



Temperature-dependent trade-offs in maternal investments: An experimental test with two closely related soil microarthropods

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ABSTRACT

Organisms face trade-offs in their reproductive investment due to energetic constraints. Yet, little is known about how such investments may change at different temperatures, and particularly so in soil invertebrate organisms. Here, we studied two Collembola species (*Folsomia candida* and *Proisotoma minuta*) using a long term (several generations) temperature incubation experiment (separately at 15 and 20 °C) to investigate how egg size and egg numbers and the trade-off between the two are affected in two temperature regimes. Both species are known to grow at these temperatures, but the variation in their reproductive strategies are little known. Our results show that egg sizes of *F. candida* were larger in colder temperature whereas no such patterns were found in *P. minuta*. By contrast, we found no effect of the two temperatures on egg numbers (per clutch) in any of the species. Moreover, we observed a negative correlation (indication of a potential trade-off) between egg size and egg numbers (per clutch) at colder temperature in *F. candida*, which disappeared in warmer temperature in the same species. No such trade-offs were found in *P. minuta*. Our results highlight that temperature effects on maternal investments are both trait- and species-specific, particularly when Collembola species are within their optimal thermal niches.

1. Introduction

Life-history traits, such as survival and reproduction, are fundamental to the biology of species and allow making predictions on species fitness in a given environment. Reproduction in general is related to high energetic costs for the female individuals, given that resources are often limited [1,2]. As a result, energetic investments to a given reproductive trait could lead to reduced investments in another reproductive trait [3–5]. Indeed, such life history trade-offs in organisms are dependent on energy availability in a given environment that subsequently determines their reproductive success [5]. For instance, oviparous females can increase their reproductive success in multiple ways, such as by investing in egg number or in egg size (or mass) or in egg care [6]. Female individuals are often unable to increase the clutch size (i.e., the number of eggs in a single egg laying event) without reducing the amount of resource investment in each egg [7]. Accordingly, previous studies have already shown that females generally by producing larger clutches, also produce smaller or lighter eggs and vice-versa [8,9].

However, we still know little whether in constant resource supply, other environmental variables, such as temperature, could also affect maternal investments and thereby result into trade-offs among reproductive traits in ectothermic organisms [8]. This knowledge gap is crucial to address given that climate change-induced temperature rise has often been associated to physiological adjustments in ectotherms [10,11], which impact life history traits and fitness of organisms [12, 13].

Temperature is one of the most important environmental variables determining physiological adjustments in ectothermic organisms [14–18]. Many studies have shown that higher temperature favours smaller body sized ectotherms due to their lower metabolic demands than larger ones [16,19,20]. Moreover, ectotherms can also reduce their body size at higher temperature to adjust their metabolic demands [10, 19,21]. Indeed, for such phenotypic plasticity to be true, organism's investments to certain traits need to change over multiple generations at higher temperature. To test this, we examine here how investment in two reproductive traits (egg size and egg number) changes in two soil

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microarthropod species that were kept at two different temperatures for several generations.

