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PARENTAL AND DEVELOPMENTAL TEMPERATURE EFFECTS ON THE THERMAL DEPENDENCE OF FITNESS IN *DROSOPHILA MELANOGASTER*

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Abstract.—Cross-generational effects refer to nongenetic influences of the parental phenotype or environment on offspring phenotypes. Such effects are commonly observed, but their adaptive significance is largely unresolved. We examined cross-generational effects of parental temperature on offspring fitness (estimated via a serial-transfer assay) at different temperatures in a laboratory population of *Drosophila melanogaster*. Parents were reared at 18°C, 25°C, or 29°C (T_{par}) and then their offspring were reared at 18°C, 25°C, or 29°C (T_{off}) to evaluate several competing hypotheses (including an adaptive one) involving interaction effects of parental and offspring temperature on offspring fitness. The results clearly show that hotter parents are better; in other words, the higher the temperature of the parents, the higher the fitness of their offspring, independent of offspring thermal environment. These data contradict the adaptive cross-generational hypothesis, which proposes that offspring fitness is maximal when the offspring thermal regime matches the parental one. Flies with hot parents have high fitness seemingly because their own offspring develop relatively quickly, not because they have higher fecundity early in life.

Key words.—Cross-generational effects, developmental temperature, *Drosophila melanogaster*, fitness, maternal effects.

Cross-generational (parental) effects are a type of phenotypic plasticity in which the environment of parents has nongenetic influences on the phenotypes of their offspring. Parental effects are important evolutionarily not only because they influence short-term responses to selection (Falconer 1989; Kirkpatrick and Lande 1989; Riska 1989), but also because they are potentially adaptive (Mousseau and Dingle 1991; Rossiter 1996; Fox et al. 1997). For example, if the parental environment is correlated with that of their offspring, then parents could enhance their own fitness by activating developmental programs that tune their offspring's phenotype for that environment (Fox et al. 1997; Donohue and Schmitt 1999).

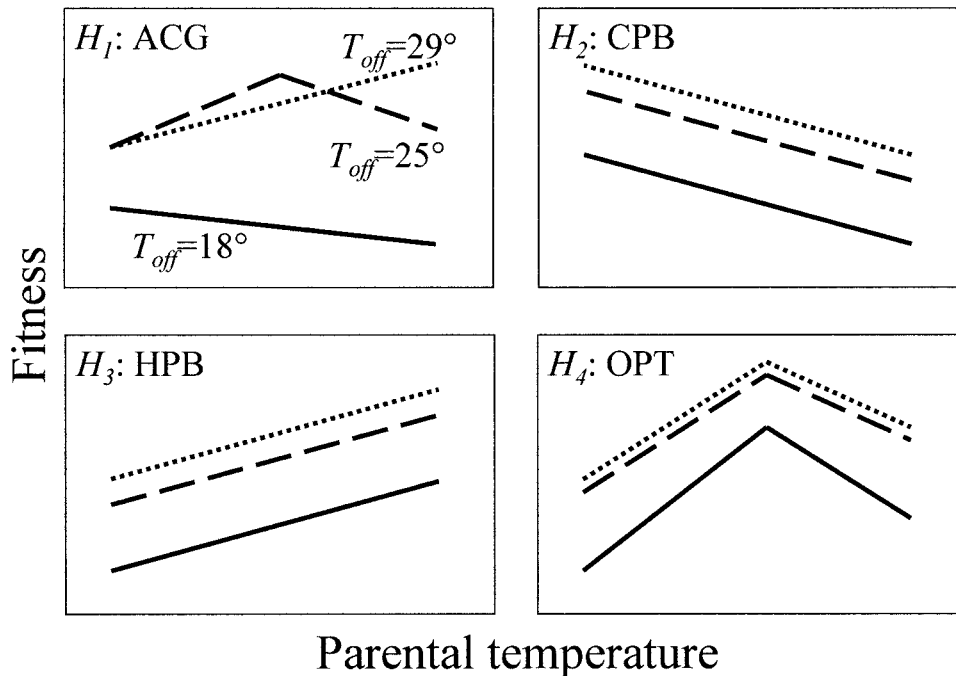Many recent studies have shown that parental environ-

FIG. 1. Graphical representations of the adaptive cross-generational (ACG), colder parents are better (CPB), hotter parents are better (HPB), and optimal parental temperature (OPT) hypotheses.

ments have important phenotypic effects on offspring, and several studies show that parental effects often enhance life-history or physiological correlates of offspring fitness (reviews in Rossiter 1996; Mousseau and Fox 1998). To our knowledge, however, no study of a eukaryotic organism has yet examined whether parental effects actually enhance offspring fitness itself, as estimated by the per capita rate of population increase.

