

Life history traits of *Aporrectodea caliginosa* in a 8-year laboratory experiment

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Abstract

Earthworms are key soil organisms used as bioindicators of soil fertility. They are also used as model organisms in soil ecology and ecotoxicology, including population dynamics modeling approaches which are based on life history traits. However, little is known about the effects of environmental conditions on their life history traits such as their life span, growth and reproductive capabilities in the long terms. The aim of this study was to bring new data and knowledge on the effects of different conditions of food resource and earthworm density on life history traits (i.e., survival, growth, reproduction) of *Aporrectodea caliginosa* individuals during an 8-year laboratory experiment. For that, a cohort of 20 hatchlings *A. caliginosa* were synchronized from a breeding culture, fed with normal food conditions or *ad libitum* (three times the normal food conditions) and monitored individually once a month. Once adults, they were kept isolated or pooled at different densities. Individual weight and cocoons were assessed every 14 days the first year and then once a month. The lifespan of *A. caliginosa* can exceed 8 years under laboratory conditions. Moreover, individuals had a longer life span when pooled with congeners than when kept isolated. An individual kept alone and fed *ad libitum* from its birth kept growing continuously, with individuals reaching more than 10 times the regular body mass known for *A. caliginosa*. Pooled earthworms stopped growing and allocate their energy to reproduction. Pooled or isolated, individual body mass of earthworms was found to be a proxy of the amount of organic matter in the soil. These data can be used in modelling approaches to infer the earthworm biomass based on soil organic matter content, or to predict *A. caliginosa* population dynamics based on life history traits.

Keywords Earthworms | food resource | soil engineer | biomass | soil organic matter

1 Introduction

Earthworms are ecosystem engineers (Jones et al., 1994; Kumar et al., 2023) that represent one of the most important living biomasses in terrestrial ecosystems (Kooch and Kuzyakov, 2024). They influence soil structure and improve water regulation, nutrient cycling, and primary production (Blouin et al., 2013). They are widely used for

soil monitoring as bioindicators of soil fertility (Phillips et al., 2021; Edwards and Arancon, 2022) and as model organisms in soil ecology and ecotoxicology for more than 40 years (OECD, 1984; Spurgeon et al., 2003). They are also used in modelling approaches for predicting the effects of contaminants or agricultural management practices on population dynamics, based on life history traits (Johnston et al., 2014, 2015; Bart et al., 2020).

Although they have been studied for decades, and at a time where earthworms are recognised as vital for soil health and processes (Lavelle and Spain, 2024), we still not have much information on very basic life history traits in the long-terms such as lifespan, reproductive capabilities along their life, and growth in different conditions. This can hinder the development of accurate mechanistic earthworm population dynamics models that can be used to predict earthworm's impacts on terrestrial ecosystems (Mathieu, 2018).

The median longevity of *Eisenia andrei* individuals was found at 4.25 years and the oldest reported specimen was 8.73 years (Mulder et al., 2007). For earthworms that live in mineral soils, Gerard (1967) found that *Aporrectodea longa* could survived 5 to 10 years in laboratory cultures. However, this age may never be reached in the field due to mortality related to predation or unfavourable environmental conditions of e.g., food, temperature, moisture, contamination. An average of 1 to 2 years was reported for adults of several common species in field conditions (Edwards and Lofty, 1977; Lee, 1985). Reproduction of earthworms, and in particular of *A. caliginosa* has been extensively studied in different situations but on a short time step (e.g., Bart et al., 2018; Khalil et al., 2016). Therefore, the continuity of reproductive effort throughout the life of organisms is still unknown, just as the effects of environmental drivers on that ability to reproduce. Finally, the abundance and individual body mass of earthworms can be seen as an indicator of their environment, fitness and functional impact (Hoeffner et al., 2019). Keys for identification of earthworms provide general information on the average or the range of individual body mass for the different species (Bouché, 1972; Sims and Gerard, 1999) but there is a real lack of knowledge about the actual weight range of populations under different resource conditions (e.g., food and space).

