

The contribution of individual and maternal experience in shaping *Daphnia* life history

Andrzej Mikulski · Joanna Pijanowska

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Abstract Maternal effects are among the key mechanisms generating phenotypic diversity in natural populations, but no general explanation has been found for why maternal effects are involved in shaping some, but not all, phenotypic traits. We investigated experimentally the relative importance of maternal and own risk perception in multi-trait response of a small planktonic crustacean *Daphnia magna* to the presence of fish. It appears that maternal effect is involved in shaping some key traits relating to adaptive changes in life history, such as duration time of egg holding in the brood chambers, age and size of mothers at first reproduction, and the number of first-clutch neonates. Other life history parameters, such as duration time of the release of the first clutch of neonates from the brood chamber and the size of neonates, were determined upon direct exposure to environmental risk. The relative contribution of maternal and own perception of risk in shaping individual phenotype depends on the time needed to

express particular life history trait. Long onset time increases the importance of maternal risk perception in the shaping of offspring phenotype.

Keywords Phenotypic plasticity · Maternal effect · Fish kairomone · Life history · *Daphnia magna*

Introduction

Maternal effects are among the key mechanisms generating phenotypic diversity in natural populations (Barnardo, 1996; Mousseau & Fox, 1998). They are involved in the shaping of the human phenotype and play a role in etiology of a number of diseases (see, e.g., Patterson, 2007). The adaptive role of maternal effects is discussed in a number of recent reviews and book chapters (e.g., Badyaev & Uller, 2009; Inchausti & Ginzburg, 2009; Cameron & Garcia, 2013) and the most commonly described is situation when mother adjusts the reaction norm of her descendant to anticipated conditions in the future. It is a so-called anticipatory maternal effect (AME; for review see Marshall & Uller, 2007).

The role of experience, both of the mother and the individual's own, in the formation of phenotype has been described for a number of species living over a wide range of environmental contexts. Conditions favoring adaptive phenotypic plasticity (within one generation or inter-generational) have also been the

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A. Mikulski (✉) · J. Pijanowska
Department of Hydrobiology, Faculty of Biology,
Biological and Chemical Research Center, University of
Warsaw, Żwirki i Wigury 101, 02-089 Warsaw, Poland
e-mail: a.mikulski@uw.edu.pl

focus of recent research interest (Berrigan & Scheiner, 2004; Marshall & Uller, 2007). There are still no data, however, elucidating the relative role played by maternal and the individual's own experience in shaping the phenotypic traits especially those involved in multi-trait adaptive mechanisms. No general explanation has been found for why maternal effects are involved in shaping some, but not all, adaptive traits. In order to answer this question, it is necessary to make use of an appropriate model system, one in which a single well-defined environmental factor can induce multi-trait adaptive transformations in the phenotype of an individual. The response of the small planktonic crustacean *Daphnia* to the presence of fish perfectly meets this criterion.

The anti-predator defenses in *Daphnia* constitute a well-known example of adaptive phenotypic plasticity (Tollrian & Dodson, 1999; Lass & Spaak, 2003). When confronted with the presence of chemicals released into their environment by a predator (kairomones; Von Elert & Stibor, 2006), *Daphnia* are capable of responding with noticeably changed behavior (Dawidowicz & Loose, 1992), morphology (Dodson & Havel, 1988; Dodson, 1989), and life history (Riessen, 1999). In the presence of fish, for example, *Daphnia* individuals may mature and reproduce earlier and at a smaller size (Stibor, 1992; Weider & Pijanowska, 1993). They hold their first-clutch embryos in the brood chamber for a shorter time (Mikulski et al., 2004), and release smaller neonates (Macháček, 1991) more quickly (Mikulski, 2001). In accordance with life history theory, early maturation in *Daphnia* results in a shortening of the average lifespan (Dawidowicz et al., 2010). These adaptations likely serve to either reduce vulnerability to predation, or to allow for better survival and reproduction under stress. In *Daphnia*, the role of maternal effect in the expression of phenotypic reactions to environmental factors by offspring has been extensively discussed (Rossiter, 1996; Mousseau & Fox, 1998). Maternal effects have also been investigated in the context of predator-induced shifts in morphology (Agrawal et al., 1999), resting egg production induced by deteriorating environmental conditions (Boersma et al., 2000; Alekseev & Lampert, 2001; LaMontagne & McCauley, 2001; Mikulski & Pijanowska, 2009), and enhancing *Daphnia* tolerance to toxic Cyanobacteria (Gustafsson et al., 2005; Jiang et al., 2013) and parasitic disease (Little, 2003; Mitchell & Read, 2005;

