ORIGINAL RESEARCH

Transgenerational and within-generation plasticity shape thermal performance curves

Grisel Cavieres1,2 | José M. Alruiz1 | Nadia R. Medina1 | José M. Bogdanovich1 | Francisco Bozinovic1

1Center of Applied Ecology and Sustainability (CAPES), Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile
2CCT-Mendoza CONICET, Grupo de Investigaciones de la Biodiversidad, CONICET, Instituto Argentino de Investigaciones de Zonas Áridas, Mendoza, Argentina

Correspondence
Grisel Cavieres, Center of Applied Ecology and Sustainability (CAPES), Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile.
Email: gcavieres@uc.cl

Funding information
Fondo de Fomento al Desarrollo Científico y Tecnológico, Grant/Award Number: FB0002-2014 line 3 to FB; Fondo Nacional de Desarrollo Científico y Tecnológico, Grant/Award Number: 1170017 and 3140450

Abstract
Thermal performance curves (TPCs) compute the effects of temperature on the performance of ectotherms and are frequently used to predict the effect of environmental conditions and currently, climate change, on organismal vulnerability and sensitivity. Using Drosophila melanogaster as an animal model, we examined how different thermal environments affected the shape of the performance curve and their parameters. We measured the climbing speed as a measure of locomotor performance in adult flies and tested the ontogenetic and transgenerational effects of thermal environment on TPC shape. Parents and offspring were reared at 28 ± 0°C (28C), 28 ± 4°C (28V), and 30 ± 0°C (30C). We found that both, environmental thermal variability (28V) and high temperature (30C) experienced during early ontogeny shaped the fruit fly TPC sensitivity. Flies reared at variable thermal environments shifted the TPC to the right and increased heat tolerance. Flies held at high and constant temperature exhibited lower maximum performance than flies reared at the variable thermal environment. Furthermore, these effects were extended to the next generation. The parental thermal environment had a significative effect on TPC and its parameters. Indeed, flies reared at 28V whose parents were held at a high and constant temperature (30C) had a lower heat tolerance than F1 of flies reared at 28C or 28V. Also, offspring of flies reared at variable thermal environment (28V) reached the maximum performance at a higher temperature than offspring of flies reared at 28C or 30C. Consequently, since TPC parameters are not fixed, we suggest cautiousness when using TPCs to predict the impact of climate change on natural populations.

KEYWORDS
climate change, early experience, environmental temperature, thermal performance curve, transgenerational plasticity
1 | INTRODUCTION

Climate is changing. Mean global temperatures, thermal variability, and the frequency of extreme environmental events have increased, and these have had significant impacts on biodiversity (Dawson, Jackson, House, Prentice, & Mace, 2011; Gitay, Suárez, Watson, & Dokken, 2002; Meehl & Tebaldi, 2004; Pachauri & Reisinger, 2007; Palmer et al., 2017; Vázquez, Gianoli, Morris, & Bozinovic, 2017). These changes in the thermal environment are expected to be particularly challenging for ectotherms because their physiology is directly dependent on ambient temperatures (Pörtner, 2002; Saxon, O’Brien, & Bridle, 2018; Sunday, Bates, & Dulvy, 2011). To a large extent the susceptibility and vulnerability of ectotherms to climate change has been assessed through the study of thermal performance curves (TPCs) which characterize the relationship between performance or fitness and body temperature (Sinclair et al., 2016). Indeed, TPCs have often been used to determine how ectothermic species will respond to ongoing climate change (Angilletta, 2009; Deutsch et al., 2008; Dillon, Wang, Garrity, & Huey, 2009; Estay, Lima, & Bozinovic, 2014; Huey et al., 2012). In that sense, Colinet, Sinclair, Vernon, and Renault (2015) reported that thermal variability within tolerant physiological ranges of organism improve performance. Also, Cavieres, Bogdanovich, and Bozinovic (2016) studying the effects of thermal variability in TPC indicated that flies reared in fluctuating thermal environments improved heat tolerance compared with flies from constant thermal environments. Parallelly, it has been reported that the nature of thermal variability shape TPC in ectotherms (Cavieres, Bogdanovich, Toledo, & Bozinovic, 2018; Kingsolver, Higgins, & Augustine, 2015; Kingsolver & Woods, 2016). As such, TPCs differ depending on physiological tolerance to environmental thermal conditions, and the thermal history experienced by each phenotype (Bozinovic, Medina, Alruiz, Cavieres, & Sabat, 2016; Cavieres, Nuñez-Villegas, Bozinovic, & Sabat, 2017; Huey & Berrigan, 1996; Huey et al., 2012).

