



Life history strategies of two springtails species (Hexapoda: Collembola) from saline soils

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Abstract

Springtails are a very common, widely spread component of soil fauna that play a significant role in numerous physical, chemical, and biological processes in the soil. Therefore, it is important to understand how their evolution and demographic parameters have changed throughout time. Since salinity is a relevant condition in the soils around the World and particularly in Mexico, the major goal of the current research is to understand the life cycle strategies of two springtail species from saline soils in Mexico. The studied species are *Clavisotoma filifera* and *Brachystomella gabriellae*, both widely distributed in Mexico, but their development or life history strategies are unknown. We found from laboratory cultures that *C. filifera* had a shorter life cycle and a faster reproduction rate than *B. gabriellae*. Nevertheless, both species show the same number of developmental stages, but there are interspecific differences in their duration. Although both species continuously reproduce throughout the year, the reproductive rate is lower in the months that are associated with the dry season at the source site. Additionally, we discovered variations in both the size and number of eggs in each species. It was found that the species under study had various life strategies for growth in the same environment. *Clavisotoma filifera* shows a more *r*-focused strategy (high fecundity, numerous offspring, shorter gestation and faster maturity), *B. gabriellae* shows an opposite strategy, closer to *q* strategy, with a lower fecundity, larger eggs, fewer reproductive events and slower maturity.

Keywords Scavenging · *Clavisotoma filifera* · *Brachystomella gabriellae* · Fecundity · Mortality · Survival

Introduction

Springtails are one of the most abundant groups of arthropods in soil and leaf litter (Wolters 2001). Their principal function is organic matter fragmentation in soil systems. Their feeding habits include mainly fungi (hyphae and spores), bacteria, litter, and/or decomposing vegetal tissues (Palacios-Vargas and Gómez-Anaya 1993). Springtails show sexual and asexual reproduction, the latter characterized by parthenogenesis (Jordana et al. 1997). The clutch size can vary within and between species and ranges from about 5 to more than 150 eggs per laying (Green 1964; Vail 1965; Tully 2023). These features differ between species and between individuals, according to specific biotic and abiotic factors, and as a result of genetic variation and speciation (Sengupta et al. 2016, 2017). The most used parameters to study the life history of a species are fecundity, survival, sex ratio, age of first reproduction, resource availability, dispersal capacity, and response strategies to environmental changes (Auclerc et al. 2009; Beladjal et al. 2021). Based on

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particular organisms, all these parameters can be measured using different methodologies. Springtails are organisms suitable for laboratory observations due to their small size (0.2 to 10 mm), short life cycle (from two to seven months to complete development from egg to adult), undemanding laboratory rearing, ability to reach high population size in short time, fast capability to respond to changes in environmental conditions and ease of monitoring. Thus they are adequate to evaluate changes in their life history strategies, specifically their longevity, fecundity and mortality rates (Stam et al. 1996; Mallard et al. 2015; Lee et al. 2016; Tully 2023). The abiotic parameters involved in the life history of springtails are physical, such as temperature and humidity, chemical such as pH, pollutants accumulated by herbicides and fertilizers use, and environmental and anthropogenic disturbances, such as fires or global warming (Malmström 2012; Salmon et al. 2014; da Silva et al. 2016). In relation to the biotic factors, interactions such as competition and predation (Johnson and Wellington 1980; Thakur et al. 2017) are the main force that modify the different life history strategies in springtails (Mallard et al. 2019). Temperature and humidity are the most important parameters that can change the life history of springtails; the natural variations of these parameters can be relatively stable in tropical areas or very variable in near-polar areas (Fjellberg 1975; Hagvar 2010). To characterize the life cycle of springtails, it is crucial to understand the traits associated with their fitness, including reproductive, morphologic, physiological, and ethological traits that ensure the expansion and persistence of their populations in space and time (Lamont 1954).

Brachystomella gabrielae Najt and Palacios-Vargas, 1986, was described within material collected in Xochimilco, Mexico. This species reaches a length of 0.60 mm, and is purple with dark violet ocular plates (Najt and Palacios-Vargas 1986) (Fig. 1a). It is widely distributed in Mexico, as well as *Clavisotoma filifera* (Denis, 1931). Both species have been recorded in different ecosystems,

from tropical rain forests in Veracruz (Palacios-Vargas 2003), to *Abies* and *Quercus* forests in the State of Mexico (Cutz-Pool et al. 2010); from 2830 to 3440 m asl, and also have been recorded in Pedregal de San Ángel ecological reserve in Mexico City. In the latter location, soils are scarce and without defined horizons, but the high spatial heterogeneity with hollows allows organic matter accumulation and promotes the development of complex soil community (Castellanos-Vargas et al. 2017; Palacios-Vargas et al. 2009). *Clavisotoma filifera* is about 0.67 mm in length, with greyish-blue pigment dispersed irregularly over the whole body and somewhat more darkened head capsule, with a black eye-patch (Fig. 1b). This species has also been recorded in sand dunes in Brazil, in Tropical and Boreal biogeographic regions, and in Australia (Abrantes et al. 2010). Both species show wide salinity tolerance limits because they have been recorded in extremely saline soils (Castaño-Meneses et al. 2013, 2017). In addition, other species of those genus show high thermic tolerance (Escribano-Álvarez et al. 2022) and are easily cultured in laboratory conditions (Pérez-Velazquez pers. observ.). Since these come from the same habitat, they can show similar or different life history traits to deal with the environmental challenges. Our objective was to describe and compare the life cycle strategies of two springtail species from saline soils in Mexico, and consider that, in spite of similar environmental conditions and resources requirements, species can show differences.

