	Granulocyte density	Liljedal <i>et al.</i> 1999
Reptile	Red-sided garter snake <i>Thamnophis sirtalis parietalis</i>	WC/L	Production of copulatory plugs	Energy expenditure / Resting metabolic rate	Friesen <i>et al.</i> 2015
Reptile	Red-sided garter snake <i>Thamnophis sirtalis parietalis</i>	WC/L	Number of copulations	Body mass loss	Friesen <i>et al.</i> 2015
Reptile	Adder <i>Vipera berus</i>	W	Testes growth	Body mass loss	Olsson <i>et al.</i> 1997

1304 <sup>1</sup> The sperm allocation is used as a proxy of sperm production.

1305 <sup>2</sup> The activity of the phenoloxidase is reduced but there was no effect on the hemocyte load.

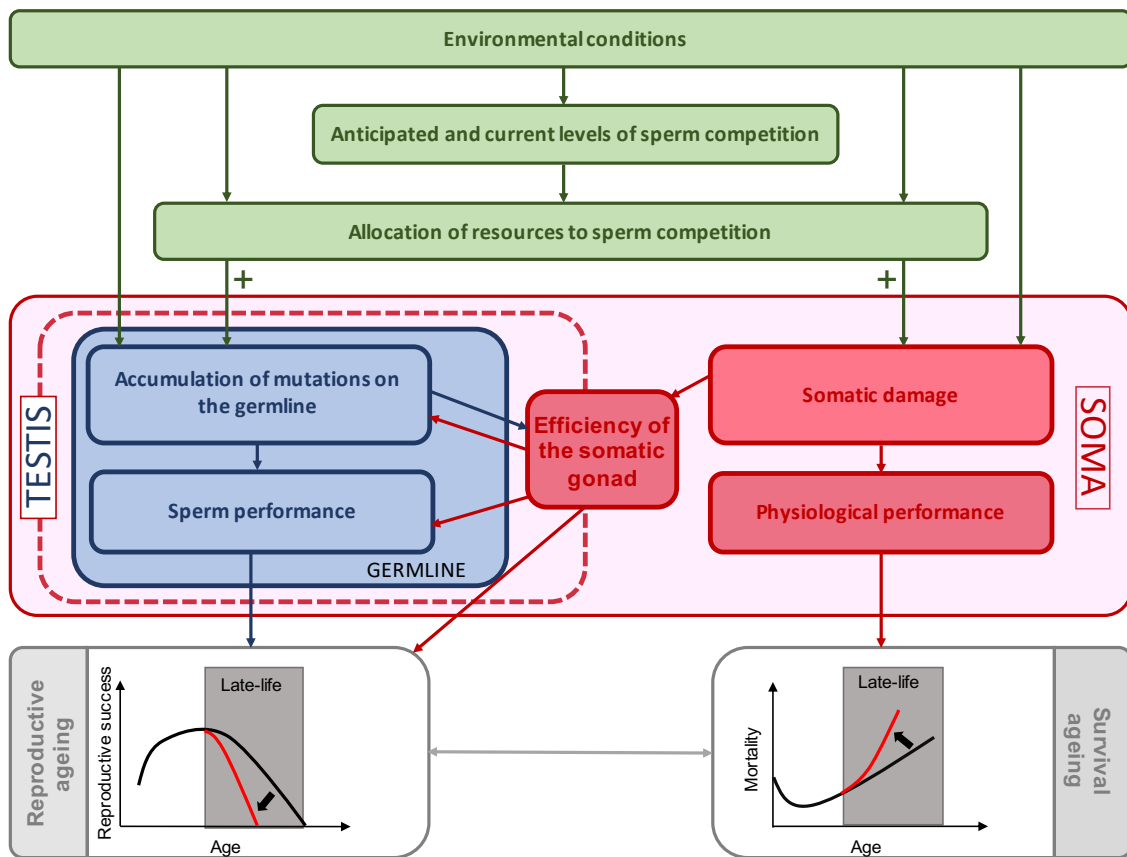
1306 <sup>3</sup> Damages found on proteins (carbonylation levels) but sexual activity of males shows an increase in anti-oxidant defences that could probably buffer oxidative costs.

1307 CAPTION FOR FIGURES

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1310 **Figure 1: Diagram of the functional relationships linking the allocation of resources to**  
 1311 **sperm competition traits with increased ageing in both reproduction and survivorship**  
 1312 **(i.e. denoted by the shift from the black to the red trajectories on the ageing curves).**  
 1313 **While some environmental conditions (e.g. pollution) can directly increase the mutation**  
 1314 **load on both germline and somatic tissues, they also largely modulate the socio-**  
 1315 **environmental context (e.g. adult sex ratio) that determines the level of sperm**  
 1316 **competition within a population. These ageing consequences are likely to be mediated by**  
 1317 **multiple physiological pathways leading to a progressive deterioration of the germline**  
 1318 **(e.g. through an accumulation of mutations on sperm DNA) and the soma (e.g. a**  
 1319 **decrease in the efficiency of the somatic gonad and an impairment of some key**  
 1320 **physiological functions such as immunity).**

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