We here assessed the effects of different conditions of food resource and earthworm density on life history traits that drive population dynamics (i.e., survival, growth, reproduction) of a common endogeic species, *Aporrectodea caliginosa*, in an 8-year laboratory experiment. Although not representative of natural conditions, this long-term study is, to our knowledge, the only one presenting repeated measurement over time of a ubiquitous earthworm species' life history traits, from hatching to death, allowing to answer the following questions: How long can these earthworms live? Does reproduction affect lifespan? To which extent two cohorts of individuals, from the same original population can vary in morphology, reproduction success according to their environment, in particular to food resource? What do we know regarding the phenotypic variation

of an earthworm population, and more importantly, to which extent the environment, especially the organic matter content, can shape earthworm morphology? We assumed that earthworms fed *ad libitum* will be larger and have a greater capacity to reproduce than individuals with less food. We also hypothesized that earthworms that reproduce will live shorter lives due to the energy expenditure involved.

2 Materials and Methods

The experiment started in June 2016, when a cohort of 20 hatchlings of *Aporrectodea caliginosa caliginosa* (Sims and Gerard, 1999) were synchronized from a breeding culture kept at INRAE, Versailles, France. They were bred separately with two different amounts of food (horse dung, frozen and defrosted twice, dried, and then milled < 1 mm; Lowe and Butt, 2005), representing two different levels of organic matter amendment: 10 individuals were fed with 1 g ind⁻¹ 14 days⁻¹ of horse dung (called “normal food”), and 10 individuals were fed with 3 g ind⁻¹ 14 days⁻¹ (called “*ad libitum*”). The “normal food” quantity was chosen according to Lowe and Butt (2005) who recommended >10 g adult⁻¹ month⁻¹ for this species, and considering that juveniles were on average five times smaller than adults. Moreover, these inputs corresponded to a daily consumption of 15 % (“normal food”) and 43 % (“*ad libitum*”) of the individual weight for an adult individual of 500 mg, which is a common weight for adults *A. caliginosa* (Bouché, 1972; Sims and Gerard, 1999). Throughout the experiment, and according to the recommendations given by Lowe and Butt (2005) and Lofs-Holmin (1982), the soil was renewed every 28 days and the moisture was set at 70 % of the water holding capacity (WHC) (corresponding to 28 % of water content). The providing food was also adjusted at the same moisture before being incorporated into the soil by mixing. Earthworm individual weight increased during the experiment, so their food requirements changed but we considered that these inputs, supplemented by food resource provided by the soil renewed every 28 days, was sufficient for both conditions. We did not add horse dung directly to the soil as we noticed in previous experiments that it was detrimental to earthworms on long terms, probably due to the progressive acidification of the substrate through horse dung addition.

Earthworms were bred individually in a 1 L plastic vessels filled with 400 g equivalent dry soil (natural Luvisol soil, FAO soil classification) in a climate room at 15 ± 1 °C. The first 31 months, the soil had the following characteristics: pH 7.5, organic matter 32.6 g kg⁻¹, C/N 12.7,