Materials and methods

This study is at the initial phase of a research project on the ability of springtails species *Clavisotoma filifera* (Collembola: Isotomidae) and *Brachystomella gabrielae* (Collembola: Brachystomellidae) to inhabit saline soils.

Fig. 1 **a** Adult of *Clavisotoma filifera*. **b** Specimen from the third molt, still immature. **c** Ovipositing female of *C. filifera*



Sampling

The federal area of the ex-lake of Texcoco, Estado de México, has soils with high salt concentrations, and both species were previously recorded at the site. On October 10, 2017 two sites near Nabor Carrillo Lake (in the ex-lake of Texcoco area) were selected. Both sites showed the presence of springtails at high salt concentrations (Castaño-Meneses et al. 2013). Both sampling points (19°27'47" N—98°56'51" W and 19°27'50" N—98° 56'24" W) are located at an altitude of 2238 m a.s.l., at a distance of 1 km from each other. Along two 12 m transects with NE-SE orientation at each site, soil samples were taken at one meter distance from each other. We followed this sampling protocol to consider the conditions in the area and increase the probability of collecting the studied species and obtaining enough material to establish the cultures, according to previous studies in the area (Castaño-Meneses et al. 2013; Pérez Velázquez 2016). In total, 24 samples were taken using a soil core of 15 cm in diameter and 10 cm deep.

Specimens collection

Soil samples were processed in Berlese-Tullgren funnels for six days at room temperature. Edaphic fauna was collected in 150 ml glass bottles; the used culture medium was a 1:10 mixture of active charcoal and gypsum, using approximately one centimeter of medium and adding on it a small soil sample to maintain certain natural conditions for the organisms. *Clavisotoma filifera* and *B. gabrielae* were the only specimens kept in the glass bottles, the remaining fauna was removed. These species were the most abundant in the samples, and they were selected to obtain abundant populations during the cultures.

Cultures

Individuals of the two species were put separately in small 35 ml glass bottles, with a 0.5 cm thick culture medium layer, without soil. This initial population was kept in 16 bottles with *C. filifera* and eight bottles with *B. gabrielae* (a total of 24 small glass bottles), and these were the breeding herd used during the study. The specimens kept in each glass bottle were of different ages. The specimens were fed with bread yeast every two days and 1 to 2 ml of water was added to keep humidity. The glass bottles with cultures were maintained in an Hinotek environment chamber, model MGC-450HPY-2, at $27.5 \pm 1^\circ\text{C}$, and a circadian cycle of 12 h of light followed by 12 h of darkness and 50% relative humidity. These conditions were established as optimal, according to previous assays performed by the first author. In reviewed literature, optimal temperature for other springtail species ranges from 17.5° to 23° (Park 2007).

To find out whether our two springtail species reproduce by parthenogenesis, we carried out an initial experiment five

weeks after the first population was established, in which we isolated hatching individuals and left them to grow until maturity to see if they were capable of laying eggs without ever having met a partner. We put 15 individuals of each species separately, each one in 35 ml glass bottles with gypsum culture medium and activated charcoal. Daily observations were made in each bottle. The egg laying date was recorded to identify individuals from the same generation for future observations.

Of the newly hatched individuals, we followed the development and growth of *C. filifera* and *B. gabrielae* for two periods: March to May and July to September 2018, in order to follow the seasonality in the sampling area (rainy season: July to November; dry season: December to May), and detect if any seasonal pattern is maintained under laboratory conditions; each one with approximately 50 eggs. In previous cultures, both species were found to be parthenogenetic, as mentioned previously. After hatching, each specimen was placed in a 35 ml glass bottle with the medium mix. Humidity was maintained by adding 1 ml of water every 48 h, since condensation in the glass bottle was observed. Each individual glass bottle was examined daily. Specimens were fed with a yeast bread pellet every three days and kept in the environmental chamber under controlled conditions. Figure 2 summarizes the methodology protocol.

