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Altitudinal variation in lifespan of *Drosophila melanogaster* populations from the Firtina Valley, northeastern Turkey

Nazli Ayhan [a,b], Pinar Güler [a,c], Banu Sebnem Onder [a,*]

[a] Hacettepe University, Faculty of Science, Department of Biology, 06800 Beytepe, Ankara, Turkey
[b] UMR Emergence des Pathologies Virales (EPV: Aix-Marseille University – IRD 190 – Inserm 1207 – EHESP), Marseille, France
[c] Institut für Zoologie, Universität Regensburg, Regensburg 93040, Germany

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A B S T R A C T

Studies of altitudinal changes in phenotype and genotype can complement studies of latitudinal patterns and provide evidence of natural selection in response to climatic factors. In *Drosophila melanogaster*, latitudinal variation in phenotype and genotype has been well studied, but altitudinal patterns have rarely been investigated. We studied populations from six different altitudes varying between 35 m and 2173 m in the Firtina Valley in northeastern part of Turkey to evaluate clinal trends in lifespan under experimental conditions. Lifespan in the *D. melanogaster* populations was examined in relation to altitude, sex, temperature (25 °C and 29 °C), and dietary yeast concentration (5 g/L and 25 g/L). As expected high temperature decrease lifespan in all populations. However, it was shown that lifespan was slightly affected by dietary stress. We found that lifespan decreases significantly under thermal stress conditions with increasing altitude. Moreover, there was a slightly negative relationship between altitude and lifespan, which was closely associated with climatic factors such as temperature and precipitation, may suggest local adaptation to climate.

1. Introduction

Life history traits represent a focal point for natural selection to produce the best lifetime strategies that increase fitness in a particular environment (Baur and Raboud, 1988). Species that occur in different environments should present different patterns of life history traits in their different populations due to different local selection pressures. This variation may be the result of either adaptation or phenotypic plasticity (Stearns, 1989).

Clinal variation is one of the most common types of geographical variation that occurs along latitude and altitude gradients in diverse groups of animals and plants (Futuyma, 1998). Geographical variation in traits related to fitness is determined by genetic differentiation in many species (Adrion et al., 2015; Karl et al., 2009; Takahashi et al., 2011; van Delden and Kamping, 1997). Analyzing these clinal patterns in fitness-related traits is one of the main objectives of studies of adaptive evolution (Sambucetti et al., 2006). Temperature is one of the significant selective factors acting on geographical clines in traits of adaptive importance (Norry et al., 2001; Reeve et al., 2000). Geographical and clinal patterns in fitness-related traits, such as morphometric, physiological, and life-history traits, have been found in *Drosophila* populations (Adrion et al., 2015; Arthur et al., 2008; Bubliy and Loeschcke, 2005; Hoffmann and Shirriffs, 2002; Pitchers et al., 2013; Robinson and Partridge, 2001; Sambucetti et al., 2006; Schmidt and Paaby, 2008). Depending on the *Drosophila* species studied, latitudinal clines have also been found in allele frequencies and chromosomal inversion frequencies (de Jong and Bochdanovits, 2003; Fabian et al., 2012; Kapun et al., 2016; Knibb, 1982; Paaby et al., 2010; Simões et al., 2012). Parallel geographical clines in molecular markers and/or quantitative traits within and among species are an important source of information for studies of local adaptation (Adrion et al., 2015; Reinhardt et al., 2014; Schrider et al., 2016).

Many life-history traits, such as lifespan, are known to correlate with external factors. Lifespan is highly variable among populations and may vary with latitude, altitude, and temperature (Duyck et al., 2010; Tatar et al., 1997). Latitudinal or altitudinal patterns in lifespan have been documented in a number of species (Munch and Salinas, 2009) including *Melanoplus sanguinipes / devastator* (Tatar et al., 1997), *Margaritifera margaritifera* (Ziuganov et al., 2000), some sub-tropical anuran species (Morrison et al., 2004), *Lycaena tityrus* (Karl and Fischer, 2009), *Ceratitis rosa* (Duyck et al., 2010), *Homo sapiens* (Burtscher, 2014), *D. buzzatii* (Norry et al., 2006), and *D. melanogaster* (Schmidt and Paaby, 2008; Sgrò et al., 2013). These studies suggest that lifespan may contribute to adaptive differentiation across habitats. However,

* Corresponding author.
E-mail address: bdalgic@hacettepe.edu.tr (B.S. Onder).

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there is relatively little information regarding to how lifespan varies with geography and with different environmental conditions (Hoffmann et al., 2003; Mitrowski and Hoffmann, 2001; Schmidt and Paaby, 2008; Trotta et al., 2006). The strong relationship between climatic factors and life-history traits is well known, and these results come mostly from investigation of organisms collected from different geographical locations, particularly from latitudinal gradients. It is possible, however, that climatic differences do not directly contribute to differences in fitness-related traits owing to the limited gene flow between distant populations (Bubliy and Loeschcke, 2005; Pitchers et al., 2013).