Schlotz et al., 2013; Garbutt et al., 2014). Maternal contributions to predator-induced changes in *Daphnia* life history were also revealed by Mikulski & Pijanowska (2009, 2010), but the relative contribution of individual's and mother's experience in shaping the eventual phenotype of the descendants has not been approached so far.

The main aims of this study were (i) to determine which traits of the *Daphnia* phenotype (focusing on those associated with first reproduction, and therefore, which are crucial for fitness under predation risk, such as size and age at maturity, time of holding eggs (THEs) in brood chamber, time of releasing neonates (TRNs) from brood chamber to the external environment, number and size of first-clutch neonates, and lifespan) depend on maternal and which on individual's own perception of danger, and (ii) to uncover the relative roles of mother and individual perception of danger in shaping the *Daphnia* phenotype.

Methods

In our experiment, we used *Daphnia magna* Straus, 1820 of a clone originating from Lake Binnensee, where *D. magna* coexists with fish. This clone was derived from ephippial egg, hatched in laboratory, and it was previously used in the study of Mikulski (2001). In pre-experimental cultures and over the course of the experiment, the animals were housed individually in glass jars containing 200 ml of aged, filtered water, from lake inhabited by fish. They were kept at 22°C under constant dim light and were fed green alga *Acutodesmus obliquus* (Turpin) Hegewald & Hanagata at a concentration of 1 mg C l⁻¹. Treatment-specific medium containing food was changed daily. The fish medium to which the *D. magna* would later be exposed was prepared by culturing one crucian carp (*Carassius carassius* Linnaeus, 1758; the same fish was used throughout the experiment) in 10 l of aged lake water (the same as used to prepare the control medium) for 24 h. During this time, the fish was fed *D. magna* (50 ind. day⁻¹). “Control” and “fish” water were filtered prior to use through a membrane filter of 0.2 µm.

Experimental design

One female (the “grandmother”: see Fig. 1) was the source of the first clutch of offspring (“mothers”: I

