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# Reproductive senescence and parental effect in an indeterminate grower

Short running title: Reproductive senescence in the woodlouse

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## Conflict of Interest

The authors declare that there is no conflict of interest.

## Abstract

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

## Keywords

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

## Introduction

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

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

So far, most studies of parental age effect focused on determinate growers (especially long-lived birds and mammals) (Fay *et al.*, 2016), which are supposed to show stronger senescence than indeterminate growers (Vaupel *et al.*, 2004). In indeterminate growers the number of offspring produced per reproductive attempt is expected to increase with age, which should counter-select reproductive senescence in terms of fecundity (Vaupel *et al.*, 2004; Jones *et al.*, 2014). For example, in fish populations, older and so bigger individuals generally have a higher reproductive success than younger and smaller individuals (Venturelli *et al.*, 2009), which might be due to the production of high quality eggs by old females (e.g. Vallin & Nissling, 2000 in the Atlantic cod, *Gadus morhua*). Age classes largely differ in size in indeterminate growers, which makes mating between individuals from distinct cohorts difficult, if not impossible. In such species, both selective pressure and physical constraints during mating can lead to a pattern of size- (and thus age-) assortative mating (Crespi, 1989). Thus, reproductive senescence can be exacerbated by the cumulative effects of both maternal and paternal ages (Lemaître & Gaillard, 2017). While investigations of reproductive senescence are mandatory to refine our current understanding of the evolution of senescence (Jones & Vaupel, 2017), such studies are still lacking, especially in invertebrates. Here, we aim to fill this knowledge gap by investigating whether reproductive senescence occurs in an indeterminate grower, the common woodlouse *Armadillidium vulgare,* and whether advanced parental age negatively influences offspring fitness components.

## Materials and Methods

### *Biological model*

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

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

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

We set up two groups of 40 breeding pairs comprising of one male and one female: one group was made up of old parents (36-months-old) and another group was made up of young ones (12-months old). The mass of each individual was initially checked to control for variation within age groups. Young individuals weighed (mean ± sd) 0.081g ± 0.027g and old ones 0.293g ± 0.044g. All 80 breeding pairs were weekly monitored throughout 7 months (i.e. during the entire reproductive season, from January to July) and when females were gravid, they were isolated and placed in boxes with wet paper towel. Only the first clutch produced was used because very few breeding pairs produced a second clutch. We computed the breeding rate according to age (the probability to produce a clutch) for each parental group (i.e. young parents and old parents). We recorded the number of offspring per clutch (hereafter called clutch size). The entire clutch was weighed and then divided by clutch size to obtain the mean offspring mass at birth. The experimental design is presented in Figure 1.

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

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

### *Statistical analysis*

All statistical analyses were performed using the software R 3.6.0 (R Core Development Team 2019). For each model, we followed a model selection procedure to identify the minimal model, or the set of adequate models (Anderson & Burnham, 2002). Starting from the full model, we ranked all the nested models based on their AIC. Among the top ranked models (delta AIC < 2), we only retained the most parsimonious ones: if one of these models was simply a more complex form of another one listed among the top rank models, for instance because it contained an additional parameter (variable or interaction term), this parameter was ignored and the more complex model was not retained (Galipaud *et al.*, 2014, Supplementary file 1). For the mean offspring mass at birth, at 12 months of age and at 18 months of age as for offspring survival at 5 months of age, between 5 and 12 months of age and at 18 months of age we first tested for an effect of clutch size. When clutch size had a statistically significant effect (see Supplementary file 2), it was systematically included in the set of considered models (see Berger *et al.*, 2015 for a similar approach).

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

Finally, reproductive senescence can be masked by the selective disappearance of low quality individuals (Nussey *et al.*, 2008). For a given age larger females produce more offspring in the common woodlouse and body mass is thus generally thought to be a good indicator of individual quality (Durand *et al.*, 2018). We tested for such relationships by modelling the breeding rate as binary data using a generalized linear model (GLM) with maternal mass set as a fixed factor within the young and old mothers separately. Then, in absence of repeated data on individuals over the life course, we tested for a putative influence of selective disappearance on our results by testing within the old parents group whether the first 50% of individuals that encounter premature death were lighter than the individuals that survived beyond the median life span. When doing this the effect of mass on survival of the old individual group has been modelled as binary data using a generalized linear model (GLM) with binomial distribution with individual mass, sex and their interaction as fixed factors.