Here we consider the effect of parental temperature on the thermal dependence of offspring fitness in a laboratory population of *Drosophila melanogaster*. Temperature is a key environmental variable for ectotherms (David et al. 1983; Hoffmann and Parsons 1991), and parental temperature has diverse phenotypic effects on the offspring in *D. melanogaster* (Zamudio et al. 1994; Crill et al. 1996; Huey and Berrigan 1996). Whether these responses actually increase fitness in this species, however, is unknown. Evolutionary physiologists have long assumed that acclimation responses within a generation are adaptive, a view codified by Leroi et al. (1994, p. 1917) as the beneficial acclimation hypothesis: "acclimation to a particular environment gives an organism a performance advantage over another organism that has not had the opportunity to acclimate to that particular environment." Recently, however, several researchers have challenged that assumption with new evidence and proposed several alternative hypotheses based on patterns observed in laboratory experiments (reviewed in Huey et al. 1999).

In this paper, we modify the statistical methods we recently developed to test the beneficial acclimation hypothesis (Huey and Berrigan 1996) to a set of related hypotheses concerning cross-generation acclimation. We use a factorial experimental design that enables us to measure the fitness of offspring as a function of interactions involving parental and offspring

temperature. We then use the resulting data to test several competing, nonexclusive hypotheses (below) that are derived from hypotheses of the effects developmental temperature on adult (i.e., within-generation) fitness.

Competing hypotheses are diagrammed in Figure 1. The adaptive cross-generational (ACG) hypothesis proposes that offspring reared and living in the same environment as that of their parents will have higher fitness than will offspring living in an environment different from that of their parents. This hypothesis is a cross-generational version of the beneficial acclimation hypothesis (Leroi et al. 1994; Huey and Berrigan 1996) or a temperature version of a general adaptive maternal effect hypothesis (Mousseau and Fox 1998). The colder parents are better (CPB) hypothesis proposes that parents reared under cool temperatures produce offspring that are invariably more fit than do parents reared under warm conditions. For example, parents reared under cool temperatures will be large and therefore will produce large offspring (Crill et al. 1996), with attendant fitness advantages. The hotter parents are better (HPB) hypothesis is just the opposite: Parents that develop under hotter temperatures will produce more fit offspring than parents grown under cooler temperatures. This hypothesis might apply if small size confers a fitness advantage through enhanced motility or an earlier age at first reproduction (McLachlan and Allen 1987). The optimum parental temperature (OPT) hypothesis proposes that parents living at intermediate temperatures produce more fit offspring than do parents living at more extreme high or low temperatures. This hypothesis derives from the intermediate developmental temperature hypothesis of Cohet and David (1978), who noted that development at intermediate temperatures produced flies with a seemingly well-integrated physiology that perform well under a variety of thermal condi-
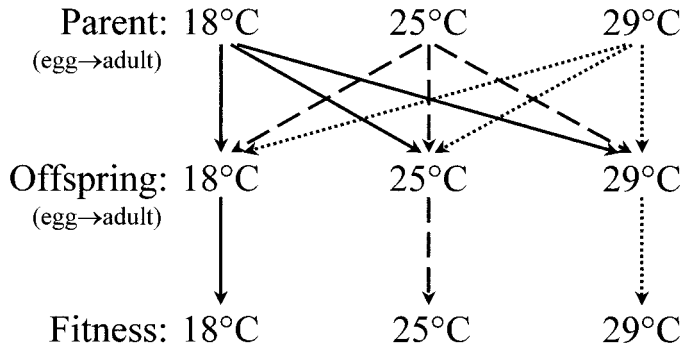
FIG. 2. Experimental design showing the temperature treatments for the parental and offspring (F_1s) generations. Fitness of the F_1s was scored using the method of Mueller and Ayala (1981) by tallying the F_2 progeny.

tions. Finally, the null hypothesis is that parental temperature (T_{par}) has no systematic effect on offspring fitness at various temperatures (T_{off}).