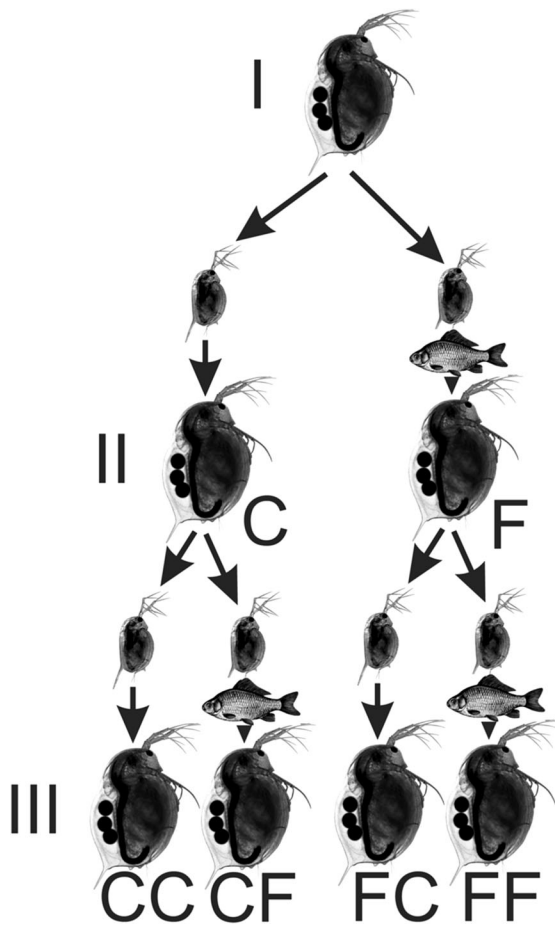


Fig. 1 Experimental design: the first clutch of offspring (mothers *I*) from a single female (the grandmother) were split into two groups. In control group *C*, the animals were not exposed to the presence of fish, whereas in the experimental group *F* they were exposed to this threat. Neonates from the first clutch of the cohort of the mothers (i.e., daughters *II*) were split into four groups. Animals from the control groups *CC* and *FC* were not exposed, while those from the two remaining groups (*CF* and *FF*) were exposed to the fish kairomone

experimental generation), which was then split into two groups. Animals from the first group were exposed from birth until vitellogenesis (until the moment when ovaries became dark) to the presence of fish kairomone, while those from the second group were not. It was done to clearly separate the direct and indirect (via maternal experience) effects of fish threat on offspring life histories. According to our observations, eggs, being already deposited in ovaries or brood chamber can, themselves, gather the information from the external environment and respond adequately.

Neonates taken from the first clutch of “mothers” from each treatment (i.e., “daughters”) were also split into two groups, each containing nine individuals. The presence of fish kairomone did not significantly affect the age at first reproduction (AFR) of the mothers, which allowed us to collect the descendants within short time and to run all treatments in the second stage of experiment in parallel. The main experiment lasted until the last female from daughters’ generation released her first-clutch offspring, and longevity measurements lasted 58 days. The sudden infection (extrinsic mortality) killed the animals that survived the 58th day of our experiment. Therefore, the “longevity part” of the experiment has been terminated.

Measurements

We studied the life history parameters of the *D. magna* from the daughters’ generation in detail. We were able to predict the schedule of key events based on the visible stage of development of eggs and/or embryos and the *D. magna* were observed every 5 min during the periods when such events might take place. In consequence, timing of birth, depositing the first-clutch eggs from the ovaries to the brood chamber, and the release of the first clutch of neonates from brood chamber were all measured with 5-min accuracy. Although the timing of *D. magna* life history parameters has earlier been measured with even higher precision (with 1-min accuracy—de facto permanently, e.g., Mikulski, 2001), our measuring period was sufficiently accurate for the purposes of this study.

We measured the daughters’ size at birth no later than 2 h after the offspring were released from the brood chamber. We measured the daughters’ size at first reproduction (SFR) when the animals were seen to be carrying their first clutch of eggs.

The duration of carrying the eggs in the brood chamber (THEs) was calculated as the time elapsed between the moment the last egg was released from the ovary into the brood chamber and the moment when the last neonate was released from the brood chamber into the external environment. The duration of neonates release (TRNs) was calculated as the time elapsed between the release of the first and the last neonate from the brood chamber into the external environment. Age at the time of release of the last first-

clutch neonate from the brood chamber was considered as the AFR.

We measured the length of the neonates [size of neonates (S-Nes)] released by the daughters during their first reproduction no later than 2 h after their birth. For statistical analysis, we used the average size of all neonates produced by each single mother. We carried out all measurements with 10- μm accuracy using the MultiScan software. *D. magna* were measured from the base of the tail spine to the top of the head. All *D. magna* neonates were counted to determine the number of neonates produced by each female (N-Ne). The females' survival rates were determined with 24-h accuracy (mortality was checked daily).

Statistics

We tested the effect of direct (via an individual's own risk assessment) and indirect (maternal, i.e., via the mother's experience) perception of the presence of fish on *D. magna* life history parameters with a multivariate analysis of variance (MANOVA). The effect of particular features on phenotypic traits was tested by ANOVA. We tested for differences in the life history parameters of the animals from the four experimental groups using Tukey's HSD test. To determine if variation in size at birth could explain the variation in the life history parameters investigated in this study, we used MANCOVA and ANCOVA models for each of the studied parameters. Maternal and direct effects of the presence of planktivorous fish on the survival of *D. magna* were tested using the Cox proportional hazard model, which allowed to overcome the problem of not normal distribution of the data, small number of replications, and closing the experiment before natural death of all individuals (Cox, 1972), and then checked for significance using Wald statistics. The model took into account the expected longevity of the animals which survived until the end of the experiment (e.g., censored data—see Bradley, 1974). All statistical analyses were conducted using the software package Statistica.