## Results

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

Old parents (40 breeding pairs) produced 16 clutches, while young parents (40 breeding pairs) produced 24 clutches. No detectable difference was found concerning the breeding rate. The model with only the intercept was selected, but if we looked the non-selected model concerning the effect of age on the breeding rate, we found that the breeding rate tended to decrease with increasing parental age (estimate ± SE=-0.76 ± 0.45, LR Chisq$_1$=2.86, P=0.09; Table 1; Figure 2). Moreover, old parents produced more and heavier offspring than young parents (estimate ± SE=45.15 ± 12.90, LR Chisq$_1$= 12.62, P<0.001; estimate ± SE=5.63e05g ± 1.77e05g, LR Chisq$_1$=12.62, P=0.001, respectively; Table 1; Figure 3).

### ***Offspring mass, survival and reproductive success***

The offspring mass at 12 and 18 months did not differ between young and old parents (estimate ± SE=0.004 ± 0.003, LR Chisq$_1$=1.94, P=0.16; estimate ± SE=0.002 ± 0.004, LR Chisq$_1$=0.11, P=0.73 for 12 and 18 months, respectively; Table 1). The cumulative survival (from 0 to 18 months) was higher for offspring born from young parents than for offspring coming from old parents (estimate ± SE=0.018 ± 0.09, LR Chisq$_1$=3.95, P=0.04; Table 1; Figure 4). More specifically, this difference did not occur for the offspring survival between birth and 5 months of age (estimate ± SE=0.18 ± 0.69, LR Chisq$_1$=0.07, P=0.79; Table 1; Figure 4) but is present for the survival from 5 to 12 months (estimate ± SE=-0.90 ± 0.41, LR Chisq$_1$=4.27, P=0.04; Table 1; Figure 4) and from 12 to 18 months (estimate ± SE=-1.06 ± 0.24, LR Chisq$_1$=8.22, P=0.004;

Table 1; Figure 4). Reproductive success of offspring was higher for offspring born from young mothers and young fathers than for offspring born from old fathers or old mothers (0.25 vs. 0 for young and old females, respectively, 0.20 vs. 0.05 for young and old males, respectively; LR $Chisq_1=15.99$, $P<0.001$ and LR $Chisq_1=5.06$, $P=0.02$; Table 1; Figure 5).

### *Selective disappearance*

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

## Discussion

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

The effect of the environmental context experienced by the parents (e.g. diet, temperature, pathogen prevalence) on offspring performance has been described for a long time (Mousseau, 1998; Curley *et al.*, 2011) but an increasing number of studies have revealed that parental age can also negatively impact offspring survival (Priest *et al.*, 2002; Fox *et al.*, 2003) and reproduction (Priest *et al.*, 2008; Bouwhuis *et al.*, 2010; Ducatez *et al.*, 2012; Schroeder *et al.*, 2015; Lippens *et al.*, 2017). For instance, in Asian elephants (*Elephas maximus*), older mothers produce offspring with impaired survival (Reichert *et al.*, 2019) and in the rotifers *Brachionus manjavacas*, maternal age negatively affects offspring survival and reproduction (e.g. egg quality) (Bock *et al.*, 2019). These results are in line with ours as we found that the parent's age has a high impact on offspring survival and reproductive prospects. Moreover, we demonstrated the occurrence of a trans-generational effect of parental age across generations. We reported that males from old parents reproduced less than males from young parents and this observed effect in males was stronger in females because females from old parents did not reproduce at all. Several mechanisms could be involved in these trans-generational effects, including oxidative stress, telomere inheritance, epigenetics, or parental care (Njajou *et al.*, 2007; Franklin & Mansuy, 2010). Most studies of the physiological basis of senescence in invertebrates (notably in *Drosophila melanogaster* and *Caenorhabditis elegans*) have focused on oxidative stress due to its well-described effect on lifespan (Golden *et al.*, 2002). Parental care could also be impacted by age (Lemaître & Gaillard, 2017) notably because the ability of acquiring and storing body reserves often decreases with increasing age, at least in vertebrates (Skogland, 1988; Lecomte *et al.*, 2010). Parental care effects are also well documented in invertebrates, in particular in insects (Wong *et al.*, 2013) but the few studies investigating the effect of age on parental care in invertebrates have provided mixed results (Ivimey-Cook & Moorad, 2018). In some organisms such as viviparous terrestrial isopods, the maintenance of the reproductive system can be very energetically expensive (Lardies *et al.*, 2004). In the woodlice, females provide nutrients to offspring during the incubation in the marsupium by a fluid called marsupial fluid (Surbida & Wright, 2001). Thus, both the quality and the quantity of nutrients provided by females in marsupium fluid could determine offspring quality and thereby their viability. Studies investigating how the marsupial fluid properties change with mother's age in the woodlouse and whether such changes might account for the decrease in reproductive success we reported in old individuals are strongly required. Overall, our knowledge on age-specific allocation to maternal and paternal care is still in its infancy in invertebrates, but we can hypothesise that a decrease in maternal care associated to increased oxidative stress and some epigenetic factors (Curley *et al.*, 2011; Guillaumet-Adkins *et al.*, 2017) could contribute to the trans-generational effect observed in woodlouse.

