In the heat of the moment

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Offspring developmental temperature is more relevant than maternal environment in determining adult temperature performance of *Drosophila melanogaster*

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Abstract

Besides inherited genes and developmental environment, an organism's phenotype can be modified by parental effects, a predictive change produced by parental influence on their offspring to better prepare them to face future environmental challenges, such as exposure to extreme temperatures. Assessing the adaptive significance of parental effects is highly interesting as consequences can be beneficial or harmful to the offspring; parental influence could produce an adaptive change if offspring conditions are similar to that of their parents. However, parental effects could also lead to non-adaptive offspring phenotypes when the environment differs or when changes are related to carry-over effects that reduce offspring phenotypical flexibility. The fruit fly *Drosophila melanogaster* has been a useful model to unravel the underlying mechanism of multiple behavioral and phenotypical characteristics. Flies live in habitats that span a wide range of temperatures and have shown apparent parental effects, such as flies from parents raised in warm environments developing faster and having a higher heat tolerance than flies with parents from colder areas. Only one study has looked specifically at temperature-related parental effects in *Drosophila*, demonstrating a strong influence of maternal thermal environment on offspring survival from egg to adult. Here, we used a split-brood match and mismatch design to estimate maternal effects on offspring response to temperature. Mothers from an inbred population of flies were exposed to a cold (18°C) or hot (29°C) environment and their brood was split between matched and mismatched conditions. We found maternal effects on offspring climbing speed. The response to gradually increasing temperatures and to heat or cold-shocks depended mostly on the phenotypic plasticity of the offspring to the environment they were raised in, independent of maternal influence.

Keywords

Maternal effect, Matched and mismatched, temperature environment, Drosophila, fitness.

Introduction

Every environment produces challenges that organisms must face to survive. When these challenges are predictable, parents may be capable of influencing the development of their offspring to better face them (Engqvist and Reinhold, 2016; Mousseau and Fox, 1998) by, for example, changing egg composition, immune factors, or stimulating epigenetic changes (Groothuis et al., 2005; Ledón-Rettig et al., 2013). This parental influence, known as 'anticipatory parental effects' or 'adaptive transgenerational plasticity', functions as a cue that directs offspring plasticity into shaping a phenotype that takes advantage of that information (Agrawal, 1999; Crean and Bonduriansky, 2014; Galloway and Etterson, 2007; Mousseau and Fox, 1998; Mousseau et al., 2009; Uller, 2008). Parental effects (Marshall and Uller, 2007), together with inherited genes and the developmental environment, determine offspring phenotype (Adrian-Kalchhauser et al., 2018; Mousseau et al., 2009). Understanding parental effects is thus important to understanding how an individual phenotype develops.

Parental effects buffer offspring resistance against environmental stressors in plants and insects (Agrawal, 1999; Agrawal, 2002; Galloway, 1995; Mousseau and Dingle, 1991), increase disease resistance of crustaceans (Mitchell and Read, 2005) and beetles (Roth et al., 2010), and benefit development and stress tolerance of fish (Munday, 2014; Salinas and Munch, 2012). However, parental effects can also be non-adaptive or even maladaptive when parental and offspring environment differ and therefore parental influence decreases offspring performance (Crean and Marshall, 2009; Marshall and Uller, 2007), or when they are merely carry-over effects of the parental environment that do not have any adaptive value for the offspring (Engqvist and Reinhold, 2016; Nettle and Batteson, 2015; Uller et al., 2013). For example, prenatal stress in mothers can lead to susceptible smaller offspring in fish (Munday, 2014), and diminish offspring learning and social coping in rodents and non-human primates (Kofman, 2002). Maternal environment can also affect germination cycles in plants (Donohue, 2009), population size of soil mites (Plaistow and Benton, 2009), and size of earwig (Raveh et al., 2016) without any anticipatory value. In addition, the potential value of parental effects depends on the time lapse between environmental cue perception by the parents and selection on the offspring, the degree of variation of said cue, the adaptive value of modifying offspring phenotype, and the plastic capacity of the offspring (Auge et al., 2017; Engqvist and Reinhold, 2016). Thus, anticipatory and adaptive parental effects are expected to evolve only when parental and offspring environment sufficiently correlate, and when offspring plasticity is limited and parental input would confer an advantage (Adrian-Kalchhauser et al., 2018; Auge et al., 2017; Engqvist and Reinhold, 2016; Gibert et al., 2001). Although parental effects could be fundamental in understanding how species could adapt to rapidly changing environments, the prevalence and significant of parental effects still remains poorly understood (Sultan, 2007; Uller et al., 2013).