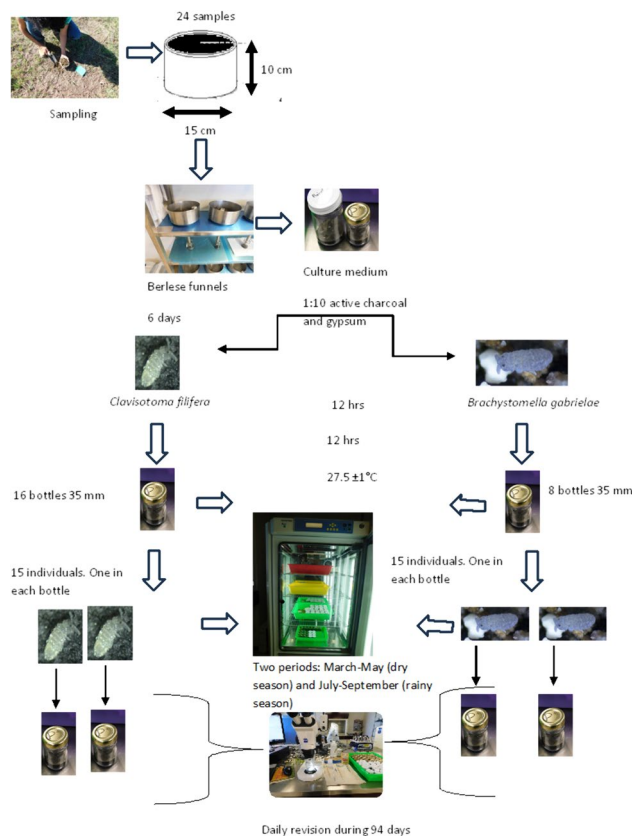


Fig. 2 Summary of the methodology used in the study

For 94 days, the individual glass bottles (each one with one springtail individual, for a total of 150) were examined every 24 h under stereomicroscope, Zeiss model Stemi 2000-C, recording molts, color, oviposition time, egg number, egg hatching time, and behavior. The observation time varied for each individual, according to its activity, 10 min on average. AxioVision Software 4.8.2SP2 (2012) was used to photograph all developmental stages and behavior. When the springtails reached the adult stage, they were put in isolated glass bottles. In addition, individual egg diameter and head width were measured. The head measures helped to determine the changes between the different juvenile stages. Measures were made with digital micrometer from pictures taken under microscope. We used an average of 30 individuals or eggs (Fig. 3). To test the effect of species and season on egg size and fecundity, an ANOVA test was performed using Statistica 9.0 software (Statsoft 2009). The average of hatching time and number of molts during the studied period by species were compared by t-test (Statsoft 2009). Hatching success was referred to as the relationship between number of eggs deposited and number of individuals hatched.

Registered data were used to produce life tables to estimate the survival rate ($l_x = n_x/n_0$), proportion of dead individuals by time Interval in each stage ($d_x = n_x/n_{x+1}$), mortality rate ($q_x = d_x/l_x$), fecundity ($m_x = Fx/nx$) and net reproductive rate ($R_0 = \sum l_x * m_x$), and generation time, that is, the period of time in which one female is replaced by another ($l_x * m_x * n_x$). Where n_x is the population size at time x , n_0 is the population size at time 0, and n_{x+1} is the population size at the next time interval.

Results

Clavisotoma filifera

Every reproductive event, which is defined as each time a female lays eggs, results in an average of 14 eggs (14 ± 6.2 ;

average \pm standard deviation (SD)) laid by each female (this species displays at least 8 reproductive events).

The hatching success was 90% (number of hatched versus the total number of eggs). Unhatched eggs changed color from hyaline white to orange, in some cases growing fungal hyphae observed inside. From March to May the reproductive events (oviposition) decreased in this species (Table 1) compared to the values obtained from July to September (Table 2).

Viable eggs have a hyaline white color at oviposition, after one day they change to dull beige. Eggs hatched 5.9 ± 0.54 days after laying. During oviposition several females tend to group the eggs, forming a clutch of more than 100 eggs. No behavior pattern for the oviposition site was observed. A few hours before the egg hatches, a line is observed on the egg, which will be the subsequent exit site of the organisms.

Newly hatched individuals show a transparent white color. After the first two molts their colour changes to light matte gray with a velvety appearance, and after five molts their color becomes dark gray (Fig. 1).

Brachystomella gabriela

This species completes its development from egg to adult in approximately 34 days. We observed 31.03 ± 1.26 molts on average during 90 days of observation; molting continues during the organisms' life. Newly hatched individuals are clear white in color. After 24 h they change to matte white and after the first two molts their colour changes to light lilac; at the fifth molt, their color is dark lilac, which persists for the remaining life cycle. This species shows an oviposition pattern in which the clutch of eggs laid by each female is well-differentiated, who tend to group them when the population density increases. An interesting behavior is that they look for pores or some holes to oviposit, and they can oviposit under small crusts of the culture medium that come off the walls and form ideal refuges for them. They can use the bottle walls to oviposit, thus making observations and

Fig. 3 Example of measuring the head width of two recently hatched springtail individuals. **a** *B. gabriela*, **b** *C. filifera*

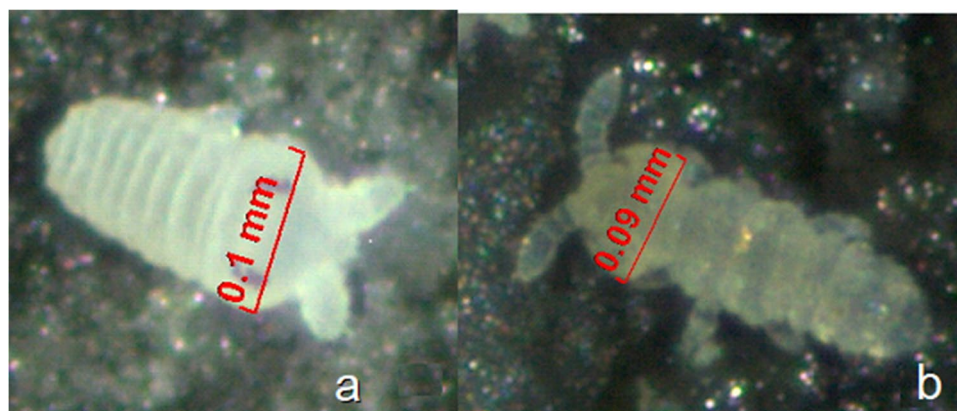


Table 1 Life table of *C. filifera*. The measured parameters of a generational cohort from its egg to adult stage, survival, mortality, and net reproduction rate are presented in the months of March to May 2019. Time starts on the day of the first hatching