Organisms may react to environmental inputs through phenotypic plasticity (Burggren, 2018; Sultan, 2015). Plasticity is heritable and appears to evolve through natural selection (Forman, 2015; Scheiner & Lyman, 1989). The modification of an organism by the environment is often hypothesized to be responsible for allowing organisms to adjust to changing environmental conditions through improving organismal function and fitness (Kelly, Panhuis, & Stoehr, 2012; Nunney, 2016; Nunney & Cheung, 1997). When environmental conditions change over short time scales, individuals can exhibit continuous and reversible phenotypic transformations (Piersma & Drent, 2003). During the early ontogeny, organisms are highly sensitive to environmental cues (Burggren & Mueller, 2015; Saxon et al., 2018; Spicer, Rundle, & Tills, 2011). Thus, developmental conditions can induce modifications in phenotype and potentially lead to irreversible changes (Burggren, 2018; Cooper, Tharp, Jernberg, & Angilletta, 2012; Dufty, Clobert, & Møller, 2002). In that sense, Cavieres et al. (2017) studying the putative effects of early life experience on physiological plasticity, reported an ontogenetic dependence of plastic response in rodents. That is, environmental conditions experienced during the development determined the ability to modify the phenotype during adulthood (see Weinig and Delph (2001)). Moreover, the plastic response is a property of the trait, not the individual and may be constrained by the costs of maintenance and production of plastic structures (DeWitt, Sih, & Wilson, 1998; Gilbert & Epel, 2008; Pigliucci, 2001; Sultan, 2015).

Phenotypic changes in early ontogeny have long-term implications on an organism’s performance (Jablonska & Raz, 2009; Mousseau & Dingle, 1991), and may persist over generations despite a lack of alterations in gene sequences (Badyaev & Uller, 2009; Ho & Burggren, 2010). The transgenerational transfer also called parental effects (Badyaev & Uller, 2009), transgenerational plasticity (Marshall & Uller, 2007) and transgenerational memory (Molinier, Ries, Zipfel, & Hohn, 2006) is used to describe the transmission of traits, factors, and/or information that induces phenotypic changes from one generation to the next (Ho & Burggren, 2010). Such effects could enable offspring receive information early during the development and modify the phenotype adaptively according to parental information to best respond to their environment (Engqvist & Reinhold, 2016; Klosin, Casas, Hidalgo-Carcedo, Vavouri, & Lehner, 2017; Mousseau & Fox, 1998; Salinas, Brown, Mangel, & Munch, 2013; Schmalhausen, 1938; Young & Badyaev, 2007). For instance, Rodríguez-Romero, Jarrold, Massamba-N’Sila, Spicer, and Calosi (2016) reported that transgenerational plasticity drove the increase of reproductive output in the marine polychaete Ophryotrocha labronica after three generations under low pCO2 conditions. Also, Crill, Huey, and Gilchrist (1996) have found that the ambient temperature experienced by parents influences heat tolerance in the fruit fly D. melanogaster. Thus, transgenerational transfer appears as a valuable source of variation between individuals, influencing short-term selection and the evolutionary trajectory of a population (Bonduriansky, Crean, & Day, 2012; Mousseau & Dingle, 1991; Rodríguez-Romero et al., 2016; Young & Badyaev, 2007). Overall, the transgenerational transfer may depend on the physiological status of parents, duration of exposure, and environmental signal (Burggren, 2014; Donelson, Wong, Booth, & Munday, 2016).

