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1 **The population determines whether and how life-history traits vary between**
2 **reproductive events in an insect with maternal care.**

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11 **Declaration of authorship:** TR, JK, MV and JM designed the experiment. MV collected the
12 individuals in the field. TR and JK conducted the experiment. TR and JM analysed the data.
13 JM wrote the first draft of the manuscript, which was then commented and corrected by all
14 co-authors.

Abstract

The last reproductive event of a female is often associated with major changes in terms of both maternal and offspring life-history traits. However, the nature of these changes and the importance of population-specific environmental constraints in shaping their expression are difficult to predict and, as a consequence, poorly understood. Here, we investigated whether and how life-history traits vary between reproductive events and whether this variation is population-dependent in the European earwig *Forficula auricularia*. In this insect species, females produce up to two clutches during their lifetime and express extensive forms of maternal care. We conducted a common garden experiment, in which we measured 11 life-history traits of the first and second clutches of 132 females originating from three populations. Our results showed that clutch size was higher - and the level of care expressed towards juveniles lower - in second as compared to first clutches in all three populations. By contrast, we found a population-specific effect on whether and how the reproductive event shaped juvenile quality and a trade-off between egg developmental time and female weight at hatching. Overall, these findings emphasize that the last reproductive event of a female entails both positive and negative effects on various life-history traits of the female herself and her clutch of juveniles. Moreover, our study stresses the importance of population idiosyncrasies on the expression and nature of such cohort-specific effects.

Keywords: senescence, terminal investment, parental care, family life, semelparity, insect

Introduction

Life-history traits are crucial phenotypic variants that reflect how an organism allocates time and energy to optimise its development and maximise its reproduction (Roff 1992; Stearns 1992; Flatt and Heyland 2011). These traits can be divided in a great diversity of categories, including the reproductive capability and success of an individual (e.g. age and size at maturity, number and size of offspring), as well as its physiology (e.g. immunocompetence and senescence) and behaviours (e.g. aggressiveness, reproductive tactics and parental care; Southwood 1977, Brommer 2000, Reznick et al. 2000). Studying the determinants of life-history traits is thus a pivot of evolutionary biology and ecology, as it helps to better understand the evolutionary constraints that shape the multiple aspects of an individual's fitness and, more generally, the factors that drive the evolution of populations and species (Stearns 1992; Schluter 2001; Rundle and Nosil 2005).

Numerous factors are known to either positively or negatively influence an individual's life-history traits (see examples in Stearns 1992; Nylinä and Gotthard 1998; Flatt and Heyland 2011). The nature of the effects of being produced during the late reproductive period of a female (thereafter called 'cohort'), however, remains controversial. On the one hand, offspring can benefit from being produced in a late cohort. This is mostly because parental effort into reproduction is predicted to increase when the parents' prospects for survival and future reproduction decline (the 'terminal investment' hypothesis; (Williams 1966; Clutton-Brock 1984; Javoiš 2013)) and this might benefit offspring if the increase is allocated to parental care (rather than to the production of additional offspring). Over the last decades, numerous studies conducted across species and taxa provided empirical support for this prediction (Fox and Czesak 2000; Hasselquist and Nilsson 2009; Royle et al. 2012; Santos and Nakagawa 2012). For instance, females of the North American red

squirrels *Tamiasciurus hudsonicus* and the burying beetle *Nicrophorus orbicollis* have been shown to produce juveniles of better quality (and/or more juveniles) in late compared to early cohorts (Descamps et al. 2007; Creighton et al. 2009). Similarly, parents showed higher levels of parental care for late- as compared to early-produced juveniles in the collared flycatcher *Ficedula albicollis* and in *N. orbicollis* (Part et al. 1992; Creighton et al. 2009).

On the other hand, offspring may also suffer from being produced in a late cohort. This cost often results from physiological constraints that hamper the expression of parental investment and thus ultimately decrease offspring quality (reviewed in Javoiš 2013). Maternal senescence is a well-known physiological constraint that negatively and specifically affects juveniles of late cohorts, as aging females usually become unable to increase or even maintain their reproductive efforts (McNamara and Houston 1996; Nussey et al. 2013; Kowald and Kirkwood 2015). For instance, in the grey seal *Halichoerus grypus*, maternal and offspring body mass, weaning mass and the level of lactation have all been shown to decline with age due to physiological degeneration (Bowen et al. 2006).

Importantly, (often population-specific) environmental constraints such as food restriction and pathogen presence can either promote or hamper the expression of a terminal investment and may thus have a substantial influence on the traits of late cohort offspring. For instance, low food intake has been shown to inhibit the expression of terminal investment by females of the Alpine chamois *Rupicapra rupicapra* (Mason et al. 2011), whereas food restriction and pathogen presence favoured its expression in males of the yellow mealworm beetle *Tenebrio molitor* (Krams et al. 2015) and of the blue-footed booby *Sula nebouxii* (Velando et al. 2006), respectively. Although environmental constraints often vary between populations, the occurrence of population-specific differences in the life-history traits expressed by individuals from early and late cohorts remains surprisingly

poorly studied (see Mason et al. 2011; Javoiš 2013; Vincze et al. 2013).