Within soil microarthropods, Collembola are among the most important taxonomic groups given their high density and diversity, and due to their important roles in organic matter decomposition [22–26]. Collembola further are an important component of soil food webs as they consume a wide range of soil microorganisms (e.g., fungi) and are also consumed by a number of predators [26,27]. Warming can alter the physiology of Collembola, such as through changes in their body size [28], with potential implications for ecosystem functions and stability [29]. Body size shifts among Collembola species may also vary depending on their ecology, such as their feeding habit or depending on their habitat conditions, as well as depending on biotic interactions, such as competition [21,30,31]. For instance, a previous study [21] found that the Collembola species *Folsomia candida* decreased in body size with increasing temperature, whereas such reduction in body size was not detected in *Proisotoma minuta*. The same study then showed that the species that decreased in body size at higher temperature outperformed the species unable to shift in body size, indicating ecological consequences of such body size shifts [21]. However, this study could not demonstrate whether body size reduction in *F. candida* was due to ecological filtering (one species favoured over the other) or was it due to differences in phenotypic plasticity among individuals of different species [21]. Another study in fact did suggest temperature-induced phenotypic plasticity in reproductive traits in *Orchesella cincta* - a Collembola commonly found in temperate forests [14]. This study showed that *Orchesella cincta* eggs were larger in colder temperature, and that further determined juvenile resistance and survival at low temperature [14]. Moreover, temperature-induced shifts in egg size in Collembola could also lead to life-history trade-offs. For instance, in terms of reproductive investments, a trade-off between reproduction and growth in *O. cincta* was reported [32]. Another study in the Collembola species *F. candida* showed a trade-off between fecundity and survival [33]. Given the evidence of such potential trade-offs in reproductive traits in Collembola and their warming-induced physiological adjustments, we suspect that temperature can also alter reproductive investments in Collembola.

Here we investigated how temperature differences affect the egg size-egg number relationship in two Collembola species, *Folsomia*

candida (Willem) and *Proisotoma minuta* (Tullberg), which were grown at two different temperatures (15 °C and 20 °C) for several generations. While studies have shown that both species perform well at 15 °C and 20 °C [21,34], little is known about their life history strategies at these temperatures. These species are shown to co-occur in the soil subsurface (hemi-edaphic) [35], and can compete for similar food resources [21, 36]. We measured the number of eggs per clutch and the egg size of both species at 15 °C and 20 °C. We hypothesize that the egg size should decrease with increasing temperature, however, this may only be true for *F. candida* as observed in a previous study in terms of adult mean body size [21]. Secondly, we hypothesize that there should be a negative correlation (as an indication of a potential trade-off) between the egg size and the number of eggs (per clutch) in both Collembola species because of warming-induced physiological adjustments.

2. Methods

2.1. Model organisms

Both of our model Collembola species belong to family Isotomidae. *Folsomia candida* adults have lengths ranging from 1.5 to 3 mm and show a lighter whitish colour, whereas the body length of adult *Proisotoma minuta* ranges from 0.60 to 1.50 mm and are more greyish in colour [37] (Fig. 1). *Folsomia candida* is mainly parthenogenetic [33,38], whereas *P. minuta* only reproduces sexually [35]. The founding population of *F. candida* was collected from forest soil near Berlin, Germany, and has been cultured at the Aarhus University since 1992 at 20 °C. *Proisotoma minuta* was collected in 2008 from heathland near Roskilde, Denmark, and has since been cultured at the Aarhus University also at 20 °C. In 2020, we started a new batch of cultures obtained from the Aarhus University at the University of Bern, Switzerland, and started rearing them at two different constant temperatures (no light to mimic soil sub-surface condition): 15 °C and 20 °C. Individuals of two species added to both temperatures were randomly chosen from the cultures from the Aarhus University. After seven months of rearing at 15 °C and 20 °C, we began the examination of their reproductive traits.

Usually, the generation time (from egg to adult stage) of the two species is about 3–5 weeks depending on temperature [21,37], which makes our rearing period of seven months adequate to capture several



Fig. 1. A graphical illustration of two species used in this study; with adults of *Folsomia candida* on the top panel and *Proisotoma minuta* on the bottom panel. We show two examples of clutches for each species. A closer view of egg shows how their diameters were estimated as a proxy of egg size measurement. Collembola adult pictures were taken from a KEYENCE digital microscope (VHX-970F, KEYENCE Corp., Japan). Egg pictures were taken from a Leica stereo microscope (Leica S9, Leica Microsystems, Germany).

generations in both species. Both species were reared on a mixture of plaster of Paris and charcoal substrate (ratio of 8:1) in Petri dishes (100 mm × 15 mm). The animals were fed on a weekly basis for seven months with dry yeast, and individuals were transferred to another Petri dish in such a way that populations were kept in the range of 300–500 individuals per Petri dish. The surface on the Petri dishes was kept moist by rewetting whenever necessary to avoid desiccation in collembolan individuals.