Studies of the effects of rapid environmental changes are normally based on its direct effects on organisms, minimizing the potential transgenerational ecological and evolutionary effects. Transgenerational effects on organisms may reveal the mechanisms through which populations could diminish the effects of climate change. Specifically, transgenerational impacts on thermal performance may have important implications on life-history processes since may alter the extinction risk posed by changing climate as demonstrated by Salinas and Munch (2012). Indeed, Sales et al. (2018) showed in beetles that heat waves impact populations across generations, which highlight the importance of seeing transgenerational effects when estimating ecological and evolutionary effects on organisms. Consequently, here we tested the effect of different environmental thermal regimes (constant and variable conditions) on organismal performance, measured as locomotor performance through climbing speed records in the fruit fly Drosophila.
melanogaster. Specifically, we assessed how early life exposure to thermal regime affected (or not) the TPC of one generation of adults flies as well as of a subsequent generation. Thus, we studied the entire performance curve and, we estimated their parameters to compare individuals. Many studies have documented thermal acclimation on thermal limits, but few have measured the effects on the entire performance curve, and to the best of our knowledge, none have looked at transgenerational effects on TPCs. Overall, we hypothesized that flies experiencing high temperatures and variable environments during development would have increased thermal tolerance, and their TPCs would be shifted to the right. Also, we hypothesized that the offspring of parents in the high temperature and variable temperature treatments would have increased thermal tolerance compared to controls despite not having directly experienced these conditions.

2 | MATERIALS AND METHODS

The fruit flies, Drosophila melanogaster, were used as animal model. Previously we have used this species to test hypotheses regarding the effects of thermal variability on performance and fitness (Bozinovic, Catalan, Estay, & Sabat, 2013; Bozinovic et al., 2016; Cavieres et al., 2016). Moreover, the phenotypic responses of this organism to environmental temperature and other climatic factors are well known (Bozinovic et al., 2011; Hoffmann, 2010; Ragland & Kingsolver, 2008).

Adult D. melanogaster were collected in central Chile (33°26 S; 70°39 W at 500 m above sea level) during summer 2016. Flies were identified based on morphological characters (Markow & O’Grady, 2005). After collection, ten breeding groups were made; each group consisted of approximately 10 males and 10 females. Groups were reared in controlled conditions at 24°C and L:D = 12:12. Flies were grown in 250-ml glass vials with Burdick culture medium (Burdick, 1955) to constituting the stock bottles. Third generation adult flies from the stock were randomly assigned to one of three thermal treatments set based on the limits of fruit fly egg viability (eggs-to-adult viability is near 80% at 28°C and 0%-5% at 32°C, for details see Hoffmann, 2010; Cavieres et al., 2018): (a) moderate mean and no variance (28 ± 0°C, “28C”), (b) moderate mean and high variance (28 ± 4°C, “28V”), and (c) high mean and no variance (30 ± 0°C, “30C”). Flies were maintained in each treatment in climatic chambers (PITEC, Model BIOREF) from eggs to adult; then, breeding groups were acclimated in one of three different thermal environments 28 ± 0°C (“28C”), 28 ± 4°C (“28V”), and 30 ± 0°C (“30C”). Eggs from flies reared at 30C did not hatch at 30C. Numbers in parentheses are sample size & Gilchrist, 2001; Gilchrist, Huey, & Partridge, 1997). Specifically, we quantified wall climbing speed (cm/s) by knocking down a fly in a narrow glass test tube (12 x 100 mm) and measuring the time required to walk up the tube to a height of 7.0 cm. Each fly was kept for 10 min at the test temperature. Each fly was tested at the following temperatures: 16, 20, 24, 28, 32, 36, 38, 39 and 40°C (see Cavieres et al., 2016). All animals remained in a room at 24 ± 2°C between tests (around 10 min).

A third-order polynomial function was fit to the Thermal performance curve, and its parameters were estimated: the upper and lower thermal limits (CTmax and CTmin, respectively), maximum performance (Vmax), performance breadth (Tb), according to (Gilchrist, 1996), and the temperature at which performance was maximized (Tc).

2.1 | Statistical analyses

To quantify effects of temperature on climbing speed, we fit a third-degree polynomial function for the entire TPC and performed a linear mixed model to test the impact of mean and variance of temperature TPC during ontogeny as well as in the next generation. The linear mixed model was generated for the longitudinal data; individuals (random intercept) were nested in temperature (slope) and included as a random effect. Also, we assessed the effects of temperature on TPC parameters. We test the variables using a linear model when variables follow a normal distribution and a general linear model when the variables follow a different distribution. To test the effects of temperature during ontogeny we used thermal treatment as a factor, and to examine the transgerational effects we used Parental thermal treatment×Offspring thermal treatment as factors. Multiple comparisons were restricted sets of contrasts among offspring reared at the same thermal environment. False Discovery Rate (FDR) correction for multiple comparisons was applied.