One of the grey areas of these results is the source of this trans-generational effect. While many studies have focused on the maternal effect, the paternal effect and the interaction between both effects remain relatively unknown. Among the rare studies that have investigated the influence of both maternal and paternal age, Bouwhuis and colleagues (2015) showed that the trans-generational effects are sex-specific in the common tern, *Sterna hirundo*. In this species, daughters from old mothers had a lower reproductive success than daughters from young mothers and sons from old fathers had a shorter lifespan than sons from young fathers. In the invertebrate *Drosophila melanogaster*, the effect of parent's age in offspring reproduction differs between sexes: sons were insensitive to maternal age but had reduced reproductive abilities with paternal age when daughters from old mothers showed a decrease in reproductive success (Mossman *et al.*, 2019). Offspring produced by both old mothers and fathers show a substantial modification in reproductive behaviour with an extreme egg dumping (Mossman *et al.*, 2019). Overall, both advanced maternal and paternal ages could have a negative impact on offspring lifetime reproductive success, which can be exacerbated by the strong positive age assortative mating that occurs in *A. vulgare*. In our experiment, it was not possible to tease apart the relative contribution of mother and father ages, notably because trials of mating between cross-aged individuals (e.g. 1-year-old individuals* 3-year-old individuals) were unsuccessful. Future experiments would need to investigate the effect of age directly on male or female reproductive traits (e.g. sperm, oocytes), which could play a key role in shaping reproductive senescence patterns (Fricke & Koppik, 2019; Monaghan & Metcalfe, 2019). Finally, it is important to notice that the survival of older individuals does not seem to be linked to their mass in our experiment, which suggests that the possible selective disappearance of the lightest individuals (in a given age-class) does not impact our results.

Everything else being equal, individuals reaching 3 years of age likely achieve a higher fitness than short-lived individuals, thanks to the much larger number of eggs produced throughout lifetime. However, old individuals suffer from a strong reproductive senescence in terms of offspring quality and why selection did not select for old individuals allocating to offspring quality rather than to offspring quantity can be seen as paradoxical at the light of some recent developments in evolutionary biology of aging, which suggest that reproductive senescence should be absent in indeterminate growing species (Vaupel et al., 2004). However, these results can largely be explained by classic evolutionary theories of aging: i) the proportion of individuals reaching 3 years of age in nature (<1%) is far too weak to enable the evolution a new reproductive tactic (Medawar, 1952), and ii) the selection for the production of a large quantity of offspring might come at a cost in late life in terms of offspring quality (Williams, 1957). Thus, our findings have two major implications. First, in the particular case of the woodlouse, these results run counter to studies carried out so far, which have viewed oldest individuals as playing a key role in population dynamics through their ability to produce many offspring (Paris & Pitelka, 1962; Dangerfield & Hassall, 1992). However, our study does not provide information on the consequences of reproductive senescence in terms of population dynamics in the wild. While three-year-old individuals are quite rare (< 1% of a given cohort are reaching 3 years of age) to be expected to play any detectable role in population dynamics, two-years-old individuals are more common in in the wild (i.e. 13% of individuals within a given cohort reach this age) and reproductive senescence in terms of decreased offspring viability we demonstrated in our study might negatively influence population recruitment (Paris & Pitelka, 1962). To better understand the influence of reproductive senescence from a quantitative viewpoint, data on age-specific reproductive success in the wild will be required. Our findings demonstrate that indeterminate growers are likely to show senescence but through different pathways compared to determinate growers.

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Figure's Captions

Figure 1: Experimental Design.

Figure 2: Breeding rate according to individual's age.

Figure 3: Number (A) and Mass (B) of offspring per clutch according to their parent's age.

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

Figure 4: Offspring survival according to their parent's age.
Mean proportion of offspring surviving (+/- bootstrapped 95% confidence interval) at 5 months of age, 12 months of age, and 18 months of age. Each data point corresponds to one clutch and was plotted as grey dots with a slight jitter added to distinguish adjacent points.

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