We adopt a strong inference approach (Huey and Berrigan 1996; Huey et al. 1999) to evaluate the relative merits of these hypotheses. The approach requires a 3×3 full-factorial design (Fig. 2). Specifically, we reared parents at 18°C, 25°C, or 29°C and reared and assayed fitness of their offspring at 18°C, 25°C, or 29°C. Then we used a factorial analysis of variance in which parental temperatures were treated as an ordered factor. All of the competing hypotheses (Table 1, Fig. 1, see Materials and Methods) can be tested by examining the strength and direction of the main effects, along with contrasts with a single degree of freedom on the ordered factors (orthogonal polynomials to test for linear and quadratic effects). For example, the OPT hypothesis would be supported if the quadratic contrast for parental temperature were significant and negative (Table 1). Of course, these hypotheses need not be exclusive (Huey et al. 1999), but our ANOVA approach allows us to rank in effect the relative impact of each hypothesis.

MATERIALS AND METHODS

Drosophila melanogaster (originally collected by L. G. Harshman near Davis, CA in 1996) were pulled from population cages (25°C, photoperiod 12:12 L:D) in two blocks, January 1997 and March 1998. Approximately 100 eggs were placed in each of nine bottles (30 ml of molasses/cornmeal medium) to found the parental (or P) generation. Three bottles were placed at each parental temperature (T_{par}: 18°C, 25°C, or 29°C, Fig. 2). When the adults eclosed, about 100 eggs from each parental temperature were placed in each of nine bottles, with three bottles incubated at each of the three offspring temperatures (T_{off}: 18°C, 25°C, or 29°C, Fig. 2) to form the offspring (or F_1) generation.

We used the per capita rate of population increase (λ) as an index of fitness and estimated it using Mueller and Ayala's (1981) Type 2 method (serial transfer). Approximately 24–48 h after eclosion, five F_1 males plus five F_1 females ($N = 10$) were transferred to a fresh bottle with 30 ml of medium and incubated at T_{off} for 1 week. Four replicates for each T_{par}-T_{off} combination were set up in the 1997 block and five in

TABLE 1. Predictions for the cross-generational effects hypotheses (Fig. 1). The terms in the table correspond to the main effects and contrasts with a single degree of freedom for the ordered factors in the linear model $\log(\lambda) = T_{off} + T_{par}$ (linear) + T_{par} (quadratic) + ($T_{off} \times T_{par}$) + ϵ. ACG, adaptive cross-generational; CPB, colder parents are better; HPB, hotter parents are better; OPT, optimum parental temperature.

	Cross-Generational Hypothesis				
Term	Null	ACG	CPB	HPB	OPT
T_{par} (main effect)	ns	*	*	*	*
T_{par} (linear)	ns	ns	*(−)	*(+)	ns
T_{par} (quadratic)	ns	ns	ns	ns	*(−)
($T_{off} \times T_{par}$)	ns	*	ns	ns	ns

the 1998. At the end of the first week, we counted the survivors in the F_1 generation and cleared the bottles. The bottles were then returned to the incubator. In each subsequent week, the living adults (F_2) within each bottle were counted (Y_i). Those flies were discarded and the cleared bottle was returned to the incubator. Counts were made for three weeks for the 25°C and 29°C treatments and for five weeks for the 18°C, because of the prolonged development time at lower temperatures.

Counts from each week were transformed such that $a_i = Y_i/N^*$ where N^* was the initial number of flies in the bottle. Fitness (λ) was estimated by the largest positive eigenvalue of the equation $N_t = a_1N_{t-1} + a_2N_{t-2} + \cdots + a_tN_0$. Mueller and Ayala (1981) explain the methodology and its justification. No significant effect of block on fitness was detected ($P > 0.70$), so the data from 1997 and 1998 were pooled for all subsequent analyses.

Fitness estimates for each population were analyzed using a linear model: $\log(\lambda) = T_{off} + T_{par}$ (linear) + T_{par} (quadratic) + ($T_{off} \times T_{par}$) + ϵ, where T_{par} is treated as an ordered factor allowing linear and quadratic contrasts with a single degree of freedom using orthogonal polynomials (Huey et al. 1999). The sign and significance of the various coefficients inform the significance of the hypothesis at risk (Table 1, Fig. 1). For example, if T_{par} (linear) is significant and positive, then the HPB hypothesis would be supported; or if T_{par} (quadratic) is significant and concave downward, then the OPT hypothesis would be supported.