Time (days)	Number of individuals (n_x)	Survivors proportion (l_x)	Dead individuals (d_x)	Mortality rate by age (q_x)	Mortality rate (%)	Fecundity (m_x)	$l_x * m_x$	$l_x * m_x * n_x$
6	129	1	11	0.085	8.527		0	0
7	118	0.915	14	0.119	11.864		0	0
9	104	0.806	0	0	0		0	0
13	104	0.806	6	0.058	5.769		0	0
16	98	0.759	3	0.031	3.061	13.04	9.906	970.823
19	95	0.736	4	0.042	4.211	11.23	8.27	785.665
29	91	0.705	11	0.121	12.088	12.05	8.5	773.535
39	80	0.620	10	0.125	12.5	13.24	8.21	656.868
49	70	0.543	8	0.114	11.429	14.06	5.91	534.062
59	62	0.481	18	0.290	29.032	12.31	4.124	366.819
69	44	0.341	12	0.273	27.273	12.09	2.793	181.444
79	32	0.248	19	0.594	59.375	11.26	2.999	89.382
89	13	0.101	0	0	0	0	0	0

Table 2 Life table of *C. filifera*. The measured parameters of a generational cohort from its egg to adult stage, survival, mortality, and net reproduction rate are presented in the months of July to September 2019. Time starts on the day of the first hatching

Time (days)	Number of individuals (n_x)	Survivors proportion (l_x)	Dead individuals (d_x)	Mortality rate by age (q_x)	Mortality rate (%)	Fecundity (m_x)	$l_x * m_x$	$l_x * m_x * n_x$
6	290	1	1.074	0.004	0.370		0	0
7	270	0.931	1.027	0.004	0.380		0	0
9	263	0.907	1.035	0.004	0.394		0	0
13	254	0.876	1.028	0.004	0.405		0	0
16	247	0.852	1.042	0.004	0.422	14.04	11.958	2953.677
19	237	0.817	1.072	0.005	0.452	13.05	10.665	2527.605
29	221	0.762	1.145	0.005	0.518	15.09	11.499	2541.416
39	193	0.666	1.135	0.006	0.588	13.75	9.151	1766.116
49	170	0.586	1.223	0.007	0.719	16.01	9.385	1595.479
59	139	0.479	1.241	0.009	0.893	15.23	7.2999	1014.686
69	112	0.386	1.231	0.011	1.099	14.07	5.434	608.600
79	91	0.314	1.338	0.015	1.471	12.31	3.863	351.514
89	68	0.234	0	0	0	0	0	0

counting difficult. Two days before oviposition, the organisms' abdomen widens, and during oviposition the abdomen shortens from the front to the back. Another characteristic behavior is that in order to molt they usually enter in some pore of the culture medium and in some cases could have difficulties getting out of the pore due to their size increase. Another molting strategy is that they adhere with the antennae to the substrate, and since the molting process starts on the dorsal side and, until the head is released, they detach from the exuvium that remains attached to the substrate.

The recently detached cuticle is white. On rare occasions, few individuals failed to detach completely from the molted exuvium, and pieces of the old cuticle remained on the organisms' body, mainly on the caudal area, causing the death of several individuals. In this species, it was also observed that when they were close to death, the cuticle looked clear and thinner, and the individual's body was swollen and seemed to contain a large amount of fluid. The organisms showing these characteristics did not survive more than 24 h.

The t test shows that hatching time is statistically different in both species ($t_{58} = 22.7, p < 0.05$), as well as the number of molts in each species ($t_{58} = 11.7, p < 0.05$).

Life cycle

Clavisotoma filifera completes its development from egg to reproductive adult in 15 days approximately (Fig. 4), under controlled temperature, humidity, and food availability. According to the cephalic capsule size average (Table 3), six stages appeared during its life cycle: egg, newly hatched, juvenile 1, juvenile 2, juvenile 3, and adult. The species has a reproductive capacity from the juvenile 3 stage. Two molts are needed to reach the juvenile 1 stage from newly hatched individual. There are three molts between juvenile 1 and juvenile 2; two molts between juvenile 2 and juvenile 3 and two more molts are needed to reach the adult stage. During the adult stage, molting continues until death. Thus, the total number of molts is indeterminate for adults, but we observed 40.51 ± 2.73 molts on average from 50 individuals during the total observation time (94 days).

A senile period was recorded in 400 individuals in total from the first generations obtained from the cohort. These organisms remained without reproduction or molts 90 days on average after the observation period (94 days). No changes were observed in their mobility, but in their coloration; despite being fed with the same food, the gray

color of the cuticle became darker than previously observed. Another relevant behavior observation was that, despite a constant supply of food, some individuals, adults, consumed part of the corpses of conspecifics within less than 24 h of their death. This scavenging behavior was not recorded frequently; it was rather rare, but was remarkable because it occurred at least 12 times during the observation period (12% of observations). The consumption of dead conspecifics was also observed by Tosi and Sartini (1983) in *Coecobrya caeca* (Schött, 1896) under laboratory conditions.