In this study we investigated the anticipatory nature of maternal effects in the context of temperature adaptation using the fruit fly *Drosophila melanogaster*. Temperature influences all levels of biological organization (Good, 1993) and small ectotherms, such as fruit flies, are particularly susceptible to this ambient variable (Hoffmann et al., 2003). *Drosophila* are

present in habitats that span multiple climates to which they have selectively adapted to (Jezovit et al., 2017), while still remaining plastic if developed at a different temperature. For example, populations from temperate areas are more resistant to desiccation than populations from tropical zones (Hoffmann et al., 2003; Kellermann et al., 2012) and flies from warmer areas perform better at warmer temperatures while flies from colder regions fare better in cold scenarios (Gibert et al., 2001). At the same time, flies from the same population raised in warmer temperatures are more resistant to heat-shock (Gibert et al., 2001; Gilchrist et al., 1997) and prefer higher temperatures (Good, 1993), while flies raised in cold temperatures are faster in cold environments (Gilchrist et al., 1997) and have higher survival rate when exposed to a cold-shock (Watson and Hoffmann, 1995). Apparent parental effects also affect flies. Offspring of flies raised in warm temperatures have a faster developmental speed (Crill et al., 1996; Gilchrist, 1996), a higher knockdown temperature, smaller body size (Crill et al., 1996), and reduced cold tolerance (Watson and Hoffmann, 1995) when compared to offspring of flies raised in colder temperatures. However, these studies have not specifically separated maternal effects from offspring plasticity or carry-over effects. One recent study addressed this distinction by using a match and mismatch offspring design (Mohan et al., 2018). This design allows differentiating offspring plasticity from adaptive maternal effects by exposing offspring from the same mother to different temperature environments, although it was not possible to completely eliminate the conceivable influence of temperature-dependent carry-over affecting the parents before egg laying (Engqvist and Reinhold, 2016). Results from these experiments demonstrated that only survival from egg to adult had a strong dependency on maternal influence. Developmental speed, body size, and fecundity were mostly affected by offspring environment, with a minimum influence of maternal condition. In the series of experiments presented here we used the same split-brood match and mismatch design to test maternal effect over offspring response to temperature, which was not previously tested. We exposed mothers to a cold (18°C) or hot (29°C) environment and then split their clutches among matched and mismatched scenarios. Once offspring developed to adulthood, we examined offspring response to temperature based on recovery from heat- and cold-shock, climbing speed, and speed at gradually increasing temperatures to look for potential temperature-related maternal effects.

Methods

Fly rearing and split-brood match-mismatch temperature treatment

Drosophila melanogaster Oregon-R stock flies were raised in LD 12:12 at 25°C on fly food medium containing agar (10 g/L), glucose (167 mM), sucrose (44 mM), yeast (35 g/L), cornmeal (15 g/L), wheat germ (10 g/L), soya (10 g/L), molasses (30 g/L), propionic acid and Tegosept (for food medium preparation see Gorter et al., 2016). For experiments, approximately 500 flies were transferred to an egg-laying cage with a removable egg-laying dish of 100mm x 15mm layered with 3 ml of a solution composed of 20g agar, 26g sucrose, 52g glucose, and 9% (v/v) red grape juice spotted with a fresh dab of dry yeast

mixed with water (Mohan et al. in progress) also kept at 25°C in LD 12:12 incubator. The egg-laying dish was removed after 24h and kept in the same incubator as the egg-laying cage. Larvae were collected 24h later and transferred in groups of 50 to vials of 25mm x 95mm containing 6ml of fly food medium. Flies developed to adulthood at 25°C in LD 12:12. Virgin males and females were collected under CO2 anaesthesia. Virgin males were placed in vials in groups of 20 flies inside an incubator at 25°C with LD 12:12 cycles. Virgin females were individually placed in vials with 6ml of food and transferred within 1h of collection to a walk-in climate chamber at either 18°C (±1°C range) or 29°C (±1°C range) with LD 12:12 cycles. Female flies were acclimated for 24hrs, after which they were paired with one virgin male and allowed to mate for 24hrs within their respective climate chambers. After this period, males were removed and individual females were transferred to an inverted egg-laying vial fitted on top of a 1.5 cm food medium patch. Females were changed to a new patch every 1h during 12h. For the flies at 29°C, this process started immediately after male removal. For flies at 18°C, this process started 48h after male removal as flies require a longer time to start depositing sufficient eggs for our experiments at this temperature. Eggs were collected from each batch immediately after female removal and placed in groups of 2-15 in vials containing 6ml food. The total number of eggs per vial depended on the amount of eggs deposited by each mother, as each brood was split in two equal parts. This created two matched conditions: offspring