In this study, we investigated whether maternal and offspring life-history traits vary between initial and terminal reproductive events in the European earwig *Forficula auricularia*, and whether the occurrence and nature of this variation are population-specific. In this insect species, females produce up to two clutches during their one-year lifespan: the initial clutch of eggs is generally produced in early-winter and hatches in the following early-spring, while the terminal clutch (when present) is produced in mid-spring and hatches in the following early-summer (Meunier et al. 2012). From the date of egg laying until several weeks after egg hatching, mothers provide extensive forms of care to their eggs and juveniles (called nymphs) that include the protection against predators and pathogens, as well as the provisioning of nymphs with food (e.g. through regurgitation; Lamb 1976; Kölliker 2007; Boos et al. 2014; Koch and Meunier 2014; Diehl et al. 2015; Kölliker et al. 2015).

In a previous study focusing on differences between semelparous and iteroparous *F. auricularia* females, Meunier et al. (2012) showed that the 2nd clutches of iteroparous females were smaller and developed faster than their 1st clutches. However, it remains unknown whether this variation (1) shapes other key life-history traits of earwigs, such as maternal condition and the expression of maternal care and, more importantly, whether it (2) depends on the studied population. Here, we addressed these questions by comparing a total of eleven life-history traits measured in the 1st and 2nd clutches of 132 *F. auricularia* females sampled in three distant populations in Europe. These traits encompassed measures of clutch quantity and quality, maternal condition during post-hatching family interactions, as well as the expression of brood defence and food provisioning, two important forms of post-hatching maternal care (Meunier and Kölliker 2012; Thesing et al.

106 2015).

Materials and methods

107 *Field sampling and laboratory breeding*

108 Our experiment started with 696 *F. auricularia* individuals sampled in September 2014 in
109 three populations located in Girona (Spain, n = 120 females and 118 males), Montblanc
110 (Spain, n = 118 females and 107 males) and Vincennes (France, n = 119 females and 114
111 males) (Figure 1). All these populations belong to the same *F. auricularia* genetic clade B
112 (Wirth et al. 1998)(M. Veuille and X. Espalader, unpublished data), and are subjected to
113 different environmental conditions in terms of altitude, temperature and precipitation (see
114 details in Figure 1). Note that neither of these populations corresponded to the population
115 studied in Meunier et al. (2012).

116 Individuals from all three populations were maintained under standard laboratory
117 conditions adapted from Meunier et al (2012). This allowed the expression of inherited
118 population-specific traits while controlling for plastic responses to the environment. The
119 setup started by haphazardly distributing all field-sampled individuals of each population
120 among large plastic containers to form groups of 58 ± 0.58 (mean \pm SE) individuals
121 encompassing a maximum of 30 males and 30 females. These groups were maintained at
122 20°C, 60% humidity, 14:10 h light: dark photoperiod (thereafter called summer conditions)
123 to allow uncontrolled mating (Sandrin et al. 2015). Two months later, a random sample of
124 237 females (Girona: n = 71; Montblanc: n = 59; Vincennes: n = 107) was isolated to allow
125 egg production. These females were maintained under complete darkness and 60%
126 humidity, with a temperature of 10°C for 2 weeks, and then 5°C for three months to mimic

winter conditions. Spring was subsequently simulated by first increasing the temperature to 10°C and one week later to 15°C. When the first nymph hatched, the corresponding family was transferred to and maintained under summer conditions (see above) to favour nymph development. Fourteen days later, each female was isolated to mimic natural family disruption and subsequently maintained under complete darkness to allow 2nd clutch production (Meunier et al. 2012). The laboratory rearing of 2nd clutch eggs and nymphs was similar to the above detailed rearing of the 1st clutches, except that eggs were maintained under summer temperatures. Among the 209 females that produced 1st clutch nymphs (28 females did not; Girona: n = 9; Montblanc: n = 5; Vincennes: n = 14), a total of 136 females also produced a 2nd clutch (see results) and were thus used in the present study. For a comparison of the life-history traits expressed by semelparous and iteroparous females, please see Meunier et al. (2012).

All large plastic containers (30 x 17 x 21 cm) contained humid sand as ground material and an egg cardboard as shelter. Isolated females and, upon hatching, their nymphs were set up in Petri dishes (diameters 8.5) containing humid sand as substrate and a plastic tube (cut in half) as shelter. All the tested individuals received an *ad libitum* amount of standard laboratory food (see composition in Kramer et al. 2015). However, we did not provide food to the isolated females between egg laying and hatching, as they typically stop feeding during this period (Kölliker 2007). All temperature changes were implemented gradually over four days. Note that all 14 days old nymphs (of both 1st and 2nd clutches) were discarded from the experiment.