2.2. Experimental design

From populations of both species at two temperatures, we randomly took 20 adult individuals per experimental unit from both temperatures for our reproductive trait measurement. Previous studies have shown that starting density of 20 individuals of both species increase their population size over time indicating weaker competition [21,34]. Adult individuals within the species were carefully selected for comparable body size to minimize any bias in their egg size and egg number production. For example, *F. candida* adults were between 2.30 mm and 2.50 mm in their body length (measured from their head to tail) for both temperature regimes. The adult body size at the start for *P. minuta* ranged between 1.20 mm and 1.50 mm in body length in both temperature regimes. In total, Petri dish (similar to those used for rearing) containing 20 adults were replicated four times per species per temperature, and we monitored eggs for three weeks after the addition of adults at 15 °C and 20 °C.

Egg size and egg numbers were estimated using a Leica S9i microscope (Leica Microsystems, Germany). We also counted the number of clutches per Petri dish and expressed the number of eggs per clutch (Table 1). Importantly, we only counted freshly laid eggs for which we monitored each Petri dish 3–4 days per week. Freshly laid eggs were removed from the Petri dishes after they were counted. In total, we counted 3718 eggs (1369 eggs of *F. candida* and 2349 eggs of *P. minuta*) over the three-week period of egg monitoring from the same adults. To get an average egg size per unit clutch, we randomly measured 20% of the counted eggs per clutch (magnification in the range of 40x–55x) by using the LASX software Leica application suite (version 3.0.14). Egg size was measured as egg diameter (Fig. 1).

2.3. Data analysis

We conducted all our statistical analysis using the R software version 4.1.0 [39]. Given that we had multiple measurements of eggs from the same Petri dish, we ran mixed-effects models using the Petri dish as random intercept, whereas temperature was used as the fixed effect. Mixed-effects models were run using the lme4 package [40] and the lmerTest package [41] was used to obtain the statistical significance of our mixed-effects models using the Satterthwaite degree of freedom approximation. We log-transformed the egg number and egg size data to meet the linear model assumptions. Linear model diagnostics were carried out in the performance package [42]. Statistical tests were run separately for the two species. Effect size of each mixed-effect model was determined using partial eta-squared with the effect size package [43]. We finally tested the trade-off between egg number (log-scaled) and egg size (log-scaled) using Model II regression method with ranged major

axis (RMA) regression. RMA regressions are recommended over ordinary least square regressions when two variables are random, and differ in dimensions, which were the cases with egg size and egg number data in our study [44]. RMA regressions were performed using the lmodel2 package [45]. All figures were drawn using the ggplot2 package [46].

3. Results

3.1. Average egg size and egg numbers

Our results show a significantly smaller average egg size at 20 °C in *F. candida* than those obtained from 15 °C ($F_{1,6.80} = 6.28$, p -value = 0.04, $\text{partial-}\eta^2 = 0.48$, Fig. 2A). By contrast, we did not find any significant differences in average egg size between the two temperatures in *P. minuta* ($F_{1,6.38} = 0.19$, p -value = 0.19, $\text{partial-}\eta^2 = 0.03$, Fig. 2B). The egg number (per clutch) did not significantly differ in *F. candida* ($F_{1,5.34} = 1.20$, p -value = 0.31, $\text{partial-}\eta^2 = 0.18$) nor in *P. minuta* ($F_{1,4.26} = 3.85$, p -value = 0.11, $\text{partial-}\eta^2 = 0.47$) between the two temperatures (Fig. 3).