When this species molts, individuals shake and make a trembling motion as the antennae are quickly released from the cuticle, thus allowing them to move freely through the medium. Molting starts at the head, and individuals are seen to remain still for a short period before beginning to molt. The freshly removed cuticle is white, and some individuals had a few droplets of colorless and transparent liquid on their body, which eventually disappear.

Additionally, it was observed that individuals close to death exhibited clumsy movements and their abdominal segments appeared to be distended in front-caudal orientation. Occasionally, the body would also acquire a faint orange coloration before death.

During its development, *B. gabriellae* undergoes six stages (Fig. 5; Table 4): egg, newly hatched, juvenile 1, juvenile 2, juvenile 3, and adult; between each stage, there is a different number of molts. Between newly hatched and

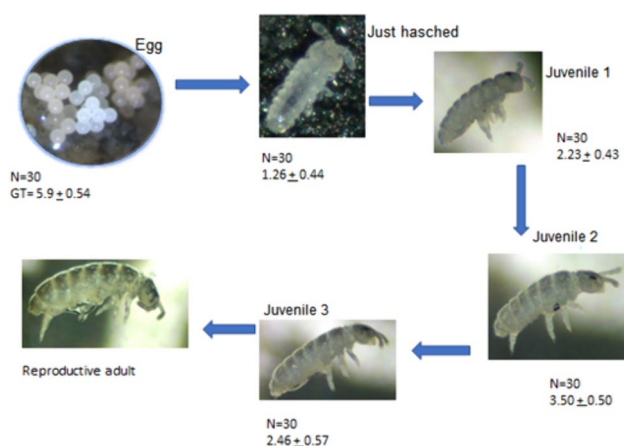


Fig. 4 *Clavisotoma filifera* life cycle. The duration of each developmental stage in days (mean \pm SD) is indicated

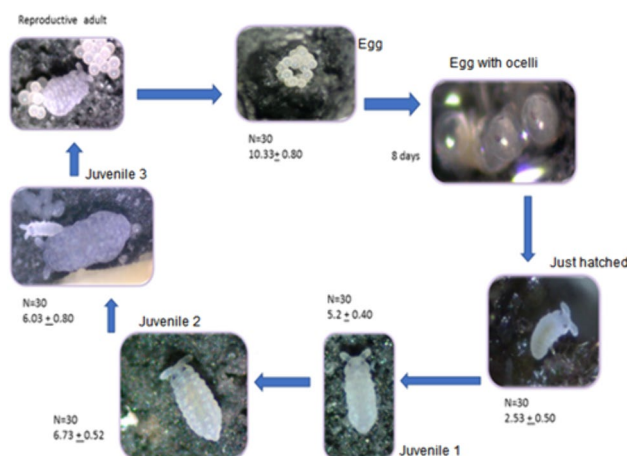


Fig. 5 Life cycle of *B. gabriellae*. The duration of each development stage in days (mean \pm SD) is indicated

Table 3 Comparison of the cephalic capsule measurements (in mm) of each stage of the life cycle of *C. filifera* and *B. gabriellae*

Stage	Just hatched	Juvenile 1	Juvenile 2	Juvenile 3	Reproductive adult
<i>C. filifera</i>	0.09 \pm 0.005	0.11 \pm 0.004	0.12 \pm 0.004	0.13 \pm 0.004	0.15 \pm 0.006
<i>B. gabriellae</i>	0.114 \pm 0.005	0.143 \pm 0.006	0.170 \pm 0.006	0.202 \pm 0.006	0.220 \pm 0.01

Table 4 Life table of *B. gabrielae*. The measured parameters of a generational cohort from its egg to adult stage, survival, mortality, and net reproduction rate are presented in the months of March to May 2019. Time starts on the day of the first hatching

Time (days)	Number of individuals (nx)	Survivors proportion (lx)	Dead individuals (dx)	Mortality rate by age (qx)	Mortality rate (%)	Fecundity (mx)	lx * mx	lx*mx*nx
11	118	1	17	0.144	14.407		0	0
14	101	0.856	7	0.069	6.931		0	0
20	94	0.797	3	0.032	3.191		0	0
27	91	0.771	7	0.077	7.692		0	0
34	84	0.712	8	0.095	9.524		0	0
40	76	0.644	8	0.105	10.526	11.31	7.284	553.615
50	68	0.576	8	0.118	11.765	12.01	6.921	470.629
60	60	0.508	14	0.233	23.333	11.42	5.807	348.407
70	46	0.389	7	0.152	15.217	10.78	4.202	193.309
80	39	0.331	16	0.410	41.026	10.03	3.315	129.285
90	23	0.195	23	1	100	0	0	0

Table 5 Life table of *B. gabrielae*. The measured parameters of a generational cohort from its egg to adult stage, survival, mortality, and net reproduction rate are presented in the months of July to September 2019. Time starts on the day of the first hatching