Measurements of 11 life-history traits

We investigated the effects of population and juvenile cohort on a total of 11 life-history

traits reflecting clutch quantity and quality, maternal condition during post-hatching family interactions, and post-hatching maternal care. These measurements started with the (1) egg developmental time, which was defined as the number of days between the first day of egg laying and the first day of egg hatching. We then counted (2) the number of eggs produced within three days after the first egg laying, (3) the number of nymphs present one day after the first egg hatching and (4) the number of nymphs alive 14 days after hatching. We used different timespans for the first two countings, because *F. auricularia* females generally need up to three days to finish the deposition of their clutch of eggs, whereas egg hatching is well synchronised within each clutch and is generally completed over a single day (Koch and Meunier 2014). We also measured the (5) mean weight of nymphs one day and (6) 14 days after egg hatching. To this end, a group of 10 nymphs (or all nymphs if brood size was lower than 10) was haphazardly sampled in each brood and weighed to the nearest 0.01 mg using a microscale (model MYA5; PESCALE, Bisingen, Germany). We then recorded (7) the developmental time of nymphs from the first to the second developmental instar, which was obtained by counting the number of days between egg laying and the emergence of the first second instar nymph in each clutch. This measurement is known to reflect the developmental time of the entire clutch in *F. auricularia* (Gómez and Kölliker 2013). Finally, changes in maternal condition over the period of post-hatching family interactions were measured by weighing each mother (8) one day and (9) 14 days after the first egg hatching.

Post-hatching maternal care was estimated by measuring food provisioning and brood defence. (10) Food provisioning was measured in 102 clutches (a haphazard sample of 34 clutches was omitted from this measurements due to time constraints; see details in table 1) using a standard method relying on the fact that ingested coloured food is visible through the partially transparent cuticle of 1st instar nymphs (Staerke and Kölliker 2008;

Kölliker et al. 2015; Kramer et al. 2015). In brief, food was removed from each family on day 5 after hatching. Twenty-four hours later, mothers were isolated and had access to a green pollen pellet (naturally yellow-coloured pollen coloured with blue dye; Hochland Bio-Blütenpollen by Hoyer; Food die by DEKO BACK) for one hour. Afterwards, mothers were returned to a standardised number of 20 of their own nymphs (or all of their nymphs if the clutch had less than 20 nymphs; mean number of nymphs used in this test \pm SE = 18.9 ± 0.21) to allow family interactions. Finally, the number of green-coloured and non-green-coloured nymphs was counted fifteen hours later using a stereomicroscope (Leica S8 APO, 10x). Note that food provisioning was not measured in clutches with less than five nymphs ($n = 5$) and that the level of food provisioning was independent of the number of recipient nymphs (Spearman correlation test, $\rho = -0.08$, $S = 23869$, $p = 0.577$). During the food provisioning test, all left-over nymphs were maintained in their original Petri dish and provided with standard laboratory food. To follow the treatments detailed above, all unused families were starved for 24 h on day 5 and fed again on day 6.

Finally, (11) brood defence was assessed using a previously established method (Thesing et al. 2015), in which each female was standardly poked on the pronotum with a glass-capillary (one poke per second) to record the number of pokes necessary to induce her running away beyond a distance of twice the female's body length. Brood defence was tested at day 4, day 8, and day 12 after hatching and the average of these three values was used as brood defence. The brood defence test was carried out under red light, as earwigs are nocturnal.

Statistical analyses

We were first interested in testing the effects of population and the juveniles' cohort on the

life-history traits of mothers and offspring. To control for possible non-independence among the 11 measured traits, we first conducted a Principal Component Analysis (PCA) to obtain non-correlated principal components (PCs) reflecting single or combinations of different life-history traits. In this PCA, the values of food provisioning were logit-transformed and the values of brood defence were log-transformed to comply with normal distributions. The PCA was conducted by scaling the data to unit variance and running a regularised iterative MFA method (with K-fold cross-validation) to handle the few missing values in the dataset (Lê et al. 2008, Husson et al. 2011). The resulting and selected PCs (Table 2) were then analysed separately using Linear Mixed Models (LMMs), in which the population, the juveniles' cohort and their interaction were entered as fixed factors and female ID was used as a random factor (Table 3). In case of significant interactions between population and the juveniles' cohort (see results), pairwise comparisons among each combination were tested using Tukey HSD tests.

To determine the occurrence of an investment trade-off between 1st and 2nd clutches, we also tested whether the life-history traits measured in 2nd and 1st clutches were negatively (i.e. reproductive trade-off) or positively (i.e. quality-dependent reproduction) correlated, and whether the occurrence and nature of these correlations were similar across populations. To this end, we conducted a series of five General Linear models (LM), in which the 2nd clutch values of each of the five above PCs were used as a response variable, while the corresponding 1st clutch values, the population and their interaction were entered as fixed variables. All statistical analyses were conducted using R v 3.2.1 (<http://www.r-project.org/>) loaded with the packages *car*, *FactoMineR*, *missMDA*, *lmerTest* and *lsmeans*.

