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1 **Reproductive senescence and parental effect in an** 2 **indeterminate grower**

3

4 Short running title: Reproductive senescence in the woodlouse

5

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24

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33

34 **Conflict of Interest**

35 The authors declare that there is no conflict of interest.

36

37 **Abstract**

38 Reproductive senescence is the decrease of reproductive performance with increasing age and
39 can potentially include trans-generational effects as the offspring produced by old parents might
40 have a lower fitness than those produced by young parents. This negative effect may be caused
41 either by the age of the father, mother, or the interaction between the ages of both parents. Using
42 the common woodlouse *Armadillidium vulgare*, an indeterminate grower, as a biological model,
43 we tested for the existence of a deleterious effect of parental age on fitness components. Contrary
44 to previous findings reported from vertebrate studies, old parents produced both a higher number
45 and larger offspring than young parents. However, their offspring had lower fitness components
46 (by surviving less, producing a smaller number of clutches, or not reproducing at all) than
47 offspring born to young parents. Our findings strongly support the existence of trans-generational
48 senescence in woodlice and contradict the belief that old individuals in indeterminate growers
49 contribute the most to recruitment and correspond thereby to the key life stage for population
50 dynamics. Our work also provides rare evidence that the trans-generational effect of senescence
51 can be stronger than direct reproductive senescence in indeterminate growers.

52

53 **Keywords**

54 Reproductive success, aging, *Armadillidium vulgare*, clutch size, indeterminate growth

55

56 **Introduction**

57 Deciphering the eco-evolutionary roots of inter-individual variation in reproductive success is a
58 long-standing objective in evolutionary biology. Many overall (e.g. temperature, photoperiod)
59 and biotic (e.g. social relationships, population density, predation, food availability) factors can
60 modulate reproductive success in both vertebrates and invertebrates (e.g. Descamps *et al.*, 2008;
61 Geister *et al.*, 2008; Schwanz, 2008; Bertram, 2009; Donelson *et al.*, 2010). Within a given
62 population, individual attributes such as age and size are also associated with reproductive
63 performance in most animals (Clutton-Brock, 1991). However, reproductive success, usually
64 measured as the number of offspring produced at some pre-defined stage, (i.e. conception, birth,
65 or independence of offspring) does not account for the entire process of reproduction. In an
66 evolutionary context where the performance of offspring matters because it shapes Darwinian

67 fitness (at the individual level) and growth (at the population level), a trans-generational approach
68 is required.

69 Among the factors that influence the fate of offspring, the role of parental age is currently
70 attracting considerable attention (see Lemaître & Gaillard, 2017 for a review). Evidence of a
71 decrease in reproductive performance at old age has accumulated in the last decades (Nussey *et*
72 *al.*, 2013) and empirical studies have reported evidence of reproductive senescence in a large
73 range of reproductive traits including clutch size (Tabata & Teshiba, 2018), juvenile mass or size
74 (Sharp & Clutton-Brock, 2010; Barks & Laird, 2016), offspring survival (Packer *et al.*, 1998),
75 offspring reproduction (Ducatez *et al.*, 2012) or offspring lifespan (Lansing, 1947; Barks &
76 Laird, 2016). Interestingly, when Lansing (1947) published his pioneering study demonstrating a
77 negative effect of parental age on offspring lifespan in rotifers, he made no explicit distinction
78 between the maternal and paternal ages. However, most studies of this process (i.e. the so-called
79 Lansing effect) have focused on maternal age (Lemaître & Gaillard, 2017) while old paternal age
80 should also negatively influence offspring performance (Lemaître & Gaillard, 2017) as a result of
81 decreasing sperm quality with increasing paternal age (Johnson & Gemmell, 2012). Studies
82 looking at the effect of both maternal and paternal ages as well as their potential interactions are
83 now strongly required (Dzyuba, 2006; Tidière *et al.*, 2018).