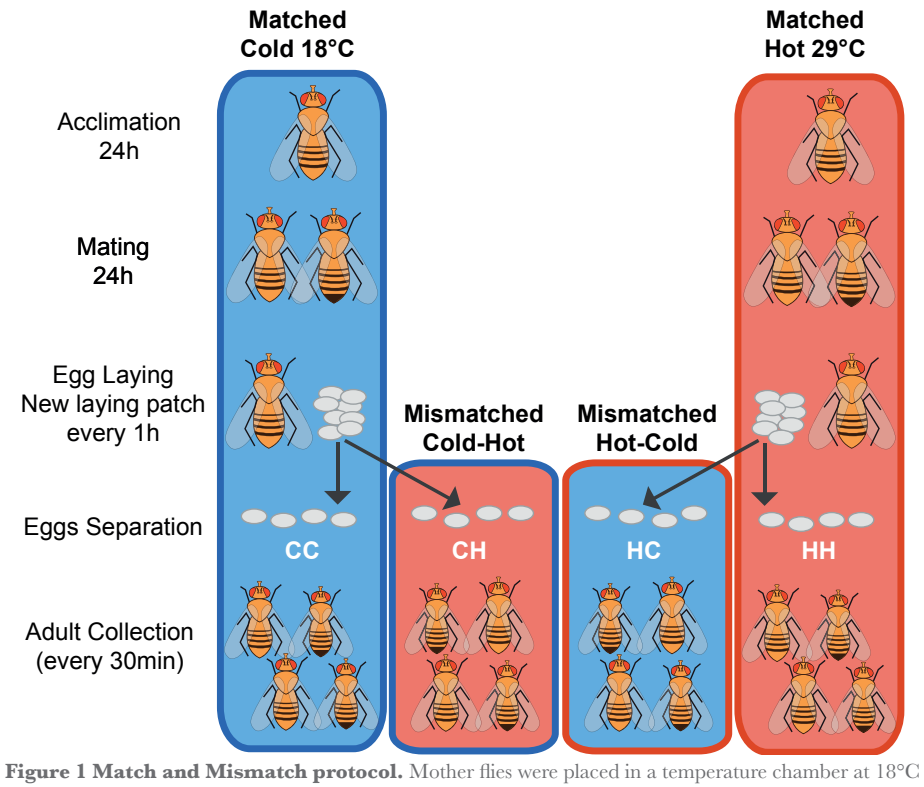

Figure 1 Match and Mismatch protocol. Mother flies were placed in a temperature chamber at 18°C or 29°C and allowed to acclimate for 24h. They were then paired with a male and allowed to mate for 24h. Eggs were separated in two groups per mother: one stayed in the same temperature chamber (matched: CC and HH), and one was taken to the opposite temperature chamber (mismatched: CH and HC). Adults were collected within 30 minutes after eclosion.

from 18°C mothers grown at 18°C (CC) and offspring from 29°C mothers grown at 29°C (HH); and two mismatched conditions: offspring from 18°C mothers grown at 29°C (CH) and offspring from 29°C mothers grown at 18°C (HC). The process is illustrated in Figure 1. Offspring were checked daily every 30min between 6:00 am and 6:00 pm from two days before expected eclosion time to two days after expected eclosion time. Vials at 29°C eclosed 7 days after egg collection while vials at 18°C eclosed 14 days after egg collection. This ensured that all offspring were collected within 30 minutes of eclosion and placed in individual vials kept in the same temperature in which they were raised before temperature response experiments.

Temperature performance measurements

Temperature performance was tested between 2h and 6h after eclosion. The delay was introduced to allow flies from both temperatures to extend their wings, as flies from 18°C matured slower than flies from 29°C, and to have a window of opportunity in which to test flies that eclosed at the same time. The first female and first male collected from each vial were used to test their response to gradually increasing temperatures in a temperature-controlled arena (as described in Soto-Padilla et al., 2018). Briefly, one fly was transferred to a 2.5 x 7.5 cm arena using a mouth aspirator and allowed to walk freely for 7 minutes at 16°C to get accustomed to the arena, after which the temperature was increased 2°C every 60 seconds until 44°C. Flies were continually video recorded with a high definition webcam (Logitech® c920, Logitech Europe S.A., Lausanne, Switzerland) and tracked using custom-made software (Python Software Foundation Version 2.7.6, http://www.python.org; Soto-Padilla et al., 2018). Fly centroid data was imported into RStudio and a custom script (RStudio Team: 2016, Version 1.0.143) was used to calculate the average speed per temperature used for analysis.

The second and third collected females of each vial were used for heat and cold-shock experiments. The similarity between the temperature reaction norms of males and females (Soto-Padilla et al., 2018; also confirmed in the similarity of sexes in the temperature curves in Supplementary Table 1) allowed us to only use female flies for these other temperature response tests. For the heat-shock recovery test, flies were placed individually in a 40x8x0.8-1 mm glass vial that was placed inside 25mm x 95mm empty vial and submerged in a hot bath set at 42°C for 7 minutes. Recovery time was measured between the moment flies were taken out of the bath and the moment they started walking again. For the cold-shock recovery test, flies were placed individually in a 40x8x0.8-1mm glass vial that was placed inside 25mm x 95mm empty vial, which was then placed in ice at 0°C for 5h 45 min. Ice temperature was measured every 3-4 h to ensure temperature consistency. Time to recovery was measured between the moment flies were taken out of the ice and the moment they started walking again.