Time (days)	Number of individuals (nx)	Survivors proportion (lx)	Dead individuals (dx)	Mortality rate by age (qx)	Mortality rate (%)	Fecundity (mx)	lx * mx	lx*mx*nx
11	274	1	25	0.091	9.124	0	0	0
14	249	0.909	6	0.024	2.409	0	0	0
20	243	0.887	11	0.045	4.527	0	0	0
27	232	0.847	3	0.013	1.293	0	0	0
34	229	0.836	5	0.022	2.183	0	9.017	0
40	224	0.818	26	0.116	11.607	11.03	8.852	2019.859
50	198	0.723	26	0.131	13.131	12.25	7.313	1752.734
60	172	0.628	32	0.186	18.605	11.65	6.668	1257.859
70	140	0.511	41	0.293	29.286	13.05	4.488	933.504
80	99	0.361	39	0.394	39.394	12.42	0	444.264
90	60	0.219	60	1	100	0	0	0

juvenile 1 there are two molts; between juvenile 1 and juvenile 2 four molts occur; between juvenile 2 and juvenile 3 there are five molts; and between juvenile 3 and adult, four molts appear. When the reproduction process starts, molting continues during the organism’s entire life span. The eggs have a hyaline white color, and after a day the color becomes brighter. The average number of eggs for each reproductive event is 11.31 ± 3.51 by a female.

In *B. gabrielae* from two cohorts (Tables 4 and 5), one from the rainy season and one from the dry season, a higher mortality rate than in *C. filifera* was observed during hatching.

Eggs

The mean number of eggs laid per week by *B. gabrielae* is lower than in *C. filifera*, but eggs are larger in size (Table 6). Significant interspecific differences were found in the egg

size (ANOVA: $F_{1,117} = 11.91, p < 0.0005$), but season had no effect (ANOVA: $F_{1,117} = 0.01, p > 0.05$).

Table 6 Comparison of four life history parameters of *C. filifera* and *B. gabrielae* species under controlled conditions. Values represent means \pm SD

Species	<i>C. filifera</i>	<i>B. gabrielae</i>
Fecundity	14.04 + 6.2	11.31 + 3.51
Hatching time (days)	6	11
Number of molts in 90 days	40.51 + 2.73	31.03 + 3.51
Size of eggs (mm)	0.13 + 0.04	0.14 + 0.01
March–May net reproduction rate	49.1368	27.5295
July–September net reproductive rate	36.3379	69.2554
March–May mortality rate	11.864	9.523
July–September mortality rate	0.404	9.124

Net reproductive rate

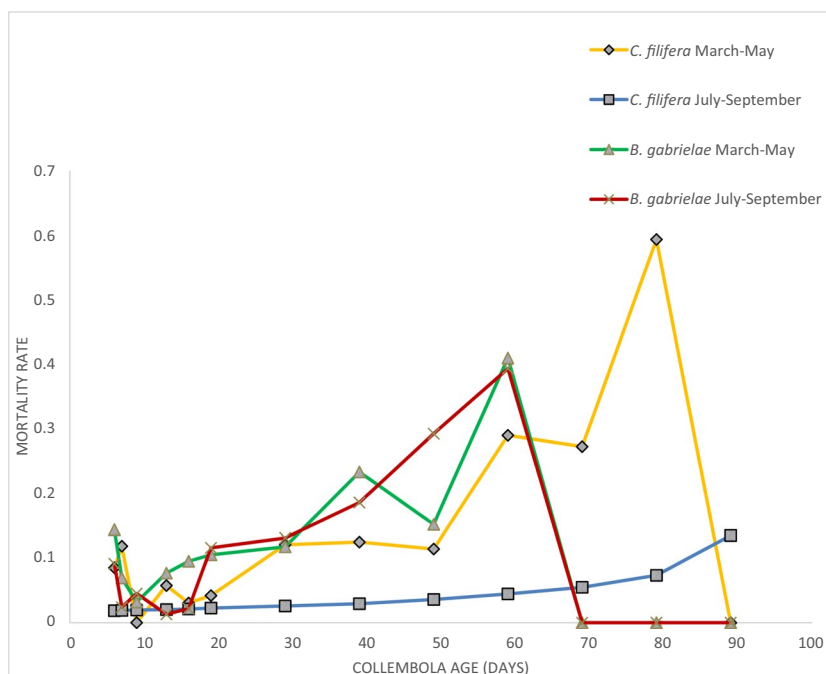
When analyzing the measured parameters of the life history of *C. filifera* from a cohort (Tables 1 and 2), we found that under controlled conditions the net reproductive rate (R_0) increased from July to September ($R_0 = 69.25$) which corresponded to the rainy season in the sampling site and was lower in March to May ($R_0 = 49.13$), which was the dry period in the sampling site. We also observed that there was less survival during the change from egg to newly hatched individuals and to juvenile 1.

The net reproduction rate of *B. gabriellae* showed lower values than *C. filifera*, but was also higher in rainy ($R_0 = 36.33$) season than in the dry season ($R_0 = 27.52$). Despite the difference, the reproduction was maintained throughout the year. Apparently, in the population maintained in culture there was a synchronization with the seasonal changes present in the sampling site. The ANOVA results show there are differences in fecundity of both species ($F_{1,32} = 7.23$, $p < 0.05$).

Survival and mortality rates

Regarding the survival and the mortality rate curves throughout the 90–94 days of observation of both species, it was recorded that mortality was higher during the first juvenile stages (Fig. 6), while pre-adults and adults had a greater survival rate (Fig. 7). Mortality in adults in both species showed an increment from day 55, and all organism died on day 90 (*B. gabriellae*) or 94 (*C. filifera*).