84 So far, most studies of parental age effect focused on determinate growers (especially long-lived
85 birds and mammals) (Fay *et al.*, 2016), which are supposed to show stronger senescence than
86 indeterminate growers (Vaupel *et al.*, 2004). In indeterminate growers the number of offspring
87 produced per reproductive attempt is expected to increase with age, which should counter-select
88 reproductive senescence in terms of fecundity (Vaupel *et al.*, 2004; Jones *et al.*, 2014). For
89 example, in fish populations, older and so bigger individuals generally have a higher reproductive
90 success than younger and smaller individuals (Venturelli *et al.*, 2009), which might be due to the
91 production of high quality eggs by old females (e.g. Vallin & Nissling, 2000 in the Atlantic cod,
92 *Gadus morhua*). Age classes largely differ in size in indeterminate growers, which makes mating
93 between individuals from distinct cohorts difficult, if not impossible. In such species, both
94 selective pressure and physical constraints during mating can lead to a pattern of size- (and thus
95 age-) assortative mating (Crespi, 1989). Thus, reproductive senescence can be exacerbated by the
96 cumulative effects of both maternal and paternal ages (Lemaître & Gaillard, 2017). While
97 investigations of reproductive senescence are mandatory to refine our current understanding of

98 the evolution of senescence (Jones & Vaupel, 2017), such studies are still lacking, especially in
99 invertebrates. Here, we aim to fill this knowledge gap by investigating whether reproductive
100 senescence occurs in an indeterminate grower, the common woodlouse *Armadillidium vulgare*,
101 and whether advanced parental age negatively influences offspring fitness components.
102

103 **Materials and Methods**

104 ***Biological model***

105 The common woodlouse is a terrestrial isopod that can live up to three years (Paris & Pitelka,
106 1962). This species exhibits indeterminate growth and as such large size differences across
107 individuals can be observed. For instance, an old individual could be up to ten times larger than a
108 newly mature individual (Brody *et al.*, 1983). Therefore, physical constraints prevent young
109 individuals to mate with old ones, leading to a pattern of assortative mating in both size and age
110 at the population level (Lefebvre *et al.*, 2019). Female parental care is energetically costly in this
111 species as females actively carry and protect their offspring in a marsupium for a month (Surbida
112 & Wright, 2001). Offspring develop in this pouch and benefit from a protected environment and
113 nutrients provided by their mother (Surbida & Wright, 2001). As the incubation of the offspring
114 takes place in the marsupium, the size of the females is closely associated with the number of
115 offspring produced (Paris & Pitelka, 1962; Dangerfield & Hassall, 1992; Durand *et al.*, 2018).
116

117 All individuals of *A. vulgare* used in our experiment came from a natural population collected in
118 Denmark (Helsingør) in 1982. All the specimens were virgin at the beginning of the study and
119 had been maintained on moistened compost and subjected to Poitiers natural photoperiod (86;
120 46° 34' 55" N; 0° 20' 10" E) at 20°C with food provided ad libitum (i.e. slices of fresh carrots and
121 dried leaves of linden, *Tilia* sp). These conditions were repeated across all experiments.
122

123 ***Differences of reproductive performance between young and old parents***

124 We set up two groups of 40 breeding pairs comprising of one male and one female: one group
125 was made up of old parents (36-months-old) and another group was made up of young ones (12-
126 months old). The mass of each individual was initially checked to control for variation within age
127 groups. Young individuals weighed (mean \pm sd) 0.081g \pm 0.027g and old ones 0.293g \pm 0.044g.
128 All 80 breeding pairs were weekly monitored throughout 7 months (i.e. during the entire

129 reproductive season, from January to July) and when females were gravid, they were isolated and
130 placed in boxes with wet paper towel. Only the first clutch produced was used because very few
131 breeding pairs produced a second clutch. We computed the breeding rate according to age (the
132 probability to produce a clutch) for each parental group (i.e. young parents and old parents). We
133 recorded the number of offspring per clutch (hereafter called clutch size). The entire clutch was
134 weighed and then divided by clutch size to obtain the mean offspring mass at birth. The
135 experimental design is presented in Figure 1.