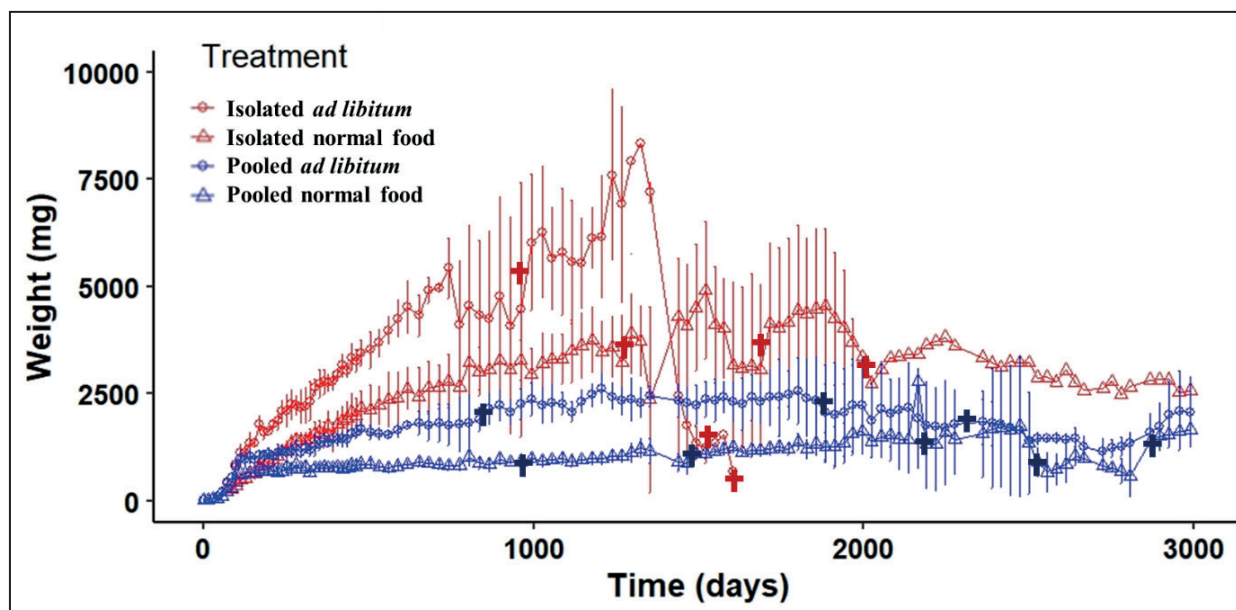


Figure 1. Growth pattern in *Aporrectodea caliginosa caliginosa* (mean weight in mg) maintained at 15°C in, isolated from birth or pooled once reach maturity, and fed with 1 (normal food) or 3 g ind⁻¹ 14 days⁻¹ (*ad libitum*) of horse dung. At the beginning of the experiment, n = 3 for “Isolated *ad libitum*”, n = 4 for “Isolated normal food”, n = 6 for pooled. A cross denotes a death, vertical bars are standard deviations.

29% sand, 48% silt, and 23% clay (see Bart et al. 2017 for more details). After 31 months, the soil was changed because we had no more access to the previous grassland. Another soil was used with close characteristics: pH 6.2, organic matter 38.6 g kg⁻¹, C/N 11.5, 20% sand, 62% silt, and 18% clay. This soil was sampled 100 m apart from the previous one, also in a grassland that had not been treated with pesticides for more than 20 years.

Once mature (appearance of a fully developed clitellum), the 10 individuals of each food level were separated into two groups. Four individuals were kept isolated in vessels in the same conditions. In order to test the effects of the earthworm density on reproduction (Bart et al. 2019), the six other individuals were pooled first by 2 for 84 days (3 vessels with 2 individuals), then by 3 for 84 days (2 vessels with 3 individuals), then by 6 for 84 days (1 vessel with 6 individuals). These “stocking density” were chosen according to Lowe and Butt (2005) who recommended 6 adults l⁻¹ for sustained culture of this species. After this period of test on reproduction, we wanted to keep on monitoring these earthworms in the long-terms. Because six individuals in one vessel was too much to ensure good conditions for earthworms, they were pooled again by 2 for 168 days (3 vessels with 2 individuals), and finally by 3 (2 vessels with 3 individuals) until the end of the experiment.

All the individuals were weighted individually every 14 days until day 476 (corresponding to one year and four months), and then once a month. The earthworms pooled in one vessel could not be differentiated so the

average weight per individual was calculated for each vessel. The cocoon production was monitored once a month for pooled individuals (by washing and sieving the soil through a 1mm mesh-size, see Bart et al. 2018). The isolated adults never produced any cocoon (Bart et al. 2019). Among the pooled individuals fed with normal food, following a death (see Fig. 1), a vessel was left with only one individual from day 1492 (i.e., 49 months). We kept monitoring this vessel to assess for how long the new isolated individual continued to produce cocoons.

A dissection was made of an individual of 1996 days (66 months), kept isolated from their birth, with a weight of 4442 mg to compare with an individual from the above-mentioned breeding culture (Fig. 2).

The effect of density (i.e., number of individuals per vessel) on cocoons production was tested using Kruskal-Wallis tests because conditions were not met for parametric tests (i.e., lack of data normality and homogeneity of variances).

3 Results

3.1 Survival

After 8 years (i.e., 2920 days) of monitoring, among the 20 individuals, 5 individuals were still alive (i.e., 25%). The pooled individuals presented a better survival than the isolated ones, with 4 out of 5 individuals still alive after