Results

The results of the MANOVA revealed that in *D. magna* several key life history parameters are strongly dependent on maternal experience, i.e., whether or not

the mothers were confronted with the fish threat [$R_{(5,12)} = 24.09$, $P < 0.0001$], as well as direct experience of the fish threat [$R_{(5,12)} = 5.03$, $P = 0.0102$], with a strong interaction between the two [$R_{(5,12)} = 7.82$, $P = 0.0017$].

Time needed to release the first clutch of offspring from the brood chamber (TRN), the size of first-clutch neonates (S-Ne, Table 1), and survival rates (see further text for details) appear to depend solely on the direct effect of fish presence, with no maternal effect involved. *D. magna* exposed to fish presence release smaller neonates (Fig. 2, lower left panel), release their neonates faster (Fig. 2, upper left panel), and live shorter (Fig. 3) than individuals that do not experience fish threat.

Maternal effect is involved in shaping all other studied parameters, but its role varies. It can work directly, influencing the phenotypic traits directionally irrespective of current environment (ANOVA shows

Table 1 Two-way ANOVA testing for the effect of indirect (i.e., maternal) and direct perception of the presence of fish on key life history traits in *Daphnia magna*

Traits	Effects	df Effect	df Error	F	P
THE	Maternal	1	21	1.01	0.3301
	Direct	1	21	14.22	0.0017
	Interaction	1	21	6.57	0.0208
AFR	Maternal	1	21	0.51	0.4864
	Direct	1	21	2.00	0.1763
	Interaction	1	21	16.76	0.0008
TRN	Maternal	1	20	2.37	0.1430
	Direct	1	20	10.05	0.0059
	Interaction	1	20	1.28	0.2739
SFR	Maternal	1	21	42.84	0.0000
	Direct	1	21	9.94	0.0062
	Interaction	1	21	5.40	0.0337
N-Ne	Maternal	1	16	48.91	0.0000
	Direct	1	16	0.00	1.0000
	Interaction	1	16	7.40	0.0152
S-Ne	Maternal	1	16	0.80	0.3848
	Direct	1	16	5.97	0.0266
	Interaction	1	16	0.04	0.8519

THE time of holding eggs in brood chamber, AFR age at first reproduction, TRN time needed to release all first-clutch neonates from the brood chamber, SFR size at first reproduction, N-Ne number of first-clutch neonates, S-Ne size of first-clutch neonates

Significant effects are bolded

Fig. 2 Life history parameters of experimental *Daphnia magna*: holding time of the first clutch of eggs in the brood chamber (*THE*), time required for the release of the first clutch of neonates from the brood chamber into the external environment (*TRN*), age at first reproduction (*AFR*), size at first reproduction (*SFR*), number of first-clutch neonates (*N-Ne*), and size of first-clutch neonates (*S-Ne*). The treatment code indicates maternal (*first letter*) or own (*second letter*) experience (*F*) or lack of experience (*C*) of fish presence; average \pm 1 SD; *significant difference from control (*CC*), Tukey's HSD test, $P < 0.05$