136

137 ***Inter-generational traits: offspring mass, survival and reproductive success***

138 We monitored the offspring during the most critical period of their lives (0-18 months). Indeed,
139 in the wild, only 11% of individuals are able to reach 2-years-old (Paris & Pitelka, 1962). To
140 estimate survival, we counted offspring from the previous breeding pairs a first time at birth, a
141 second time at 5 months of age, then at 12 months of age and finally at 18 months of age (Figure
142 1). The number of surviving offspring counted at each time allowed estimating offspring survival
143 from 0 to 5 months of age, offspring survival from 5 to 12 months of age, offspring survival from
144 12 to 18 months of age and total offspring survival (i.e. from 0 to 18 months of age). Offspring
145 were weighed as 12 (± 1) months old and then as 18 (± 1) months old to obtain the offspring
146 mass at 12 months of age and the offspring mass at 18 months of age. To estimate reproductive
147 success of offspring born from young or old parents, we set up, when they are sexually mature
148 (i.e. 1-year-old, Paris & Pitelka, 1962), 4 combinations of 20 breeding pairs (avoiding brothers
149 and sisters): (i) offspring from old parents together, (ii) female offspring from old parents with
150 male offspring from young parents, (iii) females offspring from young parents with male
151 offspring from old parents, and (iv) offspring from young parents together. To avoid pseudo-
152 replication issues (sensu Hurlbert 1984), we analyzed the reproductive status (i.e. reproduction
153 success or failure) of the pair as function of the age group of the female's parents in interaction
154 with the age group of the father' parents.

155

156 ***Statistical analysis***

157 All statistical analyses were performed using the software R 3.6.0 (R Core Development Team
158 2019). For each model, we followed a model selection procedure to identify the minimal model,
159 or the set of adequate models (Anderson & Burnham, 2002). Starting from the full model, we

160 ranked all the nested models based on their AIC. Among the top ranked models ($\Delta AIC < 2$),
161 we only retained the most parsimonious ones: if one of these models was simply a more complex
162 form of another one listed among the top rank models, for instance because it contained an
163 additional parameter (variable or interaction term), this parameter was ignored and the more
164 complex model was not retained (Galipaud *et al.*, 2014, Supplementary file 1). For the mean
165 offspring mass at birth, at 12 months of age and at 18 months of age as for offspring survival at 5
166 months of age, between 5 and 12 months of age and at 18 months of age we first tested for an
167 effect of clutch size. When clutch size had a statistically significant effect (see Supplementary file
168 2), it was systematically included in the set of considered models (see Berger *et al.*, 2015 for a
169 similar approach).

170 Breeding rate as binary data has been modelled using a generalized linear model (GLM) with
171 binomial distribution with parent's age ('young parents' vs. 'old parents') as a fixed factor.
172 Clutch size was modelled using a linear model (LM) with normal distribution with parent's age
173 as a fixed factor. The mean offspring mass at birth was modelled using a linear model (LM) with
174 a normal distribution because only the average clutch mass was recorded (i.e. individual body
175 mass within a clutch could not be measured at birth). Offspring mass at 12 months of age and
176 offspring mass at 18 months of age were analysed with a linear mixed effect models (LMM) with
177 a normal distribution, using parent's age, offspring sex and their interaction as fixed factors and
178 the breeding pairs identity as a random effect to take into account a potential genetic effect. The
179 survival to 5 months of age was modelled with a generalized linear mixed effect model (GLMM)
180 with a binomial distribution, the parent's age and clutch size were the fixed factors, and the
181 breeding pairs identity was the random effect. The offspring survival from 5 to 12 months of age,
182 from 12 to 18 months of age, and the overall survival (i.e. from 0 to 18 months of age) have been
183 modelled as binary data using generalized linear mixed effect models (GLMM) with a binomial
184 distribution, parent's age and offspring sex and their interaction added to the clutch size were the
185 fixed factors and the breeding pairs identity was used as the random effect. The breeding rate of
186 offspring was modelled with binary data using a generalized linear model (GLM), with mother's
187 age and father's age and their interaction as fixed factors.