Results

Overall, 52 (83.8%) of the 62 females from Girona, 39 (72.2%) of the 54 females from Montblanc and 45 (48.4%) of the 93 females from Vincennes produced two clutches of nymphs (Pearson's Chi-squared test, $\chi^2_2 = 22.25$, $p < 0.0001$). These proportions were significantly smaller in Vincennes compared to both Girona ($\chi^2_1 = 20.00$, $p\text{-value} < 0.0001$) and Montblanc ($\chi^2_1 = 7.93$, $p\text{-value} = 0.005$), but comparable between the two Spanish populations ($\chi^2_1 = 2.32$, $p = 0.128$).

The PCA conducted on the life-history traits measured in the 1st and 2nd clutches of these 136 females provided 11 orthogonal principal components (PCs), of which we extracted the first five ones (total variance explained = 87.2%, Table 2). The first component (PC1) was highly and positively loaded with the number of eggs as well as with the number of nymphs at day 1 and day 14, therefore overall positively reflecting clutch size. The second component (PC2) revealed a positive association between the nymphs' weights on day 1 and day 14, as well as post-hatching developmental speed, which overall reflects nymph quality. Accordingly, high values of PC2 indicate that clutches consisted of heavy nymphs which quickly moulted into the second developmental instar, whereas small values indicate clutches with light nymphs which required more time to develop into the second instar. The third component (PC3) revealed a trade-off between egg developmental time and the mother's weight at egg hatching. High values of PC3 thus represent clutches in which eggs required a long time to develop and mothers were light at egg hatching (probably because they spent more time caring for the eggs), whereas small values reflect clutches in which eggs developed fast and mothers were heavy at egg hatching. Finally, the fourth (PC4) and fifth (PC5) components were solely and positively loaded with brood defence and food

provisioning, respectively.

An interaction between population and the juvenile's cohort significantly shaped PC1, PC2 and PC3 (Table 3). For PC1, pairwise comparisons within the statistical model showed that 1st clutches were overall larger than 2nd clutches within each population, whereas the interaction emphasized that this difference was smaller in Vincennes as compared to Girona and Montblanc (Figure 2a, Table S1). By contrast, the interactive effect of population and the juveniles' cohort on PC2 revealed that 1st clutch nymphs were of lower quality than 2nd clutch nymphs in Vincennes, but not in Girona and Montblanc (Figure 2b). Similarly, the significant interaction shaping PC3 showed a slower developmental time of eggs and a lighter weight of females at hatching in the 1st compared to the 2nd clutches in Girona and Montblanc, but not in Vincennes (Figure 2c). Note that the raw values of each trait can be found in Table 1.

The values of PC4 and PC5, which respectively reflected the level of brood defence and food provisioning, were overall higher in the 2nd compared to 1st clutches (Table 3 and Figure 3). However, they were independent of the population or of an interaction between population and the juvenile's cohort (Table 3).

Finally, we found consistencies (i.e. positive associations) across the two breeding attempts (Table 4) in terms of clutch size (PC1; Model estimate \pm SE = 0.697 ± 0.039 , $t = 17.55$, $P < 0.0001$), nymph quality (PC2; estim. = 0.375 ± 0.091 , $t = 4.13$, $P < 0.0001$), the trade-off between egg developmental time and maternal weight at egg hatching (PC3; estim. = 0.335 ± 0.074 , $t = 4.55$, $P < 0.0001$) and brood defence (PC4; estim. = 0.469 ± 0.092 , $t = 5.10$, $P < 0.0001$), but not in terms of food provisioning (PC5; estim. = 0.086 ± 0.083 , $t = 1.04$, $P = 0.301$; Figure 3). The occurrence and strength of these associations were independent of the population (interaction in Table 4). These statistical models also

confirmed the results of the above analyses by showing that both clutch size and the trade-off between egg developmental time and the mother's weight at egg hatching observed in the 2nd clutches were population specific (Table 4, Figure 2).

Discussion

This study overall shows that initial and terminal clutches of the European earwig *F. auricularia* exhibit differences in life-history traits, and that the occurrence and nature of these differences depend on the trait and/or the studied population. Specifically, we found that nymph quality was higher in the 2nd compared to 1st clutches of Vincennes females only, and that egg developmental time and female weight at hatching were longer and lighter, respectively, in initial compared to terminal clutches of females from Girona and Montblanc. By contrast, clutch size was lower and maternal care – i.e. brood defence and food provisioning – higher in 1st as compared to 2nd clutches in all three studied populations. Interestingly, the expression of all traits measured in the 1st clutches (but food provisioning) was positively associated with the expression of these traits in the 2nd clutches, and the occurrence and nature of these associations were independent of the studied population.

Across species and taxa, the expression of life-history traits often varies among populations. This is the case, for instance, for offspring mass and number in the scorpion *Centruroides vittatus* (Brown and Formanowicz 1995), for the juveniles' development and survival in the Mediterranean fruit fly *Ceratitis capitata* (Diamantidis et al. 2011), and for the level of parental care in the Kentish plover *Charadrius alexandrinus* and the snowy plover *C. nivosus* (Vincze et al. 2013). In earwigs, our results do not only demonstrate that each population is characterized by a specific proportion of females producing two clutches

under identical (laboratory) conditions (see also Wirth et al. 1998; Meunier et al. 2012), but also that the population determines whether and how certain life-history traits differ between initial and terminal clutches.