Fig. 6 Mortality rate of *C. filifera* and *B. gabriellae*. A higher number of deaths is observed during the first stages in both species and in both observation periods, rainy (July–September) and dry (March–May)



Discussion

Life cycles

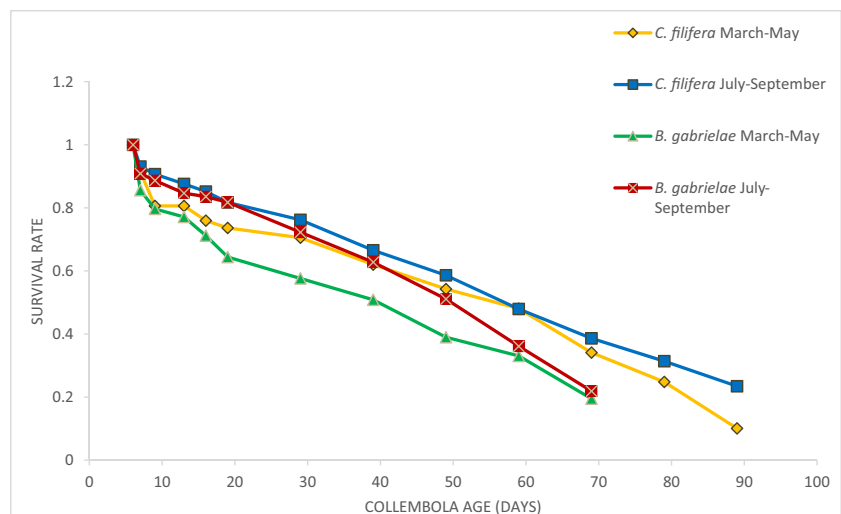
Comparison of the life strategies of two Collembola species living in similar conditions reveals that there are differences. Eggs laid by *B. gabriellae* are larger in size compared with those of *C. filifera*, and the first species shows a lower number of molts during the same observation period, which suggests that in *B. gabriellae* resources are invested mainly in egg quality. The hatching time of both springtail species also differs, being shorter for *C. filifera*, with a net reproductive rate twice that of *B. gabriellae*.

As mentioned, in *C. filifera* we observed a senile period, with the cessation of the reproduction and molt. This is an interesting discovery as in Collembola there are records of this phenomenon only in *Folsomia candida* Willem, 1902 (Tully and Lambert 2011). The findings support the existence of post-reproductive lifespan in springtails that is very rare in invertebrates well as vertebrates, except for killer whales, humans, and other primates (Tully and Lambert 2011).

Behavioral differences

Scavenging and cannibalistic behavior as observed in *C. filifera* has been recorded in several other springtail species in laboratory colonies. For example, in *Onychiurus* sp. and *Hypogastrura* sp. events of oophagy, cannibalism, and oviposition interference have been recorded as possible consequences of overcrowding and high population density

Fig. 7 Survival rate of *C. filifera* and *B. gabrielae*. Survival is greater during the rainy season (July–September) than in the dry season (March–May) for both species



(Longstaff 1976). In this context, it is important to mention that *B. gabrielae* shows two oophagy events, possibly also attributed to high population density in the colony. Population density has a strong effect on decreasing reproductive events (Longstaff 1977). Although species such as *Folsomia candida* show no changes in their reproductive behavior or in their rate of food exploitation as long as they have constant food supply (Usher et al. 1971). This could be similar for both *C. filifera* and *B. gabrielae*, since their feeding and reproduction were constant regardless of the density reached in the breeding herd culture, despite the mentioned cases. In all cases, the decline of reproduction is also related to the growth and senescence of the organisms.

Comparison with other known springtail species under laboratory conditions

One of the first springtails species whose life history was known is *Gomphiocephalus hodgsoni* Carpenter, 1908 (Hypogastruridae), in addition to its population dynamics under natural conditions in an extreme freezing-thaw habitat (Peterson 1971). *Cryptopygus antarcticus* Willem, 1901 is another species that also has been extensively studied. Both springtails are known to survive the Antarctic environment with a non-feeding period, their reproduction is restricted to the year's only season with favorable conditions (Worland and Convey 2008; Hertzberg et al. 2000), and they live as adults during the coldest season of the year. Thus, they belong to the group of species that complete their reproduction and development between spring and autumn to survive the adverse winter as adults (Materna 2002). In this sense, springtails from places with marked rainy and dry seasons, but not extreme conditions such as those mentioned above, decrease their reproductive rate without reaching zero and remain present throughout the year, maintaining their activities and interactions in the soils.

The reproductive cost can increase the mortality, since the increase in these events demands more energy that is usually subtracted from the physiological processes necessary for survival (Johansson et al. 2018). For example, it is known that the gut is partially lost with molting (Humbert 1979), so a species such as *C. filifera*, with a greater number of molts during its life, allocates a significant part of its energy to this process.

The observations of specimens of *C. filifera* close to death (clumsy movements, abdominal segments distended and faint orange coloration) are reminding of the “smurf” phenotype in *Drosophila melanogaster* PGC-1 homolog (*dPGC-1/spargel*) (Rera et al. 2011), and suggest that the increase of intestinal permeability is an important event in the aging process in a range of species (Dambroise et al. 2016) and probably is also present in Collembola.