188 Finally, reproductive senescence can be masked by the selective disappearance of low quality
189 individuals (Nussey *et al.*, 2008). For a given age larger females produce more offspring in the
190 common woodlouse and body mass is thus generally thought to be a good indicator of individual

191 quality (Durand *et al.*, 2018). We tested for such relationships by modelling the breeding rate as
192 binary data using a generalized linear model (GLM) with maternal mass set as a fixed factor
193 within the young and old mothers separately. Then, in absence of repeated data on individuals
194 over the life course, we tested for a putative influence of selective disappearance on our results by
195 testing within the old parents group whether the first 50% of individuals that encounter premature
196 death were lighter than the individuals that survived beyond the median life span. When doing
197 this the effect of mass on survival of the old individual group has been modelled as binary data
198 using a generalized linear model (GLM) with binomial distribution with individual mass, sex and
199 their interaction as fixed factors.

200

201 **Results**

202 *Differences of reproductive performance between young and old parents*

203 Old parents (40 breeding pairs) produced 16 clutches, while young parents (40 breeding pairs)
204 produced 24 clutches. No detectable difference was found concerning the breeding rate. The
205 model with only the intercept was selected, but if we looked the non-selected model concerning
206 the effect of age on the breeding rate, we found that the breeding rate tended to decrease with
207 increasing parental age (estimate \pm SE=-0.76 \pm 0.45, LR Chisq₁=2.86, P=0.09; Table 1; Figure
208 2). Moreover, old parents produced more and heavier offspring than young parents (estimate \pm
209 SE=45.15 \pm 12.90, LR Chisq₁= 12.62, P<0.001; estimate \pm SE=5.63e05g \pm 1.77e05g, LR
210 Chisq₁=12.62, P=0.001, respectively; Table 1; Figure 3).

211

212 *Offspring mass, survival and reproductive success*

213 The offspring mass at 12 and 18 months did not differ between young and old parents (estimate \pm
214 SE=0.004 \pm 0.003, LR Chisq₁=1.94, P=0.16; estimate \pm SE=0.002 \pm 0.004, LR Chisq₁=0.11,
215 P=0.73 for 12 and 18 months, respectively; Table 1). The cumulative survival (from 0 to 18
216 months) was higher for offspring born from young parents than for offspring coming from old
217 parents (estimate \pm SE=0.018 \pm 0.09, LR Chisq₁=3.95, P=0.04; Table 1; Figure 4). More
218 specifically, this difference did not occur for the offspring survival between birth and 5 months of
219 age (estimate \pm SE=0.18 \pm 0.69, LR Chisq₁=0.07, P=0.79; Table 1; Figure 4) but is present for
220 the survival from 5 to 12 months (estimate \pm SE=-0.90 \pm 0.41, LR Chisq₁=4.27, P=0.04; Table 1;
221 Figure 4) and from 12 to 18 months (estimate \pm SE=-1.06 \pm 0.24, LR Chisq₁=8.22, P=0.004;

222 Table 1; Figure 4). Reproductive success of offspring was higher for offspring born from young
223 mothers and young fathers than for offspring born from old fathers or old mothers (0.25 vs. 0 for
224 young and old females, respectively, 0.20 vs. 0.05 for young and old males, respectively; LR
225 $\text{Chisq}_1=15.99$, $P<0.001$ and LR $\text{Chisq}_1=5.06$, $P=0.02$; Table 1; Figure 5).

226

227 ***Selective disappearance***

228 The maternal mass did not influence the breeding rate within both the young mothers ($\chi^2=0.27$,
229 $df=1$, $P=0.59$) and the old mothers ($\chi^2=2.31$, $df=1$, $P=0.12$). We also did not find any link
230 between body mass and survival in the 3-years-old group ($\chi^2=1.66$, $df=1$, $P=0.20$) neither in
231 males nor in females as expressed by the absence of statistically significant interaction between
232 sex and body mass (estimate \pm SE= -17.19 ± 11.44 , $P=0.13$).

233

234 **Discussion**

235 In indeterminate growers, reproductive success should increase with age, leading to an absence or
236 a negligible reproductive senescence (Vaupel *et al.*, 2004). At first glance, our results support this
237 prediction as old parents produced clutches containing more offspring than young ones (Vaupel
238 *et al.*, 2004). However, old parents tended to produce a smaller number of clutches than young
239 ones and we detected a trans-generational effect of reproductive senescence because parental age
240 negatively influenced both survival and reproduction of offspring. As we had hardly obtained
241 clutches from offspring of old individuals, we were unable to study the quality of the
242 grandchildren.