3.2. Trade-offs between egg number and egg size

Reduced major axis regression showed a significant negative relationship between egg size and egg number at the lower incubation temperature in *F. candida* (intercept = 5.38, slope = -0.13 , p -value = 0.03, Fig. 4A). By contrast, we did not find any significant relationship between those two traits in the warmer temperature (intercept = 5.02, slope = -0.04 , p -value = 0.29, Fig. 4A) in *F. candida*. Finally, we also found no relationship between egg number and egg size in cold (intercept = 4.98, slope = -0.04 , p -value = 0.29, Fig. 4A) and in warm (intercept = 5.01, slope = -0.05 , p -value = 0.33, Fig. 4A) incubation temperatures in *P. minuta* (Fig. 4B).

4. Discussion

Our results showed a significantly larger average egg size at colder temperature (15 °C) compared to warmer temperature (20 °C), but only so in *F. candida*, which support our first hypothesis. Furthermore, our results confirm a negative relationship between egg size and egg numbers in *F. candida* indicating a trade-off between two crucial reproductive traits, but only at the colder temperature (15 °C) where egg sizes were relatively larger. Since we did not find any such trade-off at both temperatures in *P. minuta*, our second hypothesis was only partly confirmed. These results indicate that reproductive traits (egg size and number of eggs) in *P. minuta* within their optimal thermal ranges may not be thermally responsive. Our results accordingly suggest that thermal responsiveness of reproductive strategies is both trait- and species-specific.

Larger eggs at colder temperature corresponds with previous findings in the Collembola species *O. cincta*, where eggs laid at 16 °C were larger and heavier compared to eggs laid at 20 °C [14]. Among several possible explanations for the decrease of egg size in *F. candida*, we suspect that it may principally be driven by metabolic constraints [47]. As body temperature of ectotherms more or less mirrors the ambient temperature, their metabolic rate depends on the temperature of the environment [48]. As environmental temperatures increase, the metabolic rates increase, which make ectotherms consume more energy. At some point, the energy uptake of an organism is not able to compensate for the energy loss at the higher metabolism, which is why egg size might have decreased in *F. candida* as an energy compensation strategy. Given that in one of our previous studies, we reported the same species *F. candida* to decrease in its body size with increasing temperature [21], we speculate that this could likely arise from the production of smaller eggs at warmer temperatures. The decrease in egg size at higher temperature in *F. candida* partly confirms that temperature-induced reduction in body size can be a result of phenotypic plasticity, and not only due to

Table 1

Species-specific number of clutches and the average number of eggs (\pm standard error) per clutch at 15 °C and 20 °C during three weeks of observations.

Species	Temperature (°C)	Total eggs	Total number of clutches	Average number of eggs per clutch
<i>Folsomia candida</i>	15	771	28	38 \pm 8.48
	20	598	15	78 \pm 10.11
<i>Proisotoma minuta</i>	15	1178	31	28 \pm 6.44
	20	1171	15	40 \pm 20.82