To estimate the parameters of each TPC, we used the GitHub R package ThermPerf. All analyses were carried out using R (http://www.R-project.org/).
RESULTS

As expected, the locomotor performance was significantly affected by temperature (Table 1, Figure 2). High mean temperature and thermal variability shaped the TPC of *D. melanogaster*. Thermal performance was lower in flies reared at 30°C than those reared at 28°C and 28 V (Table 1 and Figure 2a). Indeed, flies reared at 30°C exhibited lower $V_{\text{max}}$ and $T_{\text{br}}$ than flies reared at 28°C and 28V. Flies developed in variable thermal conditions improved heat tolerance, that is, increased CT$_{\text{min}}$, CT$_{\text{max}}$, and $T_{0}$ in comparison to flies reared at 28°C (Table 1).

The effects of thermal conditions experienced during ontogeny were extended to the subsequent generation (Figure 2b and Figure 3). We found a significative interaction between parental and offspring thermal environment on the entire TPC (Table 2) and its parameters (Figure 3). In an environment with moderate mean and no variance (28C), the thermal performance (i.e., the entire TPC) was higher in offspring from flies reared at 28V than offspring of flies held at 30 and 28C (Figure 2b). The analyses of thermal performance parameters revealed that this increase was due to an increase in $V_{\text{max}}$ (Figure 2b). Flies reared at variable thermal environments whose parents were held at high and constant temperature (i.e., 30C) decreased heat tolerance, that is, had lower thermal limits than offspring of flies reared at 28V, shifting the TPC to the left (Figure 3d,e), with a lower $T_{0}$ than offspring of flies reared at 28V (Figure 3A respectively). Moreover, offspring from flies reared at 28V but living at 28C reached the maximum performance ($V_{\text{max}}$) at a higher $T_{0}$ than offspring of flies reared at 28C. We did not find transgenerational effects of temperature on flies reared at 30C (Figures 2 and 3).

3 | RESULTS

| Effect | Coefficient  | SE  | T    | p     |
|--------|--------------|-----|------|-------|
| (A) Entire thermal performance curve | Intercept (28C) | 1.09 | 0.03 | 31.78 | <0.001 |
| 28V | -0.04 | 0.05 | -0.71 | 0.48 |
| 30C | -0.25 | 0.05 | -5.10 | <0.001 |

The key finding was that the environmental thermal variability and high and constant temperature experienced during early ontogeny shape the thermal performance curve. Also, those effects are...
extended to the next generation but depending on the thermal environment in which offspring live. High and constant environmental temperature reduced the thermal performance of both parental and offspring generation. The thermal variability improved the heat tolerance of parents and increased thermal performance of F1 held at a constant thermal environment. Finally, in an extreme environment, the thermal experience of parents did not affect offspring’s performance.

Environmental variability through time imposes selection pressure (Gould, 1985), thus driving adaptation to different thermal
FIGURE 3  Transgenerational effects of temperature on the performance curve parameters estimated from a third-order polynomial fit. Y-axis is offspring performance ($v_{\text{max}}$, $T_{br}$, $C_{\text{max}}$, and $C_{\text{min}}$), and the X-axis is the thermal environment in which the offspring were raised. Bars indicate the response when parents were maintained in one of three different environments: 28 ± 0°C (28C), 28 ± 4°C (28V), and 30 ± 0°C (30C). Eggs from flies reared at 30C did not hatch at 30C. Different letters indicate a significant difference between groups.
environments (Kubrak, Nylin, Flatt, Nässel, & Leimar, 2017; Sultan, 2015; Young & Badyaev, 2007). The ability of organisms to produce different phenotypes under changing environmental conditions is influenced by environmental signals and the temporal window at which signals occur (Burggren & Mueller, 2015; Burggren & Reyna, 2011; Spicer et al., 2011). Here, we showed that flies experiencing environmental thermal variability during ontogeny improved heat tolerance, through changes in \( CT_{\text{max}} \), \( CT_{\text{play}} \), and \( To \) values in comparison to flies that did not experience thermal variability during development (Figure 2a, Table 1). In that sense, experimental studies have shown the benefits of thermal variability on developmental time (Ragland & Kingsolver, 2008), survival (Javal, Renault, & Colinet, 2016), and population dynamics (Clavijo-Baquet et al., 2014; Estay, Clavijo-Baquet, Lima, & Bozinovic, 2011). Brief exposure to high temperatures may induce the expression of stress-inducible heat-shock proteins (HSPs) and increase thermal tolerance in ectotherms exposed to extreme temperature or thermal variability (Colinet et al., 2015; Dong, Miller, Sanders, & Somero, 2008; Lewis et al., 2016; Tomanek, 2010). Additionally, it has been proposed that the increased performance in variable environments may be explained by recovery time between extreme events, which enable periodic opportunities to return to physiological homeostasis (Colinet et al., 2016).