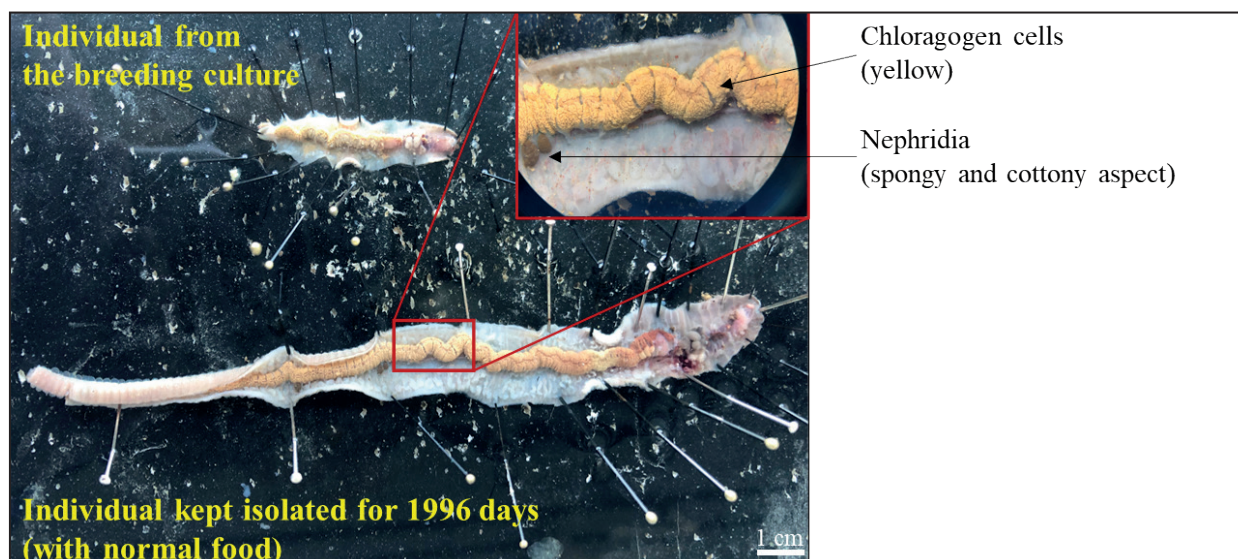


Figure 2. Picture of the dissection performed on a regular *Aporrectodea caliginosa caliginosa* (492 mg) from the breeding culture (top), and the individual isolated from birth, who never reproduced, 1996 days (i. e., 66 months) old and 4442 mg (bottom). The picture at the top right (where chloragogen cells and nephridia can be seen) is a magnified view of the red frame on the picture at the bottom.

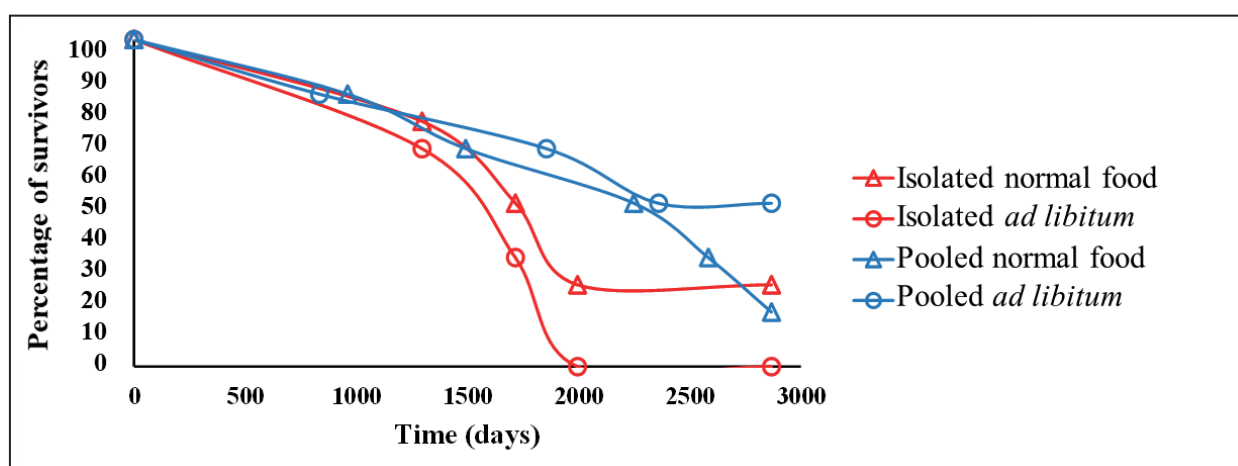


Figure 3. Percentage of *Aporrectodea caliginosa caliginosa* survivors over time (isolated $n = 4$, pooled $n = 6$).

8 years (Fig. 1 and 3). More precisely, among the 6 pooled individuals fed *ad libitum*, 3 individuals died after 27, 61 and 77 months (Fig. 1). From the 4 isolated individual fed *ad libitum*, one died at the beginning of the experiment (after 42 days) and the three others died after 33, 51 and 54 months (Fig. 1). Among the 6 pooled individuals fed with normal food, 5 individuals died after 32, 49, 74, 85 and 94 months. From the 4 isolated individuals fed with normal food, 3 died after 43, 56 and 66 months (Fig. 1).