RESULTS

Offspring fitness was significantly influenced by parental temperature (Tables 2, 3; Fig. 3). Specifically, fitness in-

TABLE 2. ANOVA of cross-generational acclimation effects. T_{off} and T_{par} are ordered factors; the linear and quadratic effects are tested using orthogonal polynomial contrasts. Fitness values (λs) were log transformed prior to analysis.

	df	MS	F	Pr(F)
T_{off}	2	36.770	4578.785	<0.001
T_{par}	2	0.149	18.556	<0.001
T_{par} (linear)	1	0.290	36.081	<0.001
T_{par} (quadratic)	1	0.008	1.031	0.313
$T_{off} \times T_{par}$	4	0.016	1.948	0.112
Residuals	72	0.008		

TABLE 3. Least squares means ± standard deviation for parental temperature effects on fitness, development time, and early fecundity. Post hoc comparisons were conducted using Tukey's method for simultaneous confidence intervals. Values with different letters are significantly different at $P < 0.05$.

T_{par}	N	λ (week^{-1})	Development time (week)	Fecundity (no. adults)
18°C	27	16.62 ± 1.088[a]	1.87 ± 0.053[a]	463 ± 53.5[a]
25°C	27	17.88 ± 1.050[b]	1.90 ± 0.075[a,b]	468 ± 46.5[a]
29°C	27	19.28 ± 1.132[c]	1.83 ± 0.077[c]	456 ± 74.1[a]

FIG. 3. Fitness (λ) of flies developing at T_{off} = 18°C, 25°C, or 29°C as a function of parental temperature (T_{par}).

creased linearly with T_{par} from 18°C to 29°C as evidenced by the significant linear contrasts (Table 2). The quadratic component of T_{par} was not significant. Neither of the interactions of T_{off} with either the linear or quadratic components of T_{par} was significant. A comparison of paired confidence intervals (Tukey's method, Table 3) reveals that fitness (λ) was highest for flies with parents reared at 29°C, intermediate for those with 25°C parents, and lowest for those from parents at 18°C (Table 3).

Our experiments were not designed to determine the specific life-history shifts underlying the observed effects of parental temperature on offspring fitness, however, we can use our data to explore this issue, albeit crudely and indirectly. Specifically, we can estimate whether parental temperature might influence either the early fecundity of offspring (F_1) or the development time of their grandoffspring (F_2). Early fecundity per bottle is simply the cumulative number of surviving adults removed from the bottle in the two weeks after the F_1 parents were removed. Mean development time of F_2 progeny of each bottle in the fitness assays is estimated by multiplying the number of surviving F_2 adults by the number of weeks since the F_1 parents were removed from the bottle. Both measurements are crude; nevertheless, they do reveal important differences among the parental temperature treatments. Flies with parents that developed at 29°C produced offspring that developed significantly more rapidly than did flies with parents at 18°C or 25°C (Table 3). Parental temperature had no significant effect on early fecundity (Table 3). Ultimately, of course, these patterns should be validated in direct experimental tests.

Within each parental temperature treatment, offspring fitness increased with test temperature (Fig. 3). Thus, flies at T_{off} of 25°C and 29°C consistently had higher fitness than those reared at 18°C (Table 2, Fig. 3). This undoubtedly results from the shorter development time of the F_2 offspring at the higher temperatures, relative to those developing at 18°C.

DISCUSSION

Parental thermal regime significantly influenced offspring fitness in *D. melanogaster*. Parents reared and living at 29°C produced offspring with higher average fitness than did parents reared at 25°C, which in turn produced offspring with higher fitness than did parents from 18°C (Table 3, Fig. 3). This pattern supports the HPB hypothesis. Moreover, it clearly contradicts an ACG hypothesis (Table 1, Fig. 1), which predicts that fitness is maximal when offspring live in the
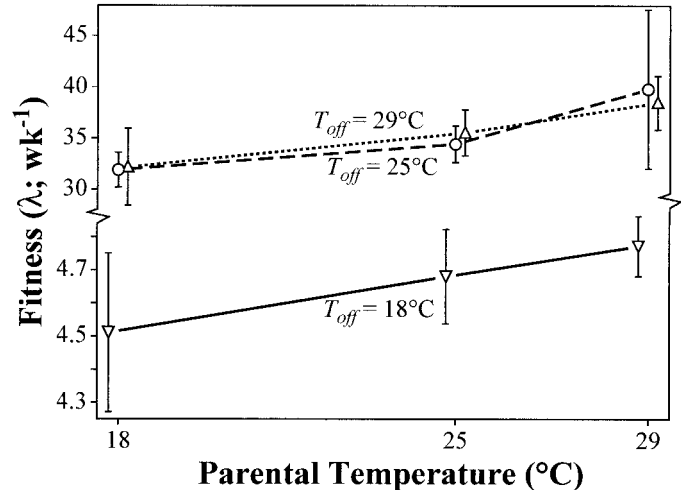
same environment as that of their parents (Mousseau and Dingle 1991; Leroi et al. 1994; Huey et al. 1999).

