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Flies developed smaller cells when temperature fluctuated more frequently

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ABSTRACT

Changes in cell size might be an important component of adaptation to thermal heterogeneity. Although *Drosophila melanogaster* develops smaller cells at fluctuating temperatures, we do not know whether this response depends on the frequency or amplitude of thermal change. In a laboratory experiment, we exposed flies to either frequent or infrequent fluctuations between 17 and 27 °C, while controlling the total exposure to each temperature. Flies emerged from these treatments with similar body sizes, but flies at more frequent fluctuations emerged earlier and had smaller epidermal cells for a given body size. Tissue built from small cells has more nuclei for transcription, shorter distances between cell compartments, and a larger surface area for transport across membranes. Therefore, we hypothesize that physiological effects of small cells reduce lags in metabolic activity and enhance performance of flies during warming. For plasticity of cell size to confer a fitness advantage, this hypothetical benefit must outweigh the cost of maintaining a greater area of plasma membrane.

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1. Introduction

To understand the potential impacts of climate change, biologists have started to consider how organisms respond to the variance of temperature as well as how they respond to the mean. Today's climates include more extreme temperatures than previous climates did (Hansen et al., 2012), and an increasing range of temperatures can be more detrimental than an increasing mean. After all, animals rarely experience the mean air temperature. Instead, environmental temperatures combine with other physical and phenotypic factors to change an organism's distribution of body temperatures (Bakken, 1976; Gates, 1980; Angilletta, 2009). For many organisms, fluctuations in temperature constitute a daily environmental stress; for example, the larvae of *Drosophila melanogaster* (Meigen) warm by as much as 20 °C in fewer than four hours while developing in rotting fruits (Feder, 1997). Such fluctuations drive ecological and evolutionary phenomena. On an ecological scale, thermal fluctuations influence the phenotypes expressed throughout the life cycle (Niehaus et al., 2012). These ecological responses to thermal variance are complicated by the nonlinear relationship between an animal's temperature and its performance (Martin and Huey, 2008; Kingsolver et al., 2009): an increase in the variance of body temperature enhances fitness at low mean temperatures but depresses fitness at high ones (Siddiqui and Barlow, 1972, 1973; Siddiqui et al., 1973; Bozinovic et al., 2011). On an evolutionary scale, thermal fluctuations select for certain physiological and life historical phenotypes (Levins, 1968; Lynch and Gabriel, 1987; Stearns, 1992; Angilletta, 2009), some of which have been documented through experimental evolution (Bennett and Lenski, 1993; Duncan et al., 2011; Cooper et al., 2012). Although we have much to learn about these ecological and evolutionary responses, one thing is certain: thermal fluctuations do matter.

Although many theories address how organisms respond to fluctuating temperatures (reviewed by Angilletta (2009)), much less attention has been focused toward cellular responses. To understand how thermal fluctuations affect cells, we focus on *D. melanogaster*, whose cellular responses to temperature have been better described than those of any other species. An increase in either the mean or the variance of temperature during development causes flies to emerge smaller (Economos and Lints, 1986; Petavy et al., 2001, 2004; Czarnoleski et al., 2013); this reduction in body size stems primarily from a reduction in size of cells rather than the number of cells (French et al., 1998; Azevedo et al., 2002; Czarnoleski et al., 2013). A theory has emerged to address the

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development of smaller cells in warmer environments. This theory assumes that smaller cells, with their greater surface area relative to volume and shorter paths for diffusion, better meet increased demands for resources (Szarski, 1983; Woods, 1999; Kozlowski et al., 2003; Atkinson et al., 2006; Hessen et al., 2013). Still, this theory cannot explain why organisms should develop smaller cells at fluctuating temperatures than they do at constant temperatures. To explain this pattern, Czarnoleski et al. (2013) proposed that flies with smaller cells benefit by completing more metabolism during brief periods at high temperature. When organisms must quickly process large quantities of resources, the relatively large plasma membrane of a small cell increases the exchange of molecules, and especially oxygen, between the cell and its environment. Although plausible, this hypothesis assumes that when temperatures fluctuate, the magnitude of thermal maxima and the time spent at these maxima drives changes in cell size.

Here, we address a simple yet important distinction about biological responses to thermal fluctuations. When animals develop smaller bodies and smaller cells in fluctuating environments, are they responding to the frequency or magnitude of thermal change? Although previous experiments showed that thermal fluctuations triggered the development of smaller cells in *D. melanogaster*, they conflated the frequency and magnitude of change (Czarnoleski et al., 2013). An environment that fluctuates between two temperatures has a greater variance than one that remains constant. Nevertheless, an environment that fluctuates frequently between two extremes can have the same mean and variance of temperature as one that fluctuates less frequently. Since natural environments differ not only in their mean and variance of temperature but also in the frequency of warming and cooling, we must decouple these effects to develop a more accurate picture of thermal plasticity. Here, we report an experiment of *D. melanogaster* in which the frequency of thermal fluctuations was manipulated independently of the magnitude to isolate its effects on development time, body size, and cell size.