The climbing speed test was done with females used for heat-shock and cold-shock recovery test prior to these experiments. Flies were taken from the climate chambers and taken to a room at 25°C to be transferred to an apparatus with six attached empty vials of 25mm x 95mm and a scale to measure distance. The apparatus was tapped once from a fixed height to force all flies to fall to the bottom of the vial. Photos were taken every

second for 5 seconds with a webcam (Logitech® c920, Logitech Europe S.A., Lausanne, Switzerland). The process was repeated 5 times for each group of six flies. Photos were imported to ImageJ (ImageJ bundled with 64-bit Java 1.8.0_112, https://imagej.nih.gov/ij/) to calculate average walking speed based on the distance moved in consecutive images. The three largest values of the five samples were used for final measurements to ensure capturing the maximum speed.

Data Analysis

Data was analyzed using Bayesian inference in R (*brms* version 2.9.0, Bürkner, 2018; *rstan* version 2.18.2, R Core Team 2018 Version 3.5.2). The (Bürkner, 2018)exposure to gradually increasing temperatures was analyzed through a hierarchical generalized additive model with a gamma hurdle distribution, with a log link function for the gamma part and a logit link for the hurdle part. The hurdle parameter (σ) and the shape parameter of the gamma distribution (k) were fitted with thin plate spline smoothers with respect to temperature as single predictor. The scale parameter of the gamma distribution (θ) was fitted with separate global smoothers with respect to temperature for each of the four treatments and an intercept that varied by sex and mother ID. For each individual fly a separate "random smoother" was fitted (factor-smoother interaction basis type; adapted from model GS in Pedersen et al., 2019). The model was run with 10 parallel chains with 2,000 iterations each, where the first 1,000 were used as warm up and discarded. Priors for population-level effects were normal distributions with a mean of 0 and a standard deviation of 10, while priors for standard deviations of group-level effects were Student's t distributions with a mean of 0, a standard deviation of 10 and 3 degrees of freedom (default *brms* prior). Trace plots, effective sample sizes (range of effective sample sizes: 485 – 6887) and R-hat (Gelman and Rubin, 1992) values (1 <R-hat < 1.02) confirmed proper convergence.

Results from heat-shock, cold-shock, and climbing speed experiments were analyzed using a multivariate Gaussian response model. For each of the three experiments, the response variable was fitted separately for the matched and mismatched conditions, yielding a multivariate model with a total of six potentially correlated response variables. Each response variable was fitted with an intercept that varied by condition, mother ID and individual ID. This setup allowed us to estimate within-mother correlations between (1) within-experiment measurements on siblings from matched and mismatched conditions, (2) between-experiment measurements on siblings, and (3) between-experiment measurements on the same individual. The multivariate model was run with 4 parallel chains, with 5,000 iterations each, where the first 1,000 were used as warm up and discarded. Priors for population-level effects and group-level standard deviations were the same as above, and for correlation coefficients the brms default prior of an LKJ (eta = 1) distribution was used. As before, trace plots, effective sample sizes (range of effective sample size: 196 – 9326) and R-hat values (1 < R-hat < 1.04) confirmed convergence.

Results

Maternal temperature affects climbing speed but not cold- or heat-shock recovery

The cold-shock (Fig. 2A) and heat-shock (Fig. 2B) recovery tests showed that offspring's environment is the main determinant of recovery speed (Table 1). Flies raised at 18°C recovered faster from the cold-shock, while flies raised at 29°C recovered faster from the heat-shock, with those from mothers kept at 18°C recovering slightly faster in both tests (Table 2). The climbing speed test showed an effect of both offspring and maternal environments (Fig. 2C; Table 1: 89% directional posterior probability of maternal condition effect and 91% directional posterior probability of offspring condition effect). Offspring raised at 29°C were faster than offspring raised at 18°C; however, offspring from mothers kept at 29°C were faster than their counterparts from mothers kept at 18°C (Table 2). The pattern of differences observed in the multiple comparison tests (Table 2) suggests there is an apparent additive effect of having a mother kept in 29°C and developing at 29°C to produce an increased climbing speed.