On the other hand, it has been reported a high cost of living in extreme environments (DeWitt et al., 1998; Kafri, Metzl-Raz, Jona, & Barkai, 2016; Piligiucci, 2001). Prolonged exposure to extreme temperatures has adverse effects on fitness, reducing survival and rate of development (Chown & Terblanche, 2006; Colinet et al., 2016; Feder & Hofmann, 1999; Krebs & Feder, 1997). Indeed, we observed that in flies exposed to 30°C during ontogeny, \( V_{\text{max}} \) was reduced, and their offspring not hatched at 30°C (Figure 1, see also Hoffmann 2010). Contrary to our predictions, offspring from 30°C flies reared at 28 V reduced heat tolerance in comparison to the progeny of 28°C and 28 V. Thus, the elevated cost of living in an extreme thermal environment reduce thermal tolerances during ontogeny (see Table 1 and Figure 2a), and on the subsequent generation (see Figure 3). Despite that studies on nongenetic inheritance mechanisms across multiple generations have increased (Donelson et al., 2016; Shama et al., 2016; Thor & Dupont, 2015), it is still unclear the impact and duration of transgenerational effects (see Burggren, 2015). Phenotypic plasticity during early ontogeny may induce the emergence of new phenotypes (Bartheld, Artacho, & Bacigalupe, 2017; Cavieres et al., 2016, 2017; Kingsolver et al., 2015; Koussoroplis, Pincebourde, & Wacker, 2017). In flies reared at 28 V, more heat tolerant phenotypes. Despite the increase of thermal performance in flies reared at 28 V, the cost of phenotypic plasticity here is unknown (not assessed in this study). Meats (2011) studying the thermal tolerance in Queensland fruit fly reared in regimes of variable and constant temperature, reported that the increased in thermal tolerance in one stage of development affected negatively the survival rate during the next stage. (see also, Messenger & Flitters, 1958; Marshall & Sinclair, 2010). Besides, Folguera et al. (2011) reported that the increase of thermal amplitude affected negatively life-history traits (longevity and growth rate), increasing metabolic cost and stress responses (synthesis of heat-shock proteins).

Thermal conditions experienced during early life affected the next generation; in this vein, the adaptive transgenerational plasticity hypothesis posits that offspring reared in the same environment of their parents will have higher fitness than offspring reared in an environment different from that of their parents (Gilchrist & Huey, 2001) showed in fruit fly that F1 of parents reared at high temperatures, exhibit higher fitness independently of the thermal environment experienced. The analyses of the entire TPC showed that flies from 28C, whose parents were reared at 28V, exhibited higher performance than F1 from flies reared in 28C or 30C (Figure 2b). Besides, in a variable environment, the offspring of flies reared in 28V and 28C increased \( T_{\text{or}} \), \( CT_{\text{min}} \), and \( CT_{\text{max}} \) compared with F1 from flies held in 30C (Figure 3). Accordingly, although our results support the transgenerational effects of temperature, it does not support the adaptive transgenerational plasticity hypothesis (see Leroi, Bennett, & Lenski 1994).