243 The effect of the environmental context experienced by the parents (e.g. diet, temperature,
244 pathogen prevalence) on offspring performance has been described for a long time (Mousseau,
245 1998; Curley *et al.*, 2011) but an increasing number of studies have revealed that parental age can
246 also negatively impact offspring survival (Priest *et al.*, 2002; Fox *et al.*, 2003) and reproduction
247 (Priest *et al.*, 2008; Bouwhuis *et al.*, 2010; Ducatez *et al.*, 2012; Schroeder *et al.*, 2015; Lippens
248 *et al.*, 2017). For instance, in Asian elephants (*Elephas maximus*), older mothers produce
249 offspring with impaired survival (Reichert *et al.*, 2019) and in the rotifers *Brachionus*
250 *manjavacas*, maternal age negatively affects offspring survival and reproduction (e.g. egg
251 quality) (Bock *et al.*, 2019). These results are in line with ours as we found that the parent's age
252 has a high impact on offspring survival and reproductive prospects. Moreover, we demonstrated

253 the occurrence of a trans-generational effect of parental age across generations. We reported that
254 males from old parents reproduced less than males from young parents and this observed effect in
255 males was stronger in females because females from old parents did not reproduce at all.
256 Several mechanisms could be involved in these trans-generational effects, including oxidative
257 stress, telomere inheritance, epigenetics, or parental care (Njajou *et al.*, 2007; Franklin &
258 Mansuy, 2010). Most studies of the physiological basis of senescence in invertebrates (notably in
259 *Drosophila melanogaster* and *Caenorhabditis elegans*) have focused on oxidative stress due to its
260 well-described effect on lifespan (Golden *et al.*, 2002). Parental care could also be impacted by
261 age (Lemaître & Gaillard, 2017) notably because the ability of acquiring and storing body
262 reserves often decreases with increasing age, at least in vertebrates (Skogland, 1988; Lecomte *et*
263 *al.*, 2010). Parental care effects are also well documented in invertebrates, in particular in insects
264 (Wong *et al.*, 2013) but the few studies investigating the effect of age on parental care in
265 invertebrates have provided mixed results (Ivimey-Cook & Moorad, 2018). In some organisms
266 such as viviparous terrestrial isopods, the maintenance of the reproductive system can be very
267 energetically expensive (Lardies *et al.*, 2004). In the woodlice, females provide nutrients to
268 offspring during the incubation in the marsupium by a fluid called marsupial fluid (Surbida &
269 Wright, 2001). Thus, both the quality and the quantity of nutrients provided by females in
270 marsupium fluid could determine offspring quality and thereby their viability. Studies
271 investigating how the marsupial fluid properties change with mother's age in the woodlouse and
272 whether such changes might account for the decrease in reproductive success we reported in old
273 individuals are strongly required. Overall, our knowledge on age-specific allocation to maternal
274 and paternal care is still in its infancy in invertebrates, but we can hypothesise that a decrease in
275 maternal care associated to increased oxidative stress and some epigenetic factors (Curley *et al.*,
276 2011; Guillaumet-Adkins *et al.*, 2017) could contribute to the trans-generational effect observed
277 in woodlouse.

278 One of the grey areas of these results is the source of this trans-generational effect. While many
279 studies have focused on the maternal effect, the paternal effect and the interaction between both
280 effects remain relatively unknown. Among the rare studies that have investigated the influence of
281 both maternal and paternal age, Bouwhuis and colleagues (2015) showed that the trans-
282 generational effects are sex-specific in the common tern, *Sterna hirundo*. In this species,
283 daughters from old mothers had a lower reproductive success than daughters from young mothers