What mechanism might explain why hotter parents are better? Mueller and Ayala's (1981) fitness assay is especially sensitive to rapid development and early fecundity. Thus, females whose parents were reared at high temperature may have greater early fecundity than do females whose parents were reared at low temperature or they may produce offspring (thus grandoffspring of the parental flies) that develop more rapidly. We found that the F_2 offspring of flies whose parents came from the high-temperature treatments completed development more rapidly than did the offspring of flies whose parents were reared at 18°C or 25°C. However, F_1 flies among the parental treatments did not differ significantly in early fecundity (Table 3).

Several insect studies support the general pattern that hotter is better in terms of developmental acclimation across generations. Using a partial-factorial design, Zamudio et al. (1994) found that male *D. melanogaster* derived from parents reared at 25°C better defended their territories at a high temperature than did males from parents reared at 18°C. Groeters and Dingle (1988) found that milkweed bugs from parents reared at 27°C attained reproductive maturity more rapidly than bugs from parents reared at 23°C.

The effects of parental temperature are likely to be complex and to affect diverse traits in diverse ways. Even though larger body size is often associated with higher fitness in *Drosophila* and other insects (e.g., Ewing 1964; Hoffmann 1987a,b; Partridge et al. 1987; Wilkinson 1987; Santos et al. 1988), individuals with a reduced size resulting from developmental and cross-generational effects of higher temperature (Zamudio et al. 1994; Crill et al. 1996) seem to have higher fitness than larger flies from low-temperature treatments. Perhaps high-temperature parents produce offspring that are physiologically more robust and more resistant to diverse stresses (Feder 1996). For example, Crill et al. (1996) showed that *D. melanogaster* offspring from parents grown at 25°C, despite their relatively small mass, had a higher knockdown temperature than did flies from parents grown at

18°C. In contrast, several studies (reviewed in Huey et al. 1995) have found that within- and between-generation effects of high temperature generally depress early fecundity. More research is needed to understand the interactions between life history, physiology, and morphology.

Using a similar factorial design and analysis, Huey et al. (1999) reanalyzed published data from several researchers to test competing hypotheses regarding developmental temperature effects on fitness. How well do those developmental temperature patterns compare with those observed here for parental temperatures? In the present experiments, the data exclusively support the HPB hypothesis. Previous experiments on developmental temperature acclimation generally supported the optimal developmental temperature hypothesis (Cohet and David 1978; Zamudio et al. 1994; Huey et al. 1999). Nevertheless, a few experiments showed limited support for selective advantage of higher temperatures (*Volvox* swimming speed: Herron 1996; *D. melanogaster* longevity: Zwann et al. 1991; *D. melanogaster* flight power output: Barnes and Laurie-Ahlberg 1986). Thus, developmental and cross-generational effects of temperature are not always parallel. However, both kinds of effects are clearly inconsistent with the common adaptive prediction that acclimation to a given environment enhances fitness.

In conclusion, parental temperatures have diverse and complex effects on offspring in *D. melanogaster* (Huey et al. 1995; Crill et al. 1996), but having hot parents seems to maximize offspring fitness. We suggest several ways in which this research can be extended. First, one could design a factorial experiment that separately manipulates parental, developmental, and adult thermal environments (as per Huey et al. 1995), and then directly estimate fitness over a range of F_1 ages (P. Gibert, R. B. Huey, and G. W. Gilchrist, unpubl. ms.) This would enable one to determine whether parental and developmental effects decay as an individual acclimates to its adult environment. Second, to make the experiments ecologically more realistic, one might use fluctuating, rather than constant, thermal regimes (Bradshaw 1980; Brakefield and Mazzotta 1995). In any case, further attention to the complex effects of temperature on parents and development definitely seems warranted.

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