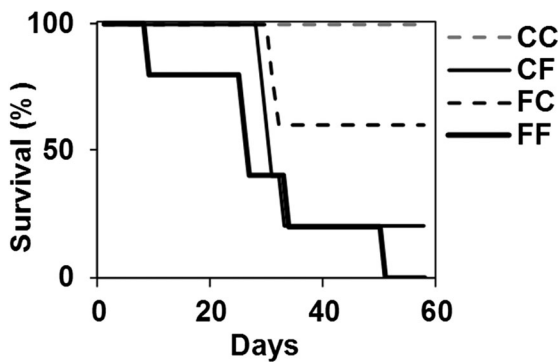
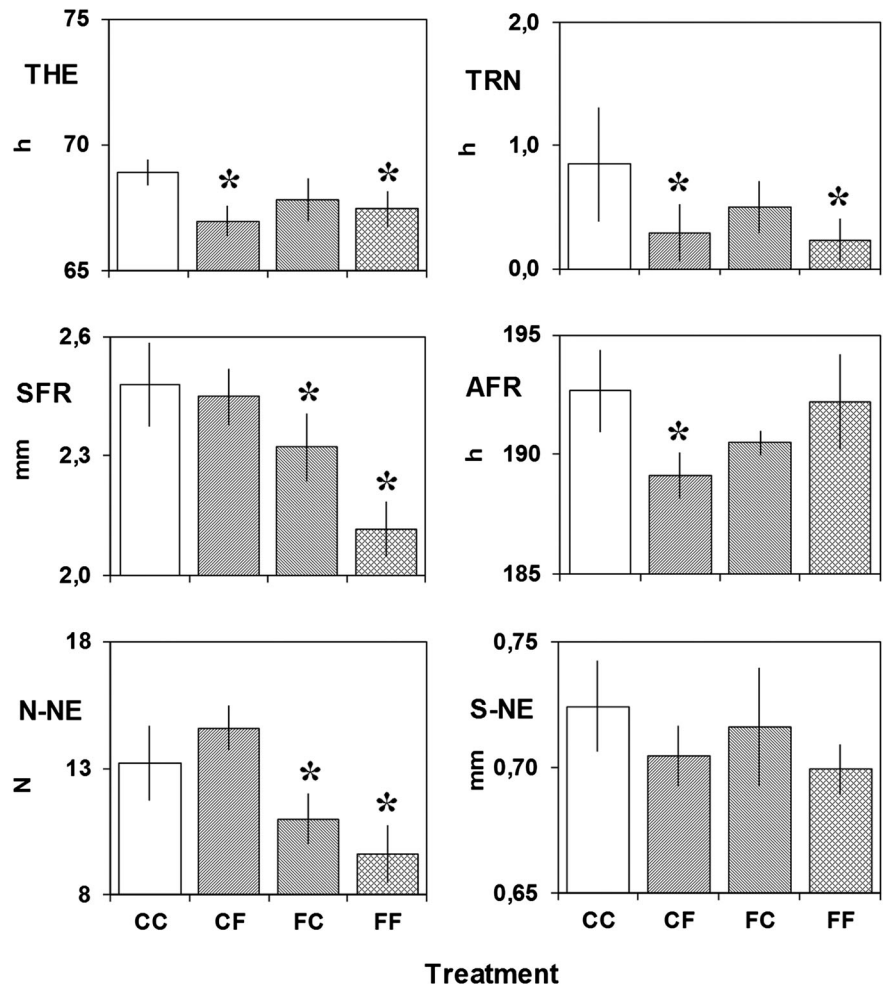


Fig. 3 Survival of experimental *Daphnia magna* offspring; treatment code indicates maternal (*first letter*) or own (*second letter*) experience (*F*) or lack of experience (*C*) of fish presence

significant effect of ME) or, indirectly, changing the direction and/or strength of *Daphnia* reaction to the presence of fish (ANOVA shows significant

interaction between direct and indirect effects—see also Fig. A attached as the electronic supplement).

Maternal experience of predator presence can decrease the direct, significant *D. magna* response to the threat in the case of THE (direct effect is related to shortening of this period; see Fig. 2, upper right panel; Table 1). It can reverse and cause insignificant direct effect of the threat in the case of the AFR (consisting in earlier reproduction, see Fig. 2, middle right panel). Maternal experience of predator presence directly decreases SFR, enhancing the direct effect of predator presence (see Fig. 2, middle left panel) and N-Ne (see Fig. 2, lower right panel).

The MANCOVA model revealed that, in general, life history parameters of individuals are not dependent on their size at birth [$R_{(7,9)} = 0.61, P = 0.7600$]. This applies to each of the studied life history parameters (ANCOVA results, Table 2).