The parental experience could result in "pre-adapted" (sensu lato) progeny that exhibits traits that allow them to respond to the environment’s challenges accurate (Engqvist & Reinhold, 2016; Salinas et al., 2013). Thus, transgenerational effects can impact mating success and reproduction (Morimoto, Simpson, & Ponton, 2017), thermal preference (So & Schwanz, 2018), growth (Salinas & Munch, 2012), among others (see Molnier et al., 2006; Herman & Sultan, 2011; Shama et al., 2016; Donelson, Salinas, Munday, & Shama, 2017). To the best of our knowledge, this is the first

| Effect                          | Coefficient | SE  | df  | T    | p     |
|-------------------------------|-------------|-----|-----|------|-------|
| Intercept (Offspring 28C      | 1.15        | 0.04| 2804| 29.35| <0.001|
| (Parents 28C)                 |             |     |     |      |       |
| Offspring 28C (Parents 28V)   | 0.17        | 0.06| 343 | 2.83 | 0.004 |
| Offspring 28C (Parents 30C)   | -0.08       | 0.06| 343 | -1.38| 0.17  |
| Offspring 28V (Parents 28V)   | 0.07        | 0.06| 343 | 1.14 | 0.25  |
| Offspring 28V (Parents 28C)   | 0.13        | 0.05| 343 | 2.26 | 0.02  |
| Offspring 28V (Parents 30C)   | 0.11        | 0.06| 343 | 1.78 | 0.07  |
| Offspring 30C (Parents 28C)   | -0.24       | 0.05| 343 | -4.28| <0.001|
| Offspring 30C (Parents 28 V)  | -0.22       | 0.06| 343 | -3.49| <0.001|

**TABLE 2.** Coefficients of the linear mixed model fitted to the entire thermal performance curve of Offspring in Drosophila melanogaster acclimated to one of three environments (28C, 28V and 30C). Thermal environment of parents in parentheses. Significant values are indicated in bold (p < 0.05) (for multiple comparisons see Figure 2)
study that tested the transgenerational effects of variable thermal environments on animals thermal performance. We showed that early life exposure to thermal variability, and extreme temperature shapes the TPCs of the fruit fly, and interestingly, these effects hold to the next generation. These results highlight the importance of incorporating ontogenetic and transgenerational effects of temperature in physiological studies to building robust predictions about the impact rapid environmental thermal fluctuations, changes in mean temperature or the effects of extreme thermal events on animal performance, and to avoid underestimating the potential plastic response of organisms. Consequently, we must consider how this might impair our ability to accurately predict the impact of climate change on natural populations when using TPCs.

ACKNOWLEDGMENTS

This work was founding by CONICYT PIA/BASAL FB0002, FONDECYT 1170017 to FB and 3140450 to GC. JG. Kingsolver provided helpful comments to an early draft.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

G.C and F.B designed the experiment. N.M, and J.M.A. performed the experiments, G.C, and J.M.B analyzed the data, G.C and F.B. wrote the paper.

DATA ACCESSIBILITY

The datasets analyzed during the current study will be available in the Dryad Digital Repository.

ORCID

Grisel Cavieres https://orcid.org/0000-0003-4230-2923
Francisco Bozinovic https://orcid.org/0000-0003-3870-9624

REFERENCES

Angilletta, M. J. (2009). Thermal adaptation: A theoretical and empirical synthesis. Oxford, UK: Oxford University Press.

Badyaev, A. V., & Uller, T. (2009). Parental effects in ecology and evolution: Mechanisms, processes and implications. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 364, 1169–1177. https://doi.org/10.1098/rstb.2008.0302

Bartheld, J. L., Artacho, P., & Bagiculaue, L. (2017). Thermal performance curves under daily thermal fluctuation: A study in helmeted water toad tadpoles. Journal of Thermal Biology, 70, 80–85. https://doi.org/10.1016/j.jtherbio.2017.09.008

Bonduriansky, R., Crean, A. J., & Day, T. (2012). The implications of nongenetic inheritance for evolution in changing environments. Evolutionary Applications, 5, 192–201. https://doi.org/10.1111/j.1752-4571.2011.00213.x

Bozinovic, F., Bastias, D. A., Boher, F., Clavijo-Baquet, S., Estay, S. A., & Angilletta, M. J. (2011). The mean and variance of environmental temperature interact to determine physiological tolerance and fitness. Physiological and Biochemical Zoology, 84, 543–552. https://doi.org/10.1086/662551

Bozinovic, F., Catalan, T. P., Estay, S. A., & Sabat, P. (2013). Acclimation to daily thermal variability drives the metabolic performance curve. Evolutionary Ecology Research, 15, 579–587.