We studied *D. melanogaster* populations from six different localities between 35 m and 2173 m in the Firtina Valley in northeastern Turkey. The valley is covered with warm deciduous forests extending without interruption in lowlands. Stands of dense trees, reaching over 30 m in height, surrounded the valley in the lowlands (0–1000 m), whereas meadows and grasslands are dominant in the subalpine and alpine zones (above 1000 m). The dense tree coverage isolates the valley from wind, and wind activity within the valley is therefore highly reduced. The valley receives abundant rainfall all year long with mean precipitation values reaching 1296.5 mm. Temperatures are usually low with a yearly mean of 13.5 °C. The highest temperatures are recorded in July and August with mean values of approximately 21.7 °C, although intra-day temperatures can vary depending on sunlight and rainfall. Relative humidity is high in the lowlands and constant throughout the year with mean values of approximately 73–82% (Saglam and Caglar, 2007). The most drastic environmental changes occur in the subalpine and alpine zones, where trees are limited and open landscapes are more common. Higher altitudes possess harsher and unstable environments with lower air temperatures and oxygen levels, and increased wind and radiation levels. High altitudes are thus typically unsuitable for insects like fruit flies that mostly feed and breed on rotting fruits. Limited vegetation leads to limited food sources for fruit flies and prevents them from occupying the highlands. These decreases in fruit supplies along altitudinal gradients may limit high-altitude colonization by fruit flies that have ripe fruit requirements. Because of all these heterogeneous environmental conditions along altitudinal transects in the valley, the Firtina Valley is well suited for studies of adaptation to different environments at narrow geographical scales.

The aim of this study was to examine the variation in lifespan in relation to local climatic variables in populations collected along a 40-km altitudinal transect in the Firtina Valley in Turkey, with an average mean annual temperature difference of 10 °C between the lowest and highest elevation points. By analyzing lifespan, we expected to identify the selectively important climatic factors under natural conditions, and by rearing the populations under different temperatures and diets, we also aimed to investigate plastic responses to temperature and diet. Phenotypic plasticity is thought to play an important role in the adaptation of populations to changing local environments (Schlichting and Pigliucci, 1998).

2. Materials and methods

2.1. Origin of the Flies Used

Fly collection was conducted in August 2012 at six different elevations along an altitudinal transect in the Firtina Valley, Rize, Turkey (Fig. 1), using banana-baited plastic bottle traps. Geographical coordinates were determined with a GPS (Table 1). The

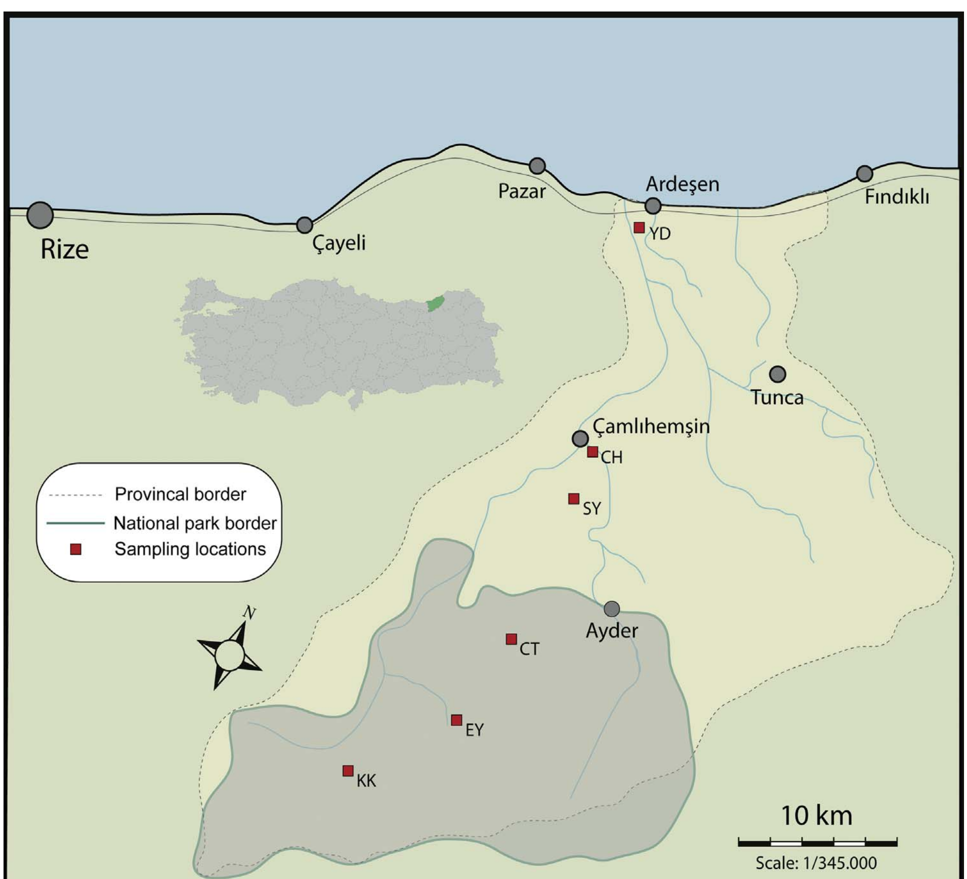

Fig. 1. Map showing the six sampling localities along the altitudinal gradient from Firtina Valley, Turkey.