3.2 Growth

Individuals isolated from their birth kept growing until their death in the treatment *ad libitum* while pooled earthworms stopped growing and allocated their energy

to reproduction (Fig. 1; Bart et al., 2019). Among isolated individuals fed *ad libitum*, the highest weight recorded was 9927.7 mg, which is more than 10 times the regular body mass known for *A. caliginosa* (i. e., 180–840 mg, Bouché, 1972). Comparatively, isolated individuals fed with normal food showed a stationary phase from month 46 with an average of 3500–4000 mg (Fig. 1), and the highest weight recorded for this treatment was 6184.8 mg. This underlines the close link between individual body mass and the amount of organic matter in the soil.

When pooled, earthworm individuals had a slower growth (Fig. 1). The average weight of individuals with normal food was 857 mg at 17 months, 923 mg at 34 months, 1107 mg at 50 months, and 1532 mg at 68 months. The remaining individual had a weight of 1656 mg after 75 months. When fed *ad libitum*, the average weight was

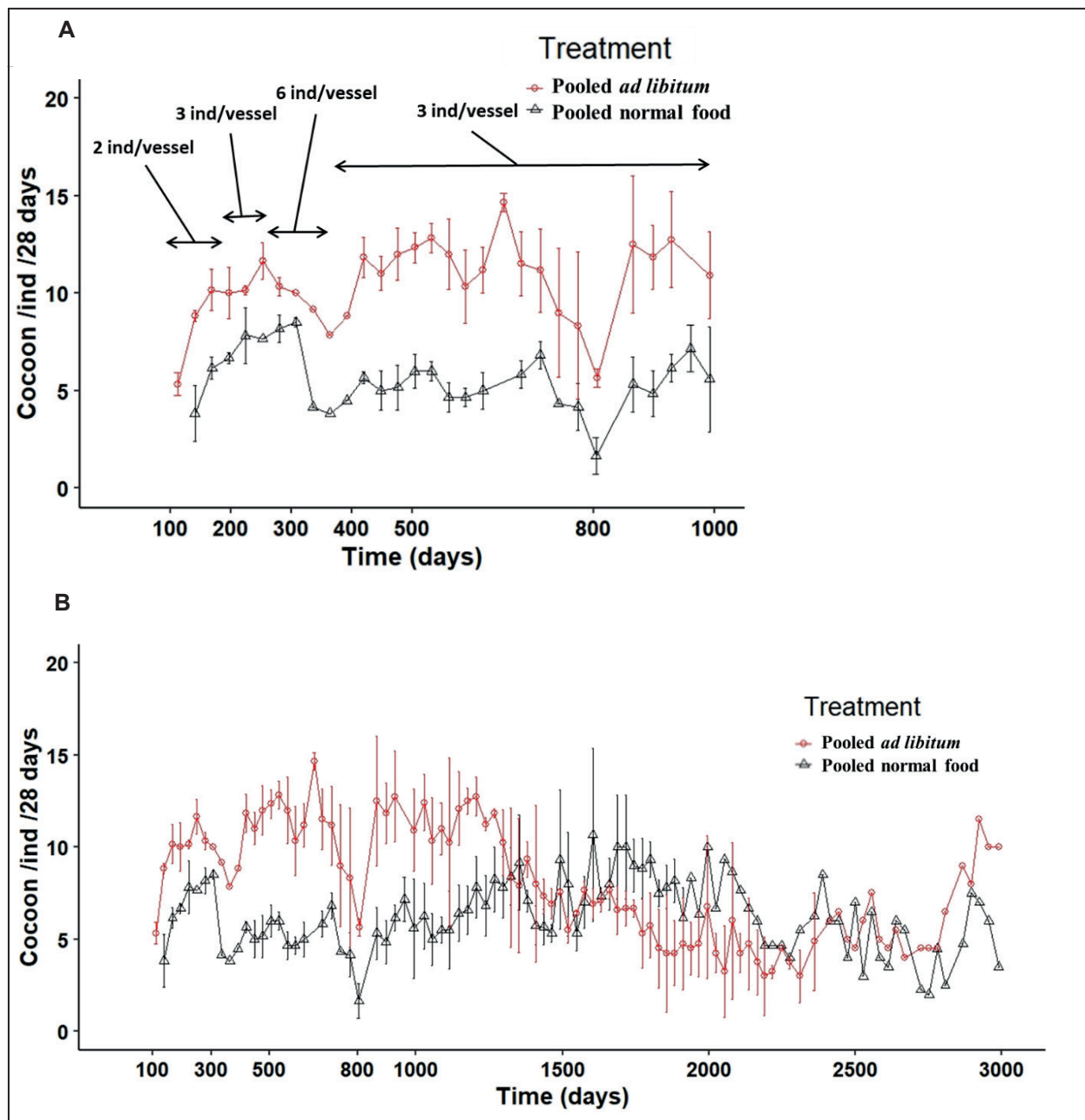


Figure 4. *Aporrectodea caliginosa caliginosa* cocoon production (mean number of cocoons ind⁻¹ 28 days⁻¹) (A) in details during the first 1000 days (i. e., 33 months), and (B) over the 2920 days (i. e., 75 months) of monitoring, at 15°C, fed with “normal” food or *ad libitum* (1 or 3 g ind⁻¹ 14 day⁻¹ of horse dung, respectively), and pooled by 2, 3 or 6 throughout the experiment. Vertical bars are standard deviations.

higher: 1596 mg at 17 months, 2227 mg at 34 months, 2371 mg at 50 months, and 2045 mg at 68 months. The average weight of the three remaining individuals after 75 months was 2071 mg $\pm$ 816 mg.