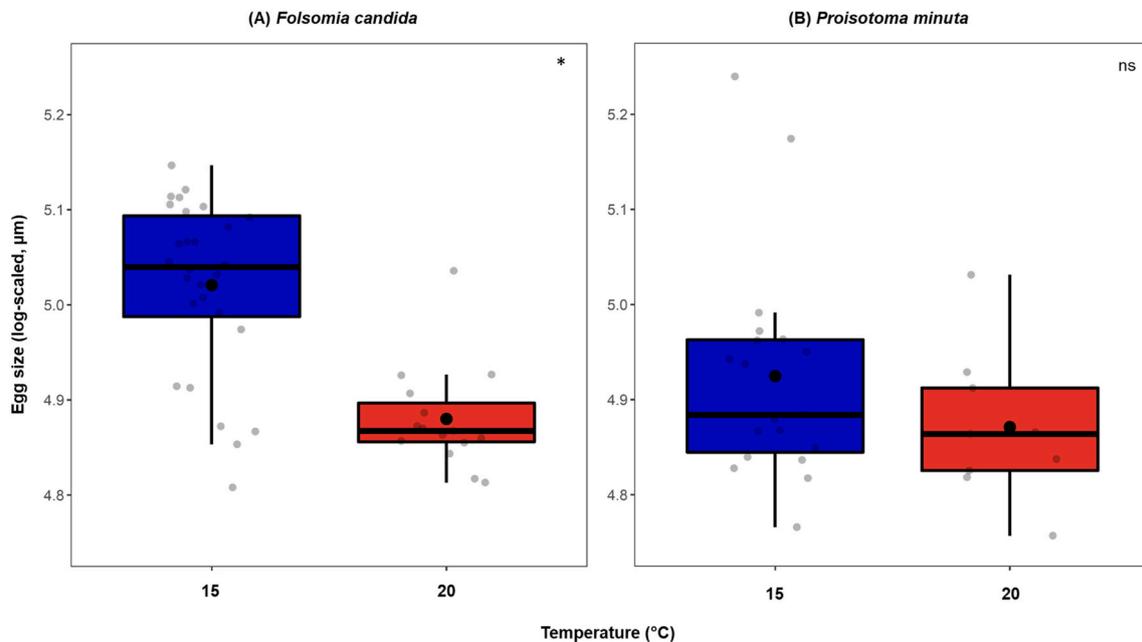


Fig. 2. Boxplots showing the difference in average egg size (log-scaled) in relation to the incubation temperature for two Collembola species. Raw data are shown as jittered points (in gray) whereas mean values are shown as black filled points. *: p-value < 0.05, ns: p-value > 0.05. Untransformed data - *F. candida*: 15 °C (mean \pm s.d. = 152.12 \pm 13.37, n = 28, median = 154.42) and 20 °C (mean \pm s.d. = 131.83 \pm 7.45, n = 15, median = 130); *P. minuta*: 15 °C (mean \pm s.d. = 126.74 \pm 20.75, n = 31, median = 126.05) and 20 °C (mean \pm s.d. = 121.01 \pm 15.50, n = 15, median = 123.77).