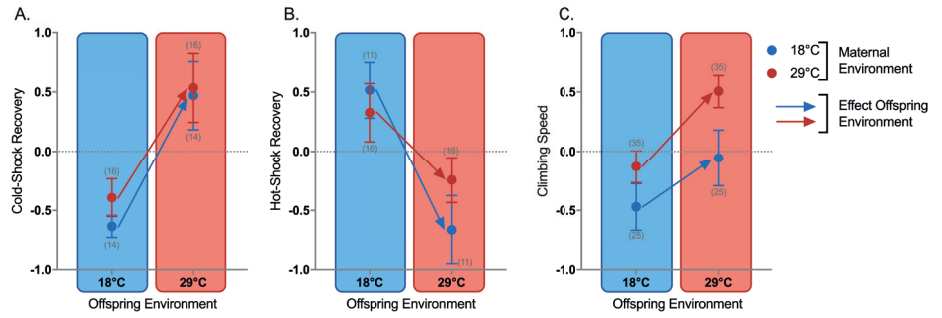

Figure 2 Response to temperature tests. A. Cold-shock recovery. Flies kept at 18°C recovered faster. **B.** Heat-shock recovery. Flies kept at 29°C recovered faster. **C.** Climbing speed. Test performed at 25°C. Flies kept at 29°C walked faster, with those from mothers also kept at 29°C walking the fastest. Data are mean and s.e.m.

Maternal temperature has a minor influence in offspring's response to gradually increasing temperature

The gradually increasing temperature curve suggests that offspring raised at 29°C from mothers kept also at 29°C were the fastest flies (Fig. 3A), consistent with the hypothesis that mothers influence the overall motility of their offspring, although this was not quite statistically significant (Fig 3B-D). Indeed, the analysis of the gradually increasing temperature curve showed that the offspring environment and the changing temperatures were the main determinants of the speed of the flies, with those raised at 29°C moving faster at relatively high temperatures than those raised at 18°C. Flies raised at 29°C also decayed later than flies raised at 18°C (Fig. 3A).

Estimate	Trait	Mean	SD	Lower 90% CI	Upper 90% CI	Directional post. prob.
Mother condition	Cold-shock Recovery	-0.25	0.35	-0.82	0.33	0.77
Offspring condition		-1.12	0.37	-1.72	-0.53	1.00
M x O interaction		-0.14	0.50	-0.97	0.67	0.61
Mother condition	Heat-shock Recovery	0.19	0.37	-0.41	0.81	0.69
Offspring condition		1.17	0.42	0.48	1.87	1.00
M x O interaction		0.60	0.53	-0.28	1.47	0.88
Mother condition	Climbing Speed	-0.34	0.27	-0.78	0.09	0.89
Offspring condition		-0.40	0.29	-0.88	0.06	0.91
M x O interaction		0.23	0.38	-0.39	0.83	0.73

Table 1 Summary of posterior distribution for multivariate model for cold-, heat-shock recovery and climbing speed

Note: Directional posterior probability represents the posterior probability that the tested effect has the same sign as the mean. Mother and offspring interaction (MxO).

Comparison	Parameter	Estimate	Estimate Error	Lower 90% CI	Upper 90% CI	Directional post. prob.
CC - CH	Cold-shock Recovery	-1.12	0.37	-1.72	-0.53	1.00
CC - HC		-0.25	0.35	-0.82	0.33	0.77
CC - HH		-1.23	0.36	-1.81	-0.65	1.00
CH - HC		0.87	0.34	0.32	1.43	0.99
CH - HH		-0.11	0.35	-0.68	0.46	0.62
HC - HH		-0.98	0.34	-1.53	-0.43	1.00
CC - CH	Heat-shock Recovery	1.17	0.42	0.48	1.87	1.00
CC - HC		0.19	0.37	-0.41	0.81	0.69
CC - HH		0.76	0.33	0.22	1.31	0.99
CH - HC		-0.98	0.44	-1.70	-0.28	0.99
CH - HH		-0.41	0.40	-1.09	0.23	0.85
HC - HH		0.57	0.32	0.04	1.10	0.96
CC - CH	Climbing Speed	-0.40	0.29	-0.88	0.06	0.91
CC - HC		-0.34	0.27	-0.78	0.09	0.89
CC - HH		-0.97	0.26	-1.39	-0.57	1.00
CH - HC		0.07	0.28	-0.40	0.53	0.59
CH - HH		-0.57	0.27	-1.00	-0.13	0.98
HC - HH		-0.63	0.24	-1.04	-0.22	0.99

Table 2 Pairwise comparisons between all four conditions for multivariate model on cold-shock recovery, heat-shock recovery and climbing speed

Note: Directional posterior probability represents the posterior probability that the tested comparison has the same sign as the mean. First letter maternal temperature and second letter offspring temperature (C=18°C; H=29°C).