3.3 Reproduction

The individuals fed with normal food switched from juvenile to adult between day 84 and 98, while individuals

fed *ad libitum* between day 98 and 112. Once adults, the cocoon production increased during the first 84 days of the experiment in both food conditions (Fig. 4a). During the first period with variation of the earthworm density (Fig. 4a, between day 112 and 560), the cocoon production was significantly impacted by the number of individuals per vessel for the individuals fed with normal food (p -value = 0.003), but not for the individuals fed *ad libitum* (p -value = 0.06). After that period, the cocoon production was relatively stable for the individuals fed

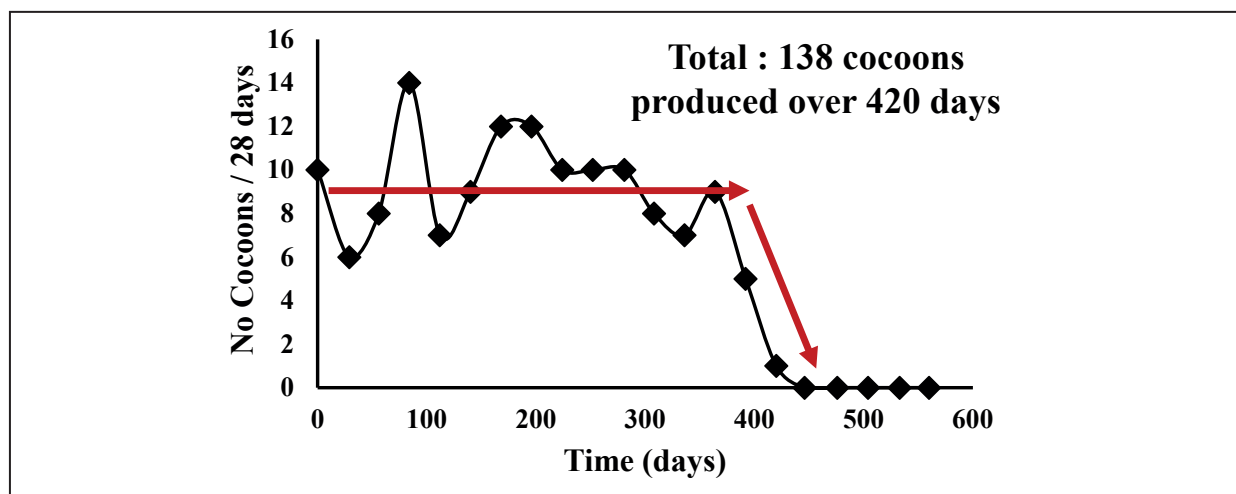


Figure 5. Cocoon production (number of cocoons 28 days⁻¹) by the individual kept alone since its isolation from other individuals. The red arrows denote the trend of quantity of cocoon produced.

with normal food with an average of 7.0 cocoons ind⁻¹ 28 days⁻¹ (Fig. 4b). The individuals fed *ad libitum* showed a relatively stable cocoon production up to 42 months with an average of 11 cocoons ind⁻¹ 28 days⁻¹ (Fig. 4b), and it continually decreased from that day, except from the 89th month when the production varied (Fig. 4b). Thus, from the beginning of the cocoon production to the 44th month, earthworms fed *ad libitum* produced more cocoons than those fed with normal food. The contrary occurred since then (Fig. 4b). After 75 months, the remaining individuals produced 3.5 cocoons ind⁻¹ 28 days⁻¹ with normal food ($n = 1$ individual) and 10 cocoons ind⁻¹ 28 days⁻¹ when fed *ad libitum* ($n = 3$ individuals) (Fig. 4b).