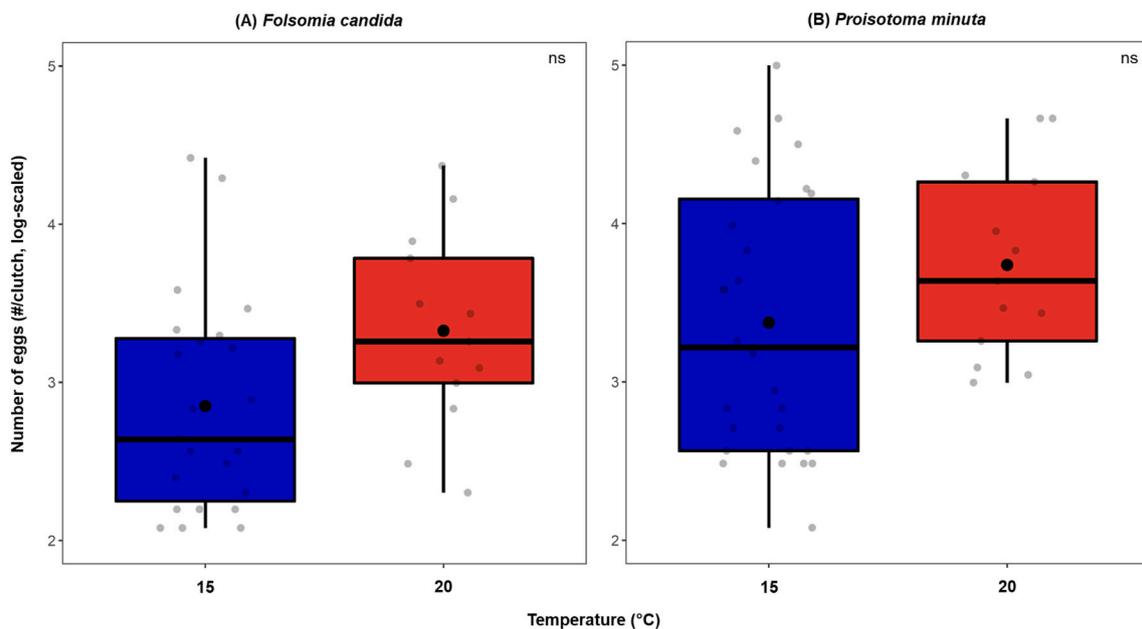


Fig. 3. Boxplots showing the average egg number per clutch (log-scaled) in relation to the different incubation temperatures individually per species. Raw data are shown as jittered points (in gray) whereas mean values are shown as black filled points. ns: p-value > 0.05. Untransformed data - *F. candida*: 15 °C (mean \pm s.d. = 27.53 \pm 44.91, n = 28, median = 13) and 20 °C (mean \pm s.d. = 39.86 \pm 39.16, n = 15, median = 26); *P. minuta*: 15 °C (mean \pm s.d. = 38 \pm 35.86, n = 31, median = 19) and 20 °C (mean \pm s.d. = 78.06 \pm 80.64, n = 15, median = 46).

ecological filtering with an assumption that small sized eggs could result in small sized adults [14,49]. There could be a number of consequences of smaller egg size production on the overall fitness of populations. For instance, smaller eggs produced by yellow dung flies at warmer temperatures eventually had lower survivorship than larger eggs [50]. Moreover, if smaller eggs lead to smaller adults, it could further affect the population size, as noted by a study with Collembola showing reduced egg production by adults that were smaller in size [51].

Contrasting egg size responses between *F. candida* and *P. minuta* may

have resulted from a number of factors. For instance, an earlier study also showed that the adult body size of *P. minuta* was not responsive to temperature [21] implying a lesser thermal responsiveness of *P. minuta* compared to *F. candida*. Another interesting difference between the two species in terms of their reproductive strategy was that *F. candida* laid overall fewer eggs than *P. minuta*, but the number of eggs per clutch was higher in *F. candida* in both temperatures (Table 1). This could relate to greater energetic investment by *F. candida* than *P. minuta* in their eggs, which merit further examination such as through testing egg quality and