Although females from the three populations were maintained under the same laboratory conditions, we found that their population of origin determined the effects of the juveniles' cohort on nymph quality and the trade-off between egg developmental time and female weight at hatching. This is important, as it reveals that these effects are not determined by the environmental conditions experienced during family life, but instead depend on the conditions experienced during female development and/or on (the conditions that have shaped) the evolutionary history of the population. In line with the first hypothesis, the quality of the environment experienced by *F. auricularia* juveniles during their development is known to affect the life-history traits of the resulting adults, for instance in terms of investment into 2nd clutch production and maternal care (Wong and Kölliker 2014; Thesing et al. 2015). Conversely, harsh winter conditions have been suggested to select for a delayed production of 1st clutch eggs (Meunier et al. 2012), which may benefit females by shortening the developmental time of their 1st clutch eggs and thus allowing the mothers to exhibit a higher condition (i.e. a higher body weight) at hatching. Ultimately, such conditions may prevent differences in the trade-off between egg developmental time/female weight at hatching between 1st and 2nd clutches (which are always produced in spring, under favourable environmental conditions), and might thus explain its absence in females from Vincennes, the population with the coldest winter (Figure 1) and the latest production of 1st clutch eggs (Table 1). Whether our results are the outcome of the interactive or independent effects of these two processes remains to be further studied.

Contrary to the population-specific effects described above, we found that earwig females expressed higher levels of post-hatching care towards 2nd compared to 1st clutches in all three tested populations. Notably, this effect was present even if the females' weight at the beginning of family life (i.e. at egg hatching) was comparable between the two clutches (see Table 1). These results are overall in line with a terminal investment of *F. auricularia* females in terms of maternal care (Williams 1966; Clutton-Brock 1984; Javoiš 2013), as found in the collared flycatcher *F. albicollis* (Part et al. 1992) and the burying beetle *N. orbicollis* (Creighton et al. 2009). Furthermore, these findings could indicate that the benefits of maternal care are more important for 2nd than 1st clutch nymphs and therefore select for higher expression of care towards late clutch nymphs across populations. In line with this idea, spring is often well advanced when 2nd clutch eggs hatch, so that the environmental conditions experienced by the resulting nymphs are likely to increase (as compared to 1st clutch nymphs) their exposure to pathogens, such as fungi, or their predators, such as other arthropods and even the 1st clutch nymphs (Dobler and Kölliker 2010). Irrespective of the mechanism mediating the increased level of maternal care towards 2nd clutch nymphs, the absence of a population-specific effect indicates that the environmental conditions experienced by females during 1st clutch family life (and egg care) are crucial in determining the subsequent expression of maternal care towards their 2nd clutch offspring. This is supported by recent studies showing that maternal condition at egg hatching determines the nature of sibling and mother-offspring interactions in *F. auricularia* (Wong and Kölliker 2012; Kramer et al. 2015; Kramer and Meunier 2016).

Interestingly, we found a reduction in size of the 2nd as compared to the 1st clutch in all three studied populations. This reduction is in line with an effect of senescence on female reproduction, but may also reflect an adaptive strategy of females. For example, the

uncertainty of surviving until 2nd clutch production could favour a higher investment into 1st clutch production independent of female age. Such an effect of the perceived risk of death on female investment into reproduction has been nicely demonstrated in the burying beetle *Nicrophorus vespilloides*, in which an experimental activation of the immune system caused females to switch from reproductive restraint to terminal investment (Cotter et al. 2011). Interestingly, our findings in earwigs reveal that although clutch sizes were different, almost all measurements of life-history traits taken in the 1st clutches were positively correlated with the corresponding measurements in the 2nd clutches. This highlights that the overall reproduction of a female is tightly linked to her own quality irrespective of whether or not senescence shapes the size of 2nd clutches (Meunier et al. 2012). Further studies should be conducted to experimentally disentangle the (mutually non-exclusive) effects on maternal investment into egg production caused by senescence and/or the perceived risk of death on the one hand, and the effects on maternal care caused by terminal investment and/or reproductive strategy (see above).

To conclude, our study demonstrates that offspring cohort and population-membership interact in determining crucial life-history traits in the European earwig. We showed in a common garden experiment that population-membership affected the expression of two cohort-specific traits only (nymph quality and the trade-off between egg developmental time and female weight at egg hatching), suggesting an important role of past environmental conditions in their expression, but also indicating a limited role of such past conditions for the expression of maternal care. Although our results are overall in line with an effect of terminal investment on maternal care, and of senescence on maternal reproduction, our findings call for further experimental studies deciphering the independent or entangled action of these mechanisms (see e.g. Cotter et al. 2011). Finally,

it is important to note that the direction and strength of the cohort-specific effects reported in this study should be interpreted with caution, as our laboratory conditions might have unwittingly favoured individuals from certain populations. Nevertheless, our results demonstrate that even within a single genetic clade (namely the *F. auricularia* clade B; Wirth et al. 1998), population idiosyncrasies may have major effects on the expression of life-history traits associated with successive reproductive attempts. The question whether these idiosyncrasies reflect the capability of individuals to develop under specific laboratory conditions, the evolutionary history of the population, and/or the biotic/abiotic constraints experienced by the juveniles during their development remains open for further studies.