Due to the small size and lack of information about patterns in the populations of soil arthropods (Athias-Binche 1989), observations under laboratory conditions are useful to improve the knowledge of soil arthropod populations and soil ecology, since under natural conditions the interactions with other organisms, particularly predators, can be one of the main important forces regulating their population size (Ferguson and Joly 2002). Other important interaction is competition as a result of the activities and symmetric requirements, not only between different springtails species but also with other edaphic groups such as oribatid mites (Ponge 1999). Models have been proposed describing the energy cost and egg's vulnerability in soil arthropods since they are exposed to biotic and abiotic factors that reduce their chances of survival, which is difficult to investigate in the field due to the restrictions inherent to their nature (Johnson et al. 2007). For example, the drought sensitivity of *Orchesella cincta* (L., 1758) (Verhoef 1977) causes a decrease in population survival. In contrast, *Entomobrya nivalis* (L., 1758) can show resistance to drought resulting

in considerable population densities despite this condition (Verhoef and Van Selm 1983). The studied species were obtained from a naturally saline soil in an area with a typical dry season during which their survival could be threatened. Under controlled conditions, they can possibly maintain their reproduction throughout the year, showing seasonal declines that may be related to the strategy they use in their natural environment. This strategy appears to be modulated by the activity of genes responsible for its functioning being maintained in the laboratory at least in the short-term. If such gene expression will be reverted after long-term laboratory culture remains to be investigated (Park 2007).

Temperature fluctuations throughout the year in locations with well-defined seasons tend to be buffered at community level, as populations decline, but in general springtail densities do not drop dramatically (Wolters 1998). *Orchesella cincta*, for example, under natural conditions does not feed in periods of drought and undergoes periods of starvation, followed by reproductive phases, but it molts even with an empty intestine and allocates its energy to growth and not to reproduction (Joosse and Testerink 1977). Other species, such as *Xenylla brevispina* Kinoshita, 1916 distributed in Sino-Japanese biogeographic region (Bellinger et al. 1996–2003), migrates to trees and the ground and has a single reproductive event per year (univoltine), during spring, and is known to live for more than three years (Itoh 1991). This is contrary to the studied species which have a shorter and faster life cycle, possibly linked to the fact that the conditions are acceptable throughout the year and that they do not have the need to resort to this type of strategy.

In relation to eggs, these are known to absorb water from the environment and can resist drought conditions, similar to the juvenile stages (Holmstrup 2019; Guimaraes et al. 2019). In the case of *B. gabriellae* the eggs' larger size may be due to a higher content of water that it is absorbed from the saturated surrounding environment, which would help it to resist lack of water in the natural environment. It is known that in forests with litter accumulation, despite the marked season, there is a higher proportion of the different stages of springtails (Kaczmarek 1977), probably related to strategies such as those of *B. gabriellae*, which oviposit in sites that offer some type of shelter. This occurs at the micro-habitat level.

Another limiting factor is the presence of pollutants, which can modify survival patterns and life history parameters under natural conditions (Posthuma et al. 1993). For example, soil cadmium concentration can reduce the populations of some mites and springtails (Van Stralen et al. 1989). The studied species come from soils with high salt concentrations, which can act as a pollutant, but both species seem to be adapted to these conditions since they maintain reproduction and growth during different seasons of the year. Tully and Ferrière (2008) have recorded that *F. candida* shows phenotypic plasticity expressed in an egg size

variation and in energy used in reproduction, with wide variations in different populations subjected to differences in the availability of food and space. Thus, we can expect similar patterns in other springtails populations.

Our results show two life strategies in the studied springtails. Although environmental conditions are the same for both species, both under natural and laboratory conditions, it was observed that *C. filifera* and *B. gabriellae* show fast-slow dynamics according to Del Giudice (2020), since their life history traits are contrasting. While *C. filifera* shows a strategy more *r*-focused strategy (high fecundity, numerous offspring, shorter gestation, and a faster maturity), *B. gabriellae* shows an opposite strategy, with a lower fecundity, larger eggs, fewer reproductive events, and a longer maturity. In addition, *B. gabriellae* has parental care with its eggs, by looking for specific places to lay the clutches, either in pores or under the remains of the culture medium. Nevertheless, *C. filifera* can provide suitable conditions for eggs by clustering them; the observations show random selection of places. The works of Sengupta et al. (2016, 2017) on different populations of *F. quadriculata* and their response to temperature variations, with differences in the number and size of eggs, depending on the location where they live, is another evidence of how the fast-slow continuum occurs in different environments. Thus, life history traits in springtails are linked to seasonality, but are also regulated by macroclimate, microhabitat and microenvironment.

Conclusions

Springtails can use different life history strategies to resolve challenges caused by the environmental conditions of the place where they live. These strategies are related to the phenotypic plasticity of the species. In the case *C. filifera* and *B. gabriellae* in this study, in the dry season, even under laboratory conditions, their reproduction rate decreases with respect to the rainy season and, in general, they show contrasting life history traits, but both reflect their adaptability to the environment. Despite both species being placed under similar, controlled, and constant laboratory conditions, these life history strategies are preserved as part of their adaptation over time to the environmental conditions from which they were sampled, and differences can reduce the competition between them.

Since both species are cosmopolites, the study of populations from other environments can be useful to recognize general patterns and if there are differences in their life history traits.

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Declarations

Conflicts of interest/Competing interests The authors have no conflicts of interest to declare.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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