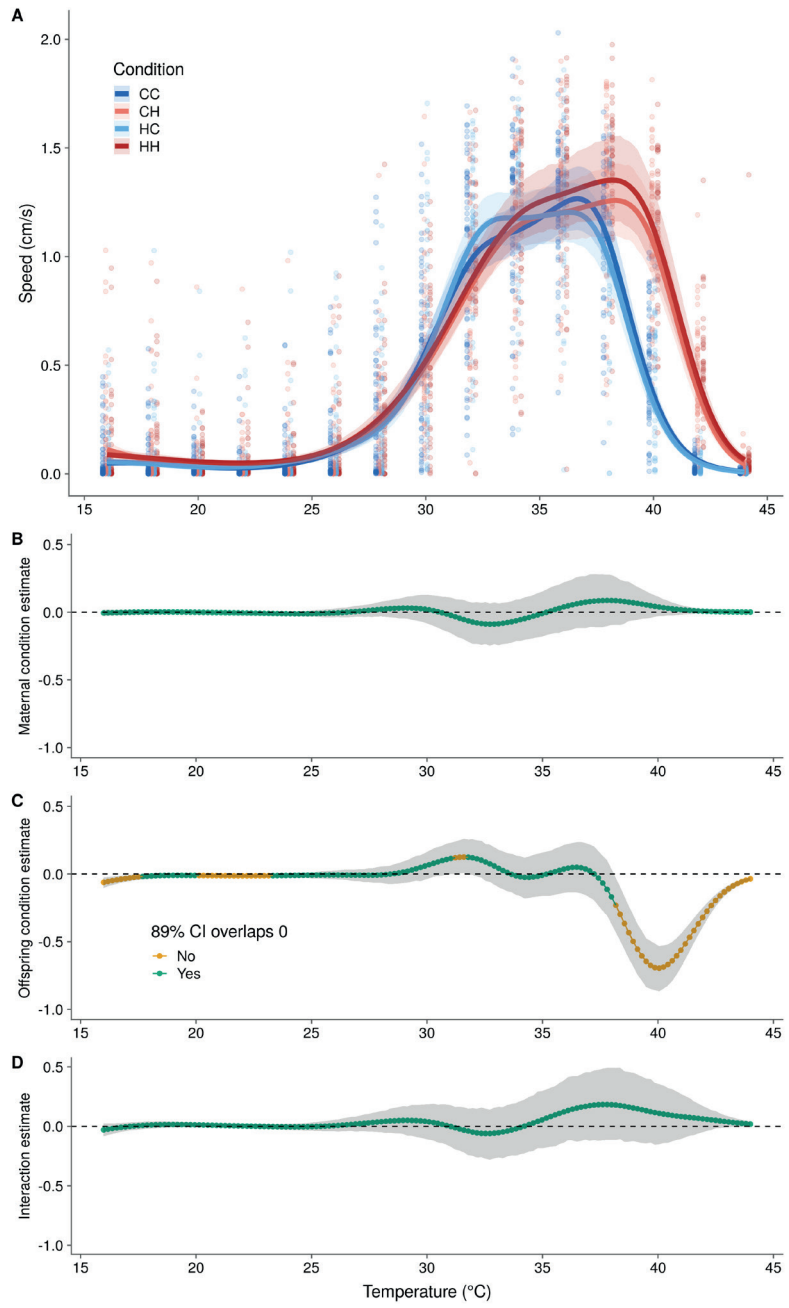

Figure 3 Temperature response curve and main effects of fitted curve. A. Fit curve of speed response to gradually increasing temperature. Flies raised at 29°C move faster at lower temperatures and decay later than flies raised at 18°C. B-D. Main effects of fitted temperature response curve for maternal condition **B.**, offspring condition **C.**, and their interaction **D.**. Ribbons represent 89% highest density interval of posterior distribution. Green points represent values not statistically different from zero and yellow points represent values statistically different from zero.

Discussion and Conclusion

We used a split-brood match and mismatch design to explore maternal effects on offspring response to temperature. We found that offspring response was mainly determined by the environment in which the offspring developed, with those raised at 18°C recovering faster from cold-shock, those raised at 29°C recovering faster from heat-shock, and those raised at 29°C moving faster in the climbing speed test and when exposed to gradually increasing temperatures (Fig. 2 and 3). Maternal effects, however, were hinted at by subtle differences between offspring raised at the same temperature but coming from 18°C mothers or 29°C mothers: offspring from 18°C mothers recovered faster in both, cold- and heat-shock test, and were slower in the climbing speed test and when exposed to gradually higher temperatures after being raised at 29°C. This could have emerged as consequence of carry-over effects of the cold temperature over mothers and not from an anticipatory maternal effect. Flies reared in cold environments have larger bodies with greater fat content and slower metabolism when compared to flies from warm environments (Adrian et al., 2016; Czarnoleski et al., 2013; Klepsatel et al., 2013; Li and Gong, 2015). It is possible that mothers exposed to a cold environment transferred these characteristics to their offspring, conferring a higher resistance to extreme temperatures due to the extra fat layer protecting the core of the fly, which could have reduced the intensity of the effect of extreme temperatures in our shock tests, accelerating recovery. A greater fat content has been linked to a slower metabolism (Brookheart and Duncan, 2016; Palu et al., 2017), which could explain the slower walking rate of offspring from 18°C mothers in the climbing speed test. As offspring effects would have emerged as a consequence of the phenotypic change due to temperature in the mothers, they could be considered carry-over effects, and not anticipatory maternal influence.