As the results of the Cox model revealed, the presence of fish had a strong effect on *D. magna* survival (Fig. 3, $\chi^2_{(2,20)} = 11.76$, $P = 0.0028$). Offspring survival depends mostly on direct [$W_{(2,20)} = 7.47$, $P = 0.0063$] rather than on maternal experience of the danger [$W_{(2,20)} = 1.49$, $P = 0.2221$]. However, as shown in Fig. 3, maternal effect seems to be important as well, and failure to obtain significant results may be due to our small sample size and the extrinsic mortality that forced us to terminate the experiment after 58 days.

Discussion

Most of the *D. magna* life history parameters which were the focus of our study, and which can be considered crucial for individual's fitness, were influenced by both maternal and direct perception of fish presence. The observed pattern of shifts in *D. magna* life history in our study was consistent with previously published data (Riessen, 1999): individuals only directly exposed to fish presence carried their eggs in the brood chamber for a shorter time (THE; Mikulski et al., 2004), released neonates into the external environment faster (TRN; Mikulski, 2001), released those neonates earlier (AFR; e.g., Stibor, 1992), and lived shorter (Dawidowicz et al., 2010) than unexposed individuals. Lack of a statistically significant direct influence of the presence of fish on the SFR and the N-Ne or S-Nes produced, respectively, earlier documented for various clones from Binnensee, can be explained in the light of known interclonal variability in the response to environmental stress (e.g., Boersma

et al., 1998; Bernatowicz & Pijanowska, 2011). In the study of Boersma et al., the decrease of SFR in response to fish kairomone has been observed in ca. 50% of the *D. magna* clones from Binnensee. Thus, different genotypes show different responses to predation cues. The phenomenon of either reduced or unreduced SFR in *D. magna* in the response to predation threat has also been previously discussed as context dependent (see, e.g., Mikulski, 2000).

Depending on the extent to which maternal effect is involved in the expression of offspring phenotypes, life history parameters in *D. magna* can be classified into two groups. The first group includes traits which depend solely on the direct effect of fish presence, such as TRN and S-Ne. The second group includes traits which are either under direct control of maternal effect or are part of the interaction of maternal effect with fish presence. These are THE, AFR, SFR, and N-Ne.

Why are some traits of the life history of *D. magna* controlled by maternal effect while others are not? In our opinion, the key reason is the moment of exposure to environmental stress in ontogenesis and the time needed for the development of a particular life history trait. For example, the S-Nes may probably be determined within a couple of hours during the process of vitellogenesis. Females may provide eggs with more or less yolk based on the direct perception of environmental conditions. Additionally, mothers are able to regulate quickly the time needed to release their offspring via direct perception of environmental risk. Alternatively, traits such as AFR and SFR, N-Nes released, and egg-holding time in the brood chamber result from a more long-term strategy of resource allocation and they may be determined 2–3 days before first reproduction (Mikulski et al., 2004).

The variability shown by *D. magna* in the expression of these different phenotypic traits allows us to postulate a strong hypothetical role for maternal effects in shaping offspring phenotype. Phenotypic reaction to environmental stress is generally not instantaneous; there is a measurable time period (lag time) between the perception of an environmental cue, the initiation of phenotypic changes (even when not yet visible), and the moment when these changes become adaptive (this problem is thoroughly discussed by Mikulski et al., 2005). When the lag time in emergence of a trait is long, there is a high probability that the risk disappears and individuals will incur the

Table 2 Effects of size at birth as a covariate in an ANCOVA model testing the effects of indirect (i.e., maternal) and direct perception of the presence of fish kairomone by *Daphnia magna*

Traits	df Effects	df Errors	F	P
THE	1	20	0.86	0.3678
AFR	1	20	0.10	0.7615
TRN	1	20	0.86	0.3696
SFR	1	20	1.53	0.2350
N-Ne	1	20	1.73	0.2087
S-Ne	1	20	0.43	0.5196

costs of the defensive mechanism without having drawn any advantage from it. In such a case, additional information is required about the nature and persistence of the hazard. We hypothesize that this information may originate from maternal experience. When a mother is subjected to long-term exposure to a predation risk, that risk will likely persist long enough to overlap with the lifespan of her descendants. This suggests that a longer lag time in the induction of adaptive phenotypic changes can promote an increased role of maternal effect.