The individual remaining isolated after the death of the two other individuals in the same vessel continued to produce the same number of cocoons (mean of 9.2 cocoons ind⁻¹ 28 days⁻¹) for 364 days after isolation (Fig. 5). Then the production of cocoons by this individual drastically dropped, and definitely stopped after 420 days of isolation, after a total of 138 cocoons produced (Fig. 5). Unfortunately, we do not know if the produced cocoons were viable as they were not kept in favorable conditions for hatching (i. e., kept for too long in the fridge).

3.4 Morphological analysis

On both individuals i. e., the individual of 66 months, kept isolated from their birth, with a weight of 4442 mg, and the individual from the breeding culture (weight of 492 mg) (Fig. 2), the male pore was on segment 15 as described in Bouché (1972). No histological aberrations were noticed and most morphological characteristics were identical between the two specimens (e. g., 129 segments for both, clitellum on segments 27–34), except the weight

(492 mg vs 4442 mg), the diameter (0.3 cm vs 0.6 cm) and the length (8.5 cm vs 15 cm). Moreover, more chloragogen cells were found all around the intestine on the biggest individual, and nephridia had a spongy and cottony aspect (Fig. 2). Chloragogen cells are star-shaped cells in annelids involved in the storage and synthesis of glycogen and fats with excretory functions, as nephridia.

4 Discussion

A. caliginosa adult individuals are described in the literature as typically composed of 120–150 segments, with an individual body mass ranging from 200 to 1200 mg, and a body length from 60 to 85 mm (Bouché, 1972; Sims and Gerard, 1999). We here found that *A. caliginosa* individuals can weight more than 10 times their regular weight when fed *ad libitum* under laboratory conditions. Although much larger, these individuals kept the same anatomy, in particular the same location of the clitellum and number of segments, two characteristics commonly used for earthworm identification at the species level. However, our study also highlighted that the size and body mass, which are also often used for species identification, are not necessarily good indicators as they depend on the environment in which the individuals live. Based on these results, we strongly encourage scientists working on earthworms to use the number of segments and the position of the clitellum for earthworm species identification, in addition with the colour which seems to be relatively conserved between our two specimens.

A. caliginosa was described as a species with an obligatory biparental reproduction (Sims and Gerard, 1999), which is supported by our results as the individuals

isolated from their birth never produced any cocoon. However, to our knowledge, this is the first time a study highlights that following a reproduction period (mating with congeners), *A. caliginosa* is able to store the gametes and produce more than 130 cocoons during more than a year after a mating event. This ability is certainly one of the keys of the success of this species to colonize new lands (Eijsackers, 2010). Moreover, our results do not support the idea of a reproductive fatigue such as that observed for *Lumbricus terrestris* after 36–52 weeks of intensive breeding (Lowe and Butt, 2007). They rather support, for *A. caliginosa*, the idea of a global stock of cocoons potentially produced during the entire life, causing a reproduction decrease when the stock is nearly depleted.

Another original result of this study is that the pooled individuals were found to live longer than the isolated individuals. Interestingly, Shen et al. (2012) highlighted that reproduction (i.e., the removal of germ cells) increased the longevity of the nematode *Caenorhabditis elegans*. The underlying molecular mechanisms is that *germ cell removal flips a “molecular switch” that extends the life span by using components of a “developmental clock”*.

Moreover, this study allowed to highlight that the maximum lifespan of *A. caliginosa* is more than 8 years as the data acquired between June 2016 and June 2024 were used here, but five earthworms are still alive to date and keep on being monitored. Data on earthworm lifespan are scarce but they are in accordance with our study as the maximum reported lifespan for *Eisenia fetida* was close to 9 years (Mulder et al., 2007), and *Aporrectodea longa* individuals have survived 5 to 10 years in laboratory cultures (Gerard 1967). Under field conditions, this age may never be reached due to mortality related to predation or unfavourable environmental conditions (e.g., temperature, drought, contamination). Populations in the field may have only one season lifespan and spend part of their cycles in embryonic dormancy in cocoons under unfavorable conditions. An average of 1 to 2 years is reported for adults of several common species in field conditions (Lee 1985).