Future studies should focus on exploring differences in metabolic processes, genetic changes, and individual factors that could affect the complex dynamics between development and maternal effects. A split-brood match and mismatch experimental protocol is still advisable, as it allows comparing offspring from the same mother instead of distinct lineages. However, the work presented here suffered from an important limitation that should be considered in future endeavors: the egg collection scheme, based on the maximum egg laying times of mothers in cold or warm environments, implied that eggs were collected from 3 day old mothers at 29°C and from 5 day old mothers at 18°C. We chose this scenario because we sought to maximize offspring production to have comparable sample sizes from each temperature. Subsequent replications of this experimental method should account for possible effects of maternal age and attempt to prevent such consequences. Moreover, designers of future experiments should consider analyzing younger flies in the larval stage instead of adults. Developmental experience could modify flies' phenotype and produce a loss of maternal influence, which is less likely to occur in younger stages. Only through the full understanding of this factor would it be possible to fully use *Drosophila* as a model of parent effects.

Authors and Contributors

A.S-P and M.S.M. designed the study, performed the experiments, interpreted the results, and wrote the manuscript. M.S.M performed the statistical analysis. I.P. gave advice regarding the statistical analysis and the writing of this chapter. J-C.B guided the development and advice on the writing of this chapter.

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Supplementary Tables

Estimate	Parameter	Mean	SD	Lower 95% CI	Upper 95% CI
Group-Level effects: Mother (70 levels)					
Intercept	θ	0.05	0.03	0.00	0.12
Population-Level effects:					
Intercept	θ	-1.86	0.06	-1.99	-1.74
Condition CH		0.43	0.08	0.26	0.59
Condition HC		0.00	0.08	-0.16	0.17
Condition HH		0.52	0.09	0.36	0.70
Sex (Male)		0.03	0.05	-0.07	0.13
Temp x Condition CC		-3.67	0.61	-4.85	-2.46
Temp x Condition CH		-6.16	0.60	-7.34	-4.98
Temp x Condition HC		-3.96	0.62	-5.19	-2.74
Temp x Condition HH		-4.73	0.67	-6.06	-3.44
Intercept	k	0.63	0.03	0.58	0.68
Temp		-0.56	0.44	-1.42	0.30
Intercept	σ	-4.37	0.29	-4.99	-3.88
Temp		4.38	1.55	1.58	7.70

Supplementary Table 1 Full summary of the results obtained from a hierarchical generalized additive model for speed

Note: Environment of mother (M) and offspring (O). Group-Level effects are the standard deviation of the maternal random effects; Population-Level effects are the fixed effects of the model. The probability of zero (σ) and the shape parameter of the gamma distribution (k) were fitted with a smooth curve where temperature was the only variable. The scale parameter of the gamma distribution (θ) was fit with a separate smooth curve for each condition, sex as a fixed effect, mother ID as a random effect, and individual ID as a random smooth.

Note: This table is divided into three sections: Group-Level effects are the standard deviation of the maternal random effects (σ) and maternal level correlations between parameters (cor); Population-Level effects are the fixed effects of the model; Family specific parameters in this model are the standard deviations (σ) of each parameter. Environment temperature of mother (M) and offspring (O). Subscript M indicates matched conditions between mother and offspring and MM mismatched conditions between mother and offspring. Subscript CR indicates Cold-shock recovery time, HR indicates heat-shock recovery time and CS indicates climb speed.