2. Materials and methods

Female flies were collected in bait traps in Marlton, New Jersey, and were shipped to Indiana State University. To form isofemale lines, each female was transferred to a vial containing standard medium (Indiana University, Bloomington). Vials were kept at 21 °C on a 12:12 light cycle. New generations were created every three weeks by transferring emerging adults to fresh vials. Females from the third generation supplied eggs for our experiment. To obtain these eggs, we allowed 12-day-old females from 31 isofemale lines to oviposit for 24 h at 22 °C. Replicate vials were used for each line, with only one female in each vial.

We raised two vials from each isofemale line in each of two environments, which were maintained by programmable incubators (Precision Scientific, Chicago, USA). Although both treatments fluctuated between 17 and 27 °C, one treatment fluctuated frequently while the other did so infrequently (six versus two shifts per 24 h; Fig. 1). Other factors were the same for both treatments: the light cycle (15 L:9D), the duration per day at each temperature (13.5 h and 10.5 h at 17 and 27 °C, respectively), and the durations at each temperature during scotophase (6.5 h and 2.5 h at 17 and 27 °C, respectively) and photophase (7 h and 8 h at 17 and 27 °C, respectively). To confirm the mean temperatures of the frequently and infrequently fluctuating treatments, we immersed iButton thermochrons (Dallas Semiconductors, Dallas, USA) in the medium within vials.

We measured development and morphological traits of flies in each treatment. The minimal developmental time was estimated as the number of days between oviposition and the first emergence. For morphological measurements, we sampled up to four females from each vial at four to six days after eclosion. An ocular micrometer of a dissecting microscope (Leica Microsystems, Buffalo Grove, USA) was used to measure thorax length to the nearest 0.025 mm. The left wing of each fly was fixed to a slide with Permount (FisherScientific, Fair Lawn, USA), and the dorsal surface was digitized by a microscopic camera (Olympus Corporation, Tokyo, Japan). We used ImageJ software (National Institutes of Health, USA) to measure the area of the wing in mm^2 (Fig. 2B). Following (Dobzhansky, 1929), we estimated the mean area of epidermal cells from the reciprocal of trichome density in the 0.01-mm^2 area between the distal segments of the fourth and fifth wing veins. Epidermal cells in wings are commonly used to infer relative cell size in drosophilids (Arendt, 2007), because their size correlates with the sizes of other cells (Stevenson et al., 1995). Moreover, the sizes of cells in different organs of flies respond in concert to developmental conditions (Azevedo et al., 2002; Heinrich et al., 2011). The discovery of strong correlations between the sizes of cells from different tissues in animals (Kozlowski et al., 2010) and plants (Brodribb et al., 2013; John et al., 2013) suggests that the mechanisms coordinating cell size in organs might be evolutionarily conserved among metazoans. Nevertheless, some cell types can change independently (Kozlowski et al., 2010; Maciak et al., 2014).

We used nlme library of the R Statistical Package (R Development Core Team, 2011) to examine the effects of thermal fluctuations on developmental time, thorax length, wing size, and cell size. Two random factors were included in our models: (1) isofemale line and (2) female nested within line and treatment. Thorax length was a covariate in the analysis of wing size, and wing size was a covariate in the analysis of cell size. AIC was used to identify the most likely model for each variable.

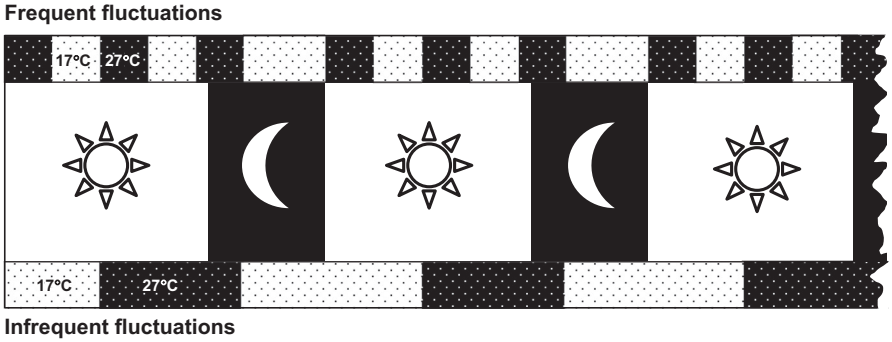

Fig. 1. Flies in our experiment experienced different frequencies of thermal fluctuations while spending the same durations at two temperatures. The central row depicts the durations of photophase and scotophase (denoted by the sun and moon, respectively). The stippled blocks depict the durations at 17 and 27 °C (denoted by white and black backgrounds, respectively).

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