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496

497 **Table 1:** Mean values of each of the 11 life-history traits measured in the three populations. For each trait, we provided the mean value, its
498 standard error (SE), as well as the number of replicates in which it has been measured (N).

	GIRONA				MONT BLANC				VINCENNES									
	First clutch		Second clutch		First clutch		Second clutch		First clutch		Second clutch							
	Mean	± SE	N	Mean	± SE	N	Mean	± SE	N	Mean	± SE	N	Mean	± SE	N			
Egg developmental time (days)	37.58	± 2.33	52	15.10	± 0.09	52	54.97	± 1.87	39	14.64	± 0.12	39	22.82	± 0.83	45	15.38	± 0.09	45
Egg number	68.63	± 1.41	52	46.83	± 1.21	52	58.95	± 1.8	39	32.21	± 1.65	39	41.22	± 1.57	45	25.11	± 1.41	45
Nymph number day 1	63.44	± 1.43	52	38.12	± 1.96	52	54.03	± 1.76	39	27.31	± 1.77	39	31.53	± 1.75	45	16.00	± 1.3	45
Nymph weight day 1 (mg)	1.44	± 0.03	52	1.38	± 0.04	52	1.58	± 0.04	36	1.42	± 0.04	39	1.35	± 0.04	45	1.49	± 0.04	45
Nymph number day 14	60.19	± 1.56	52	36.87	± 1.95	52	51.67	± 1.66	39	26.21	± 1.74	39	29.82	± 1.64	45	14.22	± 1.3	45
Nymph weight day 14 (mg)	2.83	± 0.06	52	2.93	± 0.09	52	3.04	± 0.1	36	3.01	± 0.11	39	2.60	± 0.07	45	2.90	± 0.08	45
Nymphs developmental time until 2 nd instars (days)	12.73	± 0.17	51	12.92	± 0.21	51	12.06	± 0.15	35	12.51	± 0.22	39	13.18	± 0.24	44	12.84	± 0.19	43
Mother weight day 1 (mg)	58.79	± 1.21	52	59.02	± 1.38	52	51.22	± 1.49	36	53.85	± 1.46	38	44.78	± 0.96	45	44.51	± 1.01	45
Mother weight day 14 (mg)	71.90	± 1.62	52	70.30	± 1.6	52	64.35	± 1.86	36	61.30	± 1.72	38	55.32	± 1.51	45	50.24	± 1.39	45
Brood defence	21.42	± 2.4	52	21.12	± 2.46	52	17.97	± 2.28	35	23.13	± 3.17	38	12.11	± 1.48	44	16.98	± 2.65	43
Food provisioning	11.22	± 1.48	51	11.00	± 1.95	42	15.59	± 2.61	36	13.35	± 2.89	32	11.38	± 2.41	44	17.54	± 3.54	29

499 **Table 2:** Loadings of the five first Principal Component (PCs) reflecting single or
500 combinations of eleven life-history traits. The traits having significant loadings on each PC
501 are in bold.

	PC1	PC2	PC3	PC4	PC5
Egg developmental time	0.591	0.153	0.584	0.005	-0.265
Egg number	0.931	0.032	0.129	-0.045	0.004
Nymph number d1	0.931	-0.248	0.156	-0.021	0.021
Nymph number d14	0.923	-0.243	0.151	-0.031	0.016
Nymph weight d1	-0.071	0.859	0.066	0.013	-0.238
Nymph weight d14	-0.092	0.859	0.019	0.204	-0.142
Nymphs dvpt time til 2nd instars	0.005	-0.737	-0.269	0.045	0.076
Mother weight d1	0.591	0.396	-0.631	-0.077	0.106
Mother weight d14	0.667	0.439	-0.497	-0.086	0.093
Food provisioning	-0.072	0.450	0.387	-0.059	0.790
Brood defence	0.214	-0.073	-0.053	0.962	0.098
Variance explained (%)	34.5	24.7	11.6	9.0	7.3
Cumulative variance explained (%)	34.5	59.2	70.8	79.8	87.2

502 **Table 3:** Influence of population, juvenile's cohort and their interaction on the five principal
 503 components (PC1 to PC5) based on the 11 measured life-history traits. Values obtained
 504 from LMMs. Significant p-values are in bold.

	Population		Juvenile's cohort		Interaction	
	LR χ^2_2	P	LR χ^2_1	P	LR χ^2_2	P
PC1	281.6	<0.0001	797.3	<0.0001	38.6	<0.0001
PC2	8.5	0.014	1.4	0.231	8.3	0.016
PC3	33.3	<0.0001	209.5	<0.0001	90.1	<0.0001
PC4	4.0	0.134	6.1	0.013	0.7	0.696
PC5	5.5	0.064	10.1	0.002	5.5	0.064

505 **Table 4:** Influence of first clutch values, population and their interaction on the five PCs.