The pooled individuals in the treatment with normal food were close in size and individual body mass to *A. caliginosa* individuals found in the field. However, the weight and size of the isolated individuals fed *ad libitum* of our experiment are certainly never met under field conditions as congeners are generally present and because we can assume that individuals reproduce as shortly as possible after reaching maturity. Moreover, food availability changes and the soil temperature and moisture fluctuate over time in the field. When earthworms enter diapause or quiescence at dry periods, and although they can recover their initial body weight within a few days,

they can lose considerable weight during this period of inactivity (Díaz Cosin et al., 2006). It is worth noticing that in our study, animals with less food reached sexual maturity more quickly. Accelerating sexual maturity in a resource-poor environment can be a life strategy, especially for r-strategist species such as *A. caliginosa*, which allocate energy to reproduction rather than survival (Satchell, 1980; Bart et al., 2019). Another information when comparing the pooled individuals between the normal and *ad libitum* feeding conditions, is that the individual body mass is a reliable proxy of the amount of organic matter in the soil.

Once adults and if earthworms are not isolated from each other, the energy of *A. caliginosa* individuals is entirely allocated to cocoon production, which only depends on the available food amount (Bart et al., 2019, based on the first two years of this experiment). For the individuals fed with normal food, the cocoon production was significantly impacted by the earthworm density while the difference was not significant for the individuals fed *ad libitum*. This can be due to the food available in soil, which was shared by the individuals fed with normal food. The food quantity per individual thus decreased with increasing density, leading to a decrease in cocoon production. For individuals fed *ad libitum*, because the amount of food provided (horse dung) was sufficient (the food provided by the soil is negligible in this case), the food quantity per individual remained *ad libitum*. Thus, as already shown (e.g., Lowe and Butt 2002), the development of earthworm populations and in particular *A. caliginosa* is highly related to food availability and quality. Johnston et al. (2014) underlined that the understanding of how the earthworm life cycle is influenced by ecological factors, and in particular by food supply, is needed to predict the response of populations to environmental changes.

All this knowledge on earthworm biology and ecology, and in particular on life history traits of a very common earthworm species under different food and density conditions, may help to advance studies in functional ecology and ecological modelling. Functional ecology focuses on the functions that species play in the community or ecosystem in which they occur. In this branch of ecology, morphological and life history characteristics of the species are emphasized. Functional traits are properties of individuals which affect organismal performance and govern their responses to their environment (Pey et al., 2014; Violle et al., 2007). In trait-based approaches, the data produced in the present study could help for a better understanding and assessment of earthworm role (e.g. linked to the individual biomass) and performance (e.g. reproduction) in different environmental conditions. These data could also be used in life cycle modelling as some modelling approaches with *A. caliginosa* have been

proposed (Bart et al., 2020; Johnston et al., 2014, 2015). A better parameterization of models under different environmental conditions would undoubtedly lead to better predictions of population dynamics either under laboratory or field conditions. For instance, Johnston et al. (2014) simulated *A. caliginosa* population dynamics under varying field conditions, based on laboratory data. In this model, several parameters such as mass at sexual maturity (in g), maximum asymptotic mass (in g) or growth constant (in g day⁻¹) were taken from only one medium terms (several months) laboratory study dating from the 80's (i.e., Lofs-Holmin, 1983). Data produced in our study could be used in such population dynamics models to better estimate the mentioned parameters and to account for the changes in reproduction capabilities of earthworms over time under different conditions of food and stocking rate.

5 Conclusion

Through the monthly monitoring of 20 earthworm individuals during 8 years, we brought new data and insights on the life cycle (life span, reproduction, growth) of a very common earthworm species under different experimental conditions. This study allowed to highlight that *Aporrectodea caliginosa caliginosa* can live more than 8 years under laboratory conditions and can weigh more than 10 times its basic weight, depending on the presence of conspecifics and available food, individual body mass being a proxy of the food available in our experiment. Contrarily to one of our assumptions, individuals that reproduced had a longer life span than congeners kept alone. In a context where researchers are evaluated through their scientific publications, long term experiments are not necessarily fostered. However, some very basic knowledge on biology and ecology of soil animals are lacking that require regular observations and monitoring over time. This knowledge can be used in functional ecology and population dynamics modelling approaches to better understand and predict the impacts of anthropic activities on these key soil engineers.

Conflict of Interest: The authors declare that they have no conflict of interest.

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