In our study, maternal effect caused a significant reduction in SFR and N-Ne. In these cases, this effect, itself statistically significant, was substantially modified by the direct effect of fish presence. The number of first-clutch neonates is likely to be determined during the early stages of ontogenesis, when an individual's own perception of the environment may still be impaired (Mikulski et al., 2004); this further highlights the potential importance of maternal effect in determining early fecundity. AFR is dependent on the interaction between maternal effect and direct effect of the presence of fish. Surprisingly, unlike in the case of SFR, maternal effect appears to reverse the effect of direct perception of fish presence. Both the time needed by first-clutch neonates to evacuate from the brood chamber and the S-Nes can probably be finally modified during 'pregnancy,' depending on environmental conditions (here, the presence or absence of fish kairomone). In consequence, maternal role in the induction of these two traits is negligible. Although available information on the length of lag time between the perception of environmental stimulus and appropriate adaptive response in *D. magna* is scarce (but see Mikulski et al., 2004, 2005), we claim that our reasoning well explains the role of maternal effect in the determination of individual phenotype and the phenomenon is certainly worth further experimental testing.

Although the key life history traits investigated in our study are strongly interrelated, it seems that they can be expressed independently. In our experiment, the life history parameters of individuals did not depend on their size at birth. In other words, differences in size at birth did not explain differences in other phenotypic traits expressed in later stages of ontogenesis, thus they were not the mechanism through which maternal effect operated, though they have been indicated as crucial path of maternal

influence in earlier studies (e.g., Lampert, 1993; Tollrian, 1995; Beckerman et al., 2006). Mothers, therefore, had a more subtle impact on the development of their offspring via molecular or epigenetic transfer. Indeed, nongenetic transfer of information from parental to offspring generation has gained much attention in the past years (e.g., Haussmann et al., 2012; Hayward et al., 2012; Schwarzenberger & von Elert, 2012; Wu et al., 2012; Zwier et al., 2012) due to the fact that epigenetic processes often outweigh genetic background in the shaping of phenotypes. Due to the important role of the mother during early development, there is much ongoing research on the means by which maternal effects can shape the individual, i.e., on (1) how and when maternal effects change the developmental trajectory to permanently alter the adult's phenotype, (2) molecular mechanisms associated with maternally induced life history phenotypes, and (3) the evolutionary implications of maternally mediated changes in phenotype.

Our study demonstrates that observed, maternally determined changes in the life history of *D. magna* are an excellent example of AME (Marshall & Uller, 2007). Mothers, depending on their own perception of environmental conditions (in this case, the presence of predation risk), were able to anticipate future threats and adaptively influence the phenotype of their offspring, thus increasing their relative fitness.

Although our results clearly demonstrate a link between maternal effect and the time needed to express phenotypic change, caution is required in interpretation as they were based solely on a single *D. magna* genotype. In order to formulate a more general conclusion, similar research should be repeated using more *D. magna* clones.

Conclusions

The results of our study suggest that adaptive changes, which are expressed shortly after the exposure to a predation threat, can be determined upon direct perception of environmental risk. However, developmental changes requiring longer time to be expressed in offspring depend primarily on maternal perception of the risk. Similarly, maternal effect is heavily involved in the expression of traits which are primarily or solely determined in early stages of ontogenesis. All of this evidence supports the idea that the passage of

time, which is required for the onset and expression of phenotypic traits, is an important factor with the potential to promote the evolution of adaptive inter-generational phenotypic plasticity.

The proposed mechanisms can help understand why maternal effect is entangled in such a complex way in the expression of long-term inducible mechanisms such as adaptive changes in morphology (Agrawal et al., 1999) or reproductive patterns, e.g., the formation of ephippial eggs (Alekseev & Lampert, 2001; LaMontagne & McCauley, 2001; Mikulski & Pijanowska, 2009). Additionally, our data provide an explanation why no evidence has been found so far for the role of maternal effect in the development of relatively rapid responses such as behavioral traits (e.g., locomotory response and escape, crowding, and vertical migration).

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