284 and sons from old fathers had a shorter lifespan than sons from young fathers. In the invertebrate
285 *Drosophila melanogaster*, the effect of parent's age in offspring reproduction differs between
286 sexes: sons were insensitive to maternal age but had reduced reproductive abilities with paternal
287 age when daughters from old mothers showed a decrease in reproductive success (Mossman *et*
288 *al.*, 2019). Offspring produced by both old mothers and fathers show a substantial modification in
289 reproductive behaviour with an extreme egg dumping (Mossman *et al.*, 2019). Overall, both
290 advanced maternal and paternal ages could have a negative impact on offspring lifetime
291 reproductive success, which can be exacerbated by the strong positive age assortative mating that
292 occurs in *A. vulgare*. In our experiment, it was not possible to tease apart the relative contribution
293 of mother and father ages, notably because trials of mating between cross-aged individuals (e.g.
294 1-year-old individuals* 3-year-old individuals) were unsuccessful. Future experiments would
295 need to investigate the effect of age directly on male or female reproductive traits (e.g. sperm,
296 oocytes), which could play a key role in shaping reproductive senescence patterns (Fricke &
297 Koppik, 2019; Monaghan & Metcalfe, 2019). Finally, it is important to notice that the survival of
298 older individuals does not seem to be linked to their mass in our experiment, which suggests that
299 the possible selective disappearance of the lightest individuals (in a given age-class) does not
300 impact our results.

301 Everything else being equal, individuals reaching 3 years of age likely achieve a higher fitness
302 than short-lived individuals, thanks to the much larger number of eggs produced throughout
303 lifetime. However, old individuals suffer from a strong reproductive senescence in terms of
304 offspring quality and why selection did not select for old individuals allocating to offspring
305 quality rather than to offspring quantity can be seen as paradoxical at the light of some recent
306 developments in evolutionary biology of aging, which suggest that reproductive senescence
307 should be absent in indeterminate growing species (Vaupel *et al.*, 2004). However, these results
308 can largely be explained by classic evolutionary theories of aging: i) the proportion of individuals
309 reaching 3 years of age in nature (<1%) is far too weak to enable the evolution a new
310 reproductive tactic (Medawar, 1952), and ii) the selection for the production of a large quantity of
311 offspring might come at a cost in late life in terms of offspring quality (Williams, 1957). Thus,
312 our findings have two major implications. First, in the particular case of the woodlouse, these
313 results run counter to studies carried out so far, which have viewed oldest individuals as playing a
314 key role in population dynamics through their ability to produce many offspring (Paris & Pitelka,

315 1962; Dangerfield & Hassall, 1992). However, our study does not provide information on the
316 consequences of reproductive senescence in terms of population dynamics in the wild. While
317 three-year-old individuals are quite rare (< 1% of a given cohort are reaching 3 years of age) to
318 be expected to play any detectable role in population dynamics, two-years-old individuals are
319 more common in in the wild (i.e. 13% of individuals within a given cohort reach this age) and
320 reproductive senescence in terms of decreased offspring viability we demonstrated in our study
321 might negatively influence population recruitment (Paris & Pitelka, 1962). To better understand
322 the influence of reproductive senescence from a quantitative viewpoint, data on age-specific
323 reproductive success in the wild will be required. Our findings demonstrate that indeterminate
324 growers are likely to show senescence but through different pathways compared to determinate
325 growers.

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- 475 Figure's Captions
- 476
- 477 Figure 1: Experimental Design.
- 478
- 479 Figure 2: Breeding rate according to individual's age.
- 480
- 481 Figure 3: Number (A) and Mass (B) of offspring per clutch according to their parent's age.

482 The thick line depicts the median, the box the interquartile range, and the whisker are bounded to
483 the most extreme data point within 1.5 the interquartile range. The outliers outside this range are
484 displayed as open circles. ** means $p < 0.01$.

485

486 Figure 4: Offspring survival according to their parent's age.

487 Mean proportion of offspring surviving (+/- bootstrapped 95% confidence interval) at 5 months
488 of age, 12 months of age, and 18 months of age. Each data point corresponds to one clutch and
489 was plotted as grey dots with a slight jitter added to distinguish adjacent points.

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491 Figure 5: Graphical display of the interactive effect of offspring sex and parental age on offspring
492 reproductive success.

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