Bozinovic, F., Medina, N. R., Alruz, J. M., Cavieres, G., & Sabat, P. (2016). Thermal tolerance and survival responses to scenarios of experimental climatic change: Changing thermal variability reduces the heat and cold tolerance in a fly. Journal of Comparative Physiology B, 186, 581–587. https://doi.org/10.1007/s00360-016-0980-6

Burdick, A. B. (1955). Drosophila experiments for high school biology. Am. Biol. Teach., 17, 155–159. https://doi.org/10.2307/4438704

Burggren, W. (2018). Developmental phenotypic plasticity helps bridge stochastic weather events associated with climate change. Journal of Experimental Biology, 221, 682–689. https://doi.org/10.1242/jeb.161984.

Burggren, W. W., & Mueller, C. A. (2015). Developmental critical windows and sensitive periods as three-dimensional constructs in time and space. Physiological and Biochemical Zoology, 88, 91–102. https://doi.org/10.1086/679906

Burggren, W. W., & Reyna, K. S. (2011). Developmental trajectories, critical windows and phenotypic alteration during cardio-respiratory development. Respiratory Physiology & Neurobiology, 178, 13–21. https://doi.org/10.1016/j.resp.2011.05.001

Cavieres, G., Bogdanovich, J. M., & Bozinovic, F. (2016). Ontogenetic thermal tolerance and performance of ectotherms at variable temperatures. Journal of Evolutionary Biology, 29, 1462–1468. https://doi.org/10.1111/jeb.12886

Cavieres, G., Bogdanovich, J. M., Toledo, P., & Bozinovic, F. (2018). Fluctuating thermal environments and time-dependent effects on fruit fly egg-hatching performance. Ecology and Evolution, 8, 6849–6851. https://doi.org/10.1002/ece3.4220

Cavieres, G., Nuñez-Villegas, M., Bozinovic, F., & Sabat, P. (2017). Early life experience drives short-term acclimation of metabolic and osmoregulatory traits in the leaf-eared mouse. Journal of Experimental Biology, 220, 2626–2634. https://doi.org/10.1242/jeb.149997

Chown, S. L., & Terblanche, J. S. (2006). Physiological diversity in insects: ecological and evolutionary context. Advances in Insect Physiology, 443, 931–949.

Clavijo-Baquet, S., Boher, F., Ziegler, L., Martel, S. I., Estay, S. A., & Bozinovic, F. (2014). Differential responses to thermal variation between fitness metrics. Scientific Reports, 4, 5349–5349. https://doi.org/10.1038/srep05349

Colinet, H., Renault, D., Javal, M., Berková, P., Šimek, P., & Koštál, V. (2016). Uncovering the benefits of fluctuating thermal regimes on cold tolerance of Drosophila flies by combined metabolomic and lipidomic approach. Biochimica Et Biophysica Acta (BBA) - Molecular and Cell Biology of Lipids, 1861, 1736–1745. https://doi.org/10.1016/j.bbalip.2016.08.008

Colinet, H., Sinclair, B. J., Vernon, P., & Renault, D. (2015). Insects in fluctuating thermal environments. Annual Review of Entomology, 60, 123–140. https://doi.org/10.1146/annurev-ento-010814-021017
Vázquez, D. P., Gianoli, E., Morris, W. F., & Bozinovic, F. (2017). Ecological and evolutionary impacts of changing climatic variability. Biological Reviews, 92, 22–42. https://doi.org/10.1111/brv.12216

Weinig, C., & Delph, L. F. (2001). Phenotypic plasticity early in life constrains developmental responses later. Evolution, 55, 930–936. https://doi.org/10.1554/0014-3820(2001)055[0930:PPEILC]2.0.CO;2

Young, R. L., & Badyaev, A. V. (2007). Evolution of ontogeny: Linking epigenetic remodeling and genetic adaptation in skeletal structures. Integrative and Comparative Biology, 47, 234–244. https://doi.org/10.1093/icb/icm025

How to cite this article: Cavieres G, Alruiz JM, Medina NR, Bogdanovich JM, Bozinovic F. Transgenerational and within-generation plasticity shape thermal performance curves. Ecol Evol. 2019:9:2072–2082. https://doi.org/10.1002/ece3.4900