506 Significant P-values are in bold.

2nd clutch values	Population		1st clutch values		Interaction	
	F _(2,130)	P	F _(1,130)	P	F _(2,130)	P
PC1	11.26	<0.0001	81.26	<0.0001	0.83	0.4395
PC2	0.36	0.7002	16.91	<0.0001	0.11	0.8997
PC3	35.18	<0.0001	40.27	<0.0001	0.01	0.9859
PC4	0.54	0.5841	23.97	<0.0001	0.56	0.5711
PC5	1.98	0.1428	1.00	0.3193	2.24	0.1102

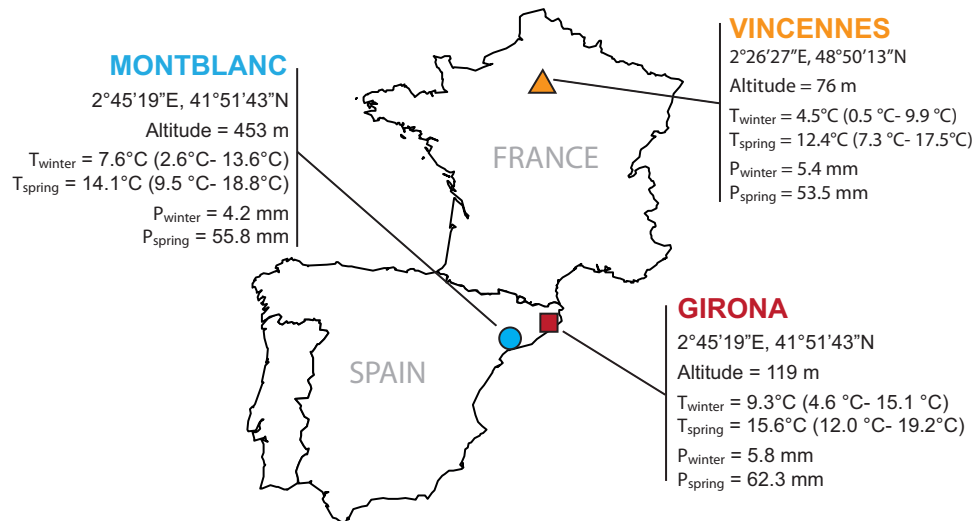


Figure 1. Location and climatic details of the three studied populations of *F. auricularia*. For each population, we provide the GPS coordinates and altitude, as well as the mean (minimum – maximum) temperatures and the mean precipitations recorded in winter and spring over the last 50 years. Information from the Worldclim data base (<http://www.worldclim.org/>).

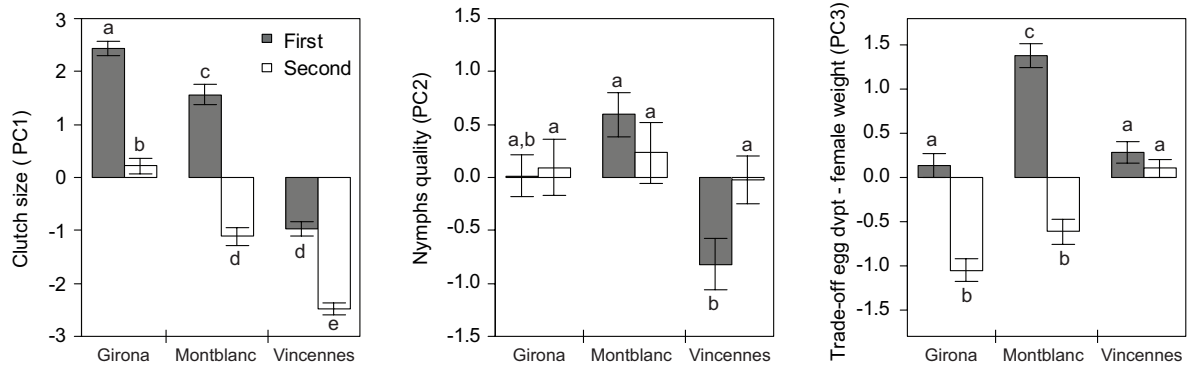


Figure 2. Interactive effects of population and the juveniles' cohort on the principal components reflecting clutch size (PC1), nymph quality (PC2) and the trade-off between egg developmental time and the mother's weight at egg hatching (PC3). Values represent means \pm s.e.m. Different letters indicate significant differences (see Table S2 for detailed values of pairwise comparisons).