Estimate	Trait	Mean	SD	Lower 95% CI	Upper 95% CI
Group-Level Effects: Mother (33 levels)					
$\sigma_{M\text{-}CR}$	Cold-shock Recovery	0.61	0.28	0.05	1.08
$\sigma_{MM\text{-}CR}$		0.58	0.25	0.06	1.01
$\sigma_{M\text{-}HR}$	Heat-shock Recovery	0.22	0.16	0.01	0.58
$\sigma_{MM\text{-}HR}$		0.41	0.27	0.02	0.96
$\sigma_{M\text{-}CS}$	Climbing speed	0.52	0.34	0.02	1.20
$\sigma_{MM\text{-}CS}$		0.24	0.17	0.01	0.63
$cor_{M\text{-}CR,M\text{-}HR}$		-0.43	0.32	-0.86	0.38
$cor_{M\text{-}CR,M\text{-}CS}$		-0.09	0.36	-0.74	0.64
$cor_{M\text{-}HR,M\text{-}CS}$		0.07	0.36	-0.63	0.72
$cor_{M\text{-}CR,MM\text{-}CR}$		-0.09	0.34	-0.70	0.59
$cor_{M\text{-}HR,MM\text{-}CR}$		0.04	0.34	-0.62	0.67
$cor_{M\text{-}CS,MM\text{-}CR}$		-0.05	0.37	-0.72	0.67
$cor_{M\text{-}CR,MM\text{-}HR}$		-0.06	0.34	-0.69	0.62
$cor_{M\text{-}HR,MM\text{-}HR}$		0.11	0.34	-0.60	0.72
$cor_{M\text{-}CS,MM\text{-}HR}$		0.04	0.37	-0.67	0.71
$cor_{MM\text{-}CR,MM\text{-}HR}$		-0.13	0.37	-0.76	0.62
$cor_{M\text{-}CR,MM\text{-}CS}$		0.06	0.36	-0.63	0.70
$cor_{M\text{-}HR,MM\text{-}CS}$		-0.14	0.36	-0.76	0.60
$cor_{M\text{-}CS,MM\text{-}CS}$		-0.01	0.38	-0.71	0.69
$cor_{MM\text{-}CR,MM\text{-}CS}$		-0.03	0.37	-0.71	0.67
$cor_{MM\text{-}HR,MM\text{-}CS}$		0.01	0.37	-0.69	0.69

Supplementary Table 2 Full summary of the results obtained from a multivariate model for matched and mismatched cold-shock recovery time, heat-shock recovery time, and climbing speed

Estimate	Trait	Mean	SD	Lower 95% CI	Upper 95% CI
Matched Offspring (60 levels)					
$\sigma_{M\text{-}CR}$	Cold-shock Recovery	0.41	0.26	0.02	0.96
$\sigma_{M\text{-}HR}$	Heat-shock Recovery	0.33	0.23	0.01	0.85
$\sigma_{M\text{-}CS}$	Climbing speed	0.49	0.28	0.03	0.97
$cor_{M\text{-}CR,M\text{-}HR}$		0.00	0.50	-0.89	0.88
$cor_{M\text{-}CR,M\text{-}CS}$		-0.22	0.45	-0.90	0.77
$cor_{M\text{-}HR,M\text{-}CS}$		0.03	0.45	-0.84	0.85
Mismatched Offspring (60 levels)					
$\sigma_{MM\text{-}CR}$	Cold-shock Recovery	0.54	0.27	0.03	1.04
$\sigma_{MM\text{-}HR}$	Heat-shock Recovery	0.53	0.34	0.03	1.18
$\sigma_{MM\text{-}CS}$	Climbing speed	0.60	0.30	0.04	1.07
$cor_{MM\text{-}CR,MM\text{-}HR}$		0.02	0.50	-0.86	0.88
$cor_{MM\text{-}CR,MM\text{-}CS}$		-0.38	0.41	-0.94	0.65
$cor_{MM\text{-}HR,MM\text{-}CS}$		-0.01	0.44	-0.84	0.83

Supplementary Table 2 (continuation) Full summary of the results obtained from a multivariate model for matched and mismatched cold-shock recovery time, heat-shock recovery time, and climbing speed

Estimate	Trait	Mean	SD	Lower 95% CI	Upper 95% CI
Population-Level effects:					
Condition CC	Cold-shock Recovery	-0.64	0.26	-1.15	-0.13
Condition HH		0.58	0.24	0.11	1.07
Condition CH		0.51	0.27	-0.02	1.04
Condition HC		-0.24	0.20	-0.64	0.16
Condition CC	Heat-shock Recovery	-0.47	0.19	-0.85	-0.09
Condition HH		0.50	0.17	0.17	0.83
Condition CH		0.47	0.25	-0.01	0.97
Condition HC		-0.39	0.24	-0.87	0.07
Condition CC	Climbing speed	-0.66	0.35	-1.36	0.02
Condition HH		0.32	0.26	-0.19	0.83
Condition CH		-0.06	0.22	-0.50	0.37
Condition HC		-0.13	0.18	-0.48	0.23
Family specific parameters:					
$\sigma_{M\text{-}CR}$	Cold-shock Recovery	0.43	0.27	0.03	0.98
$\sigma_{MM\text{-}CR}$		0.40	0.25	0.03	0.90
$\sigma_{M\text{-}HR}$	Heat-shock Recovery	0.66	0.25	0.12	1.01
$\sigma_{MM\text{-}HR}$		0.49	0.27	0.05	1.01
$\sigma_{M\text{-}CS}$	Climbing speed	0.68	0.33	0.08	1.26
$\sigma_{MM\text{-}CS}$		0.68	0.27	0.13	1.09

Supplementary Table 2 (continuation) Full summary of the results obtained from a multivariate model for matched and mismatched cold-shock recovery time, heat-shock recovery time, and climbing speed