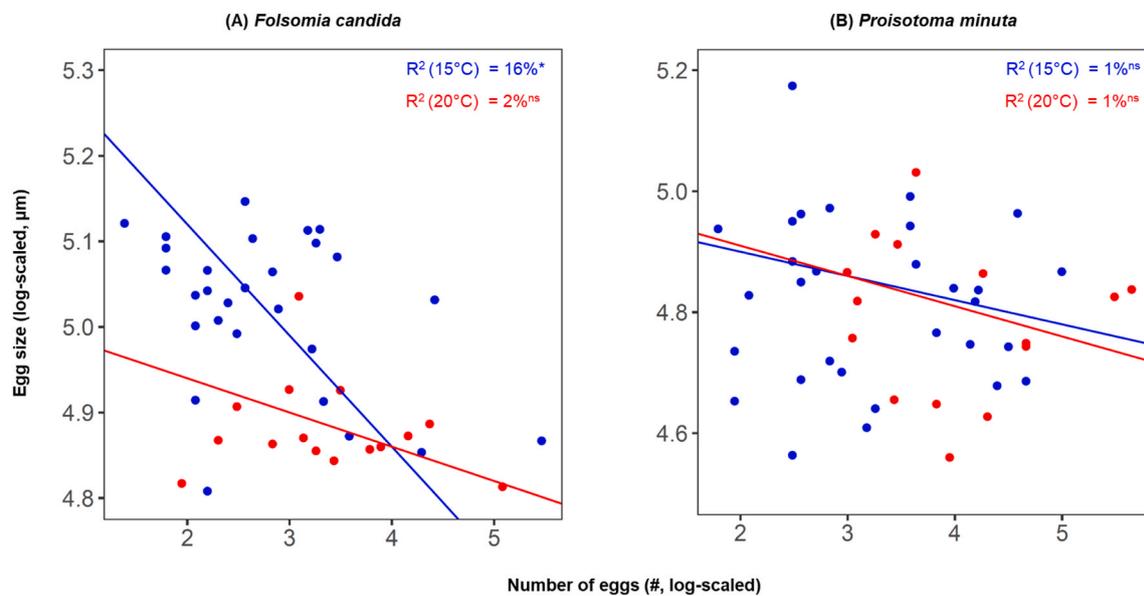


Fig. 4. The graphs showing the relationship between average egg size and average egg number in two Collembola species. The blue colour indicates the cold treatment (15 °C) and the red colour indicates the warm treatment (20 °C). Regression lines are based on the results from reduced major axis regression. *: p-value<0.05, ns: p-value>0.05. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

hatching success. *Proisotoma minuta* reproduces sexually, whereas *F. candida* reproduces asexually [38,52]. We suspect that perhaps the duration of the temperature treatment might still not have been long enough for *P. minuta* to exhibit plasticity in their egg size at the lower temperature as thermal plasticity may take longer in sexual species to occur [53]. Indeed, sexually reproducing organisms like *P. minuta* may depend more on genetic diversity to overcome environmental changes, whereas asexually reproducing Collembola species, such as *F. candida*, may rely more on phenotypic plasticity [54]. Future studies with greater number of sexual and asexual species can test this hypothesis in terms of reproductive traits.

The observed negative correlation between two reproductive traits (a potential indication of a trade-off) in *F. candida* at 15 °C and lack of it at 20 °C could relate to optimum growing temperature of the same species. It is often shown that the optimal growth temperature of *F. candida* as well as for *P. minuta* is around 21 °C [35,38]. Hence, it is likely that energetic costs for investments in reproductive traits are minimal when organisms grow close to their optimal growth temperature. Indeed, abiotic environments (temperature in our study) have been associated with maternal investments to their offspring. For instance, a study of Salmon (*Salmo salar*) eggs showed that their average egg sizes were larger in unfavourable environments, which subsequently affected trade-off between egg size and fecundity in Salmon females [55]. Another study with the large milkweed bug (*Oncopeltus fasciatus*) showed females fed on poor food had a higher level of ovarian apoptosis (therefore lower reproductive success). However, they did not show a reduced life span which indicates the insurance of survival at the cost of reproductive success [56]. Such trade-offs in soil organisms are far less known, and our results provide some insights for both the emergence and the disappearance of an important trade-off between two reproductive traits in one of the commonly studied soil model organisms [38] which are suggested to have higher reproductive flexibility [52].

In conclusion, our study demonstrates that reproductive trait trade-offs can occur in a soil invertebrate organism at a given temperature and the same may disappear when the background temperature gets closer to its optimal growth temperature. Moreover, the temperature-induced reduction in egg size in one of the Collembola species indicate potential warming-induced phenotypic plasticity that could likely result in smaller body sized individuals in warmer temperatures. The fitness consequences of smaller eggs, and how they may affect

population stability merit further examination. Furthermore, whether natural populations of Collembola species exhibit similar reproductive trade-offs when faced with different temperature regimes is little known, and we believe that our results with lab-reared populations provide testable hypotheses for natural collembolan populations. Moreover, weak effects of two temperature regimes on egg numbers in both species need further exploration, such as whether they will remain the same if food availability changes. This is also a more realistic scenario to mimic natural variability. We further emphasize that climate change studies need to link how such population level responses and (reproductive) trait trade-offs can affect organismal contributions to ecosystem functions. We conclude that temperature could be an important driver of phenotypic plasticity in reproductive traits, however, this could depend on several factors ranging from optimal growth temperature of a species to their mode of reproduction. Soil microarthropods like Collembola used in this study could help address these questions to advance the thermal biology of ectotherms.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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