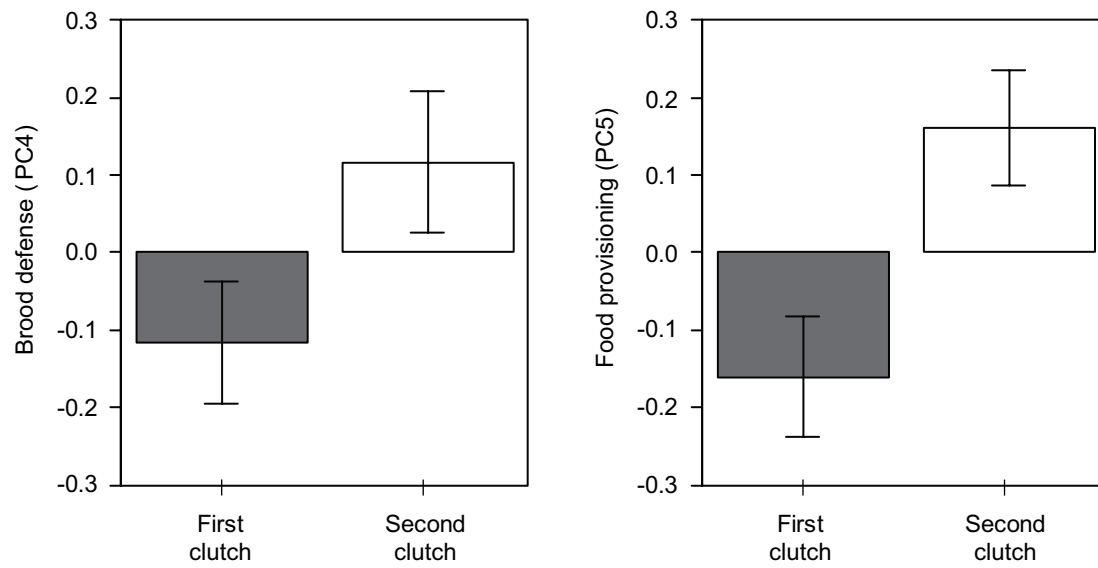
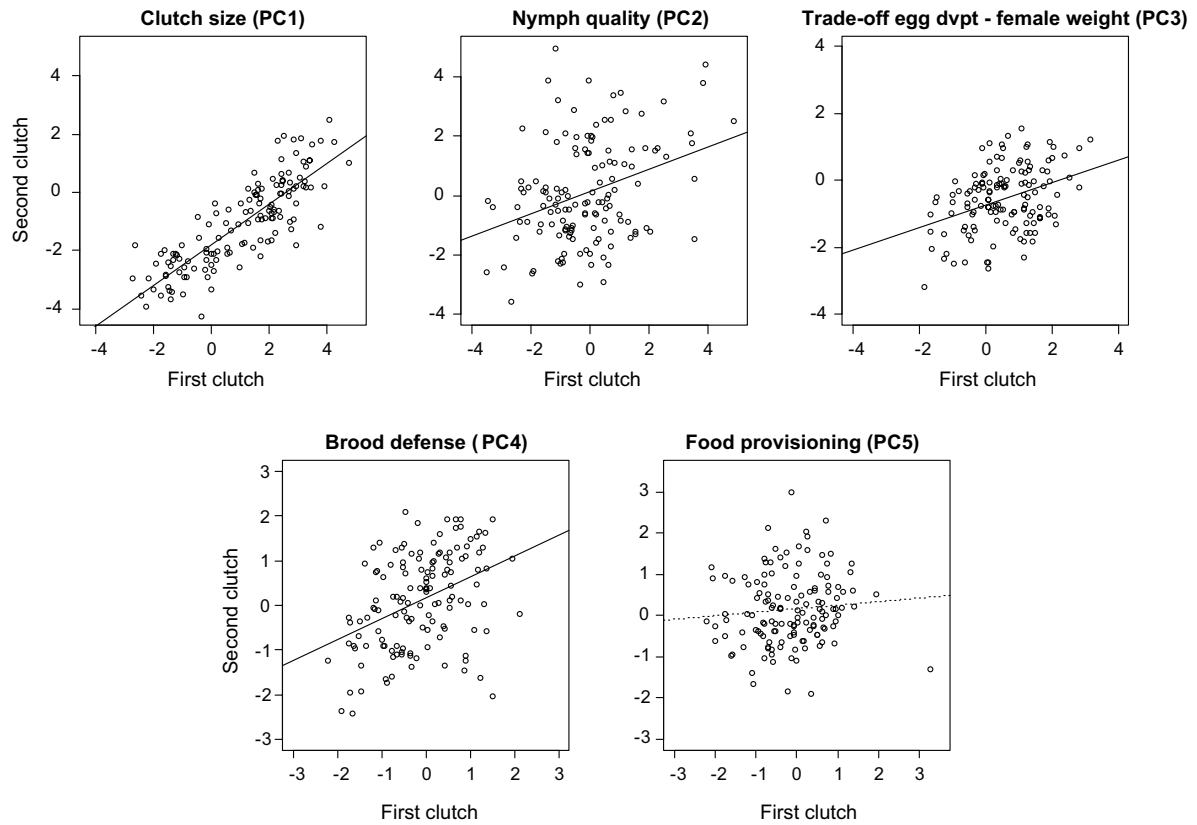


Figure 3. Influence of juveniles' cohort on the principal components reflecting brood defence (PC4) and food provisioning (PC5). Values represent means \pm s.e.m.



524 **Figure 4.** Associations between PC-values of the 1st and 2nd clutches.