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Phenotypic plasticity in thermal tolerance in the Glanville fritillary butterfly

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ABSTRACT

Ambient temperature is an ubiquitous environmental factor affecting all organisms. Global climate change increases temperature variation and the frequency of extreme temperatures, which may pose challenges to ectotherms. Here, we examine phenotypic plasticity to temperature and genotypic effects on thermal tolerance in the Glanville fritillary butterfly (*Melitaea cinxia*). We found no significant difference in heat or cold tolerance in populations originating from a continental climate in China and from Finland with moderate temperature variation. Acclimation to large-amplitude temperature variation increased heat tolerance in both populations, but decreased cold tolerance and increased *hsp70-2* expression in the Chinese population only. The latter result indicates a genotypic effect in the response to temperature variation. In the Finnish population, a non-synonymous SNP in the *phosphoglucose isomerase* (*Pgi*) gene was associated with heat knock-down time.

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1. Introduction

Temporal variation in ambient temperature and other environmental factors poses challenges especially to ectothermic organisms (Clarke, 2003; Hoffmann et al., 2003). On-going climate change increases mean temperature, but there is also emerging evidence that climate change leads to increasing variability of temperature and increasing frequency of extreme weather conditions (Coumou and Rahmstorf, 2012; Easterling et al., 2000; Walther et al., 2002). The ability to cope with temperature extremes rather than with mean temperatures may be critical in thermal adaptation and survival of species (Hoffmann et al., 2002).

Organisms respond to changes in environmental temperature conditions via phenotypic plasticity (Ayrinhac et al., 2004; Zeilstra and Fischer, 2005), and genetic (Latimer et al., 2011; Norry et al., 2009) and epigenetic adaptations (Freitak et al., 2012; Pezer and Ugarkovic, 2012). Phenotypic plasticity involves acclimation (Fischer and Karl, 2010), defined as facultative modification of a physiological trait in response to changes in an environmental variable (Wilson and Franklin, 2002). For instance, *Drosophila melanogaster* reared in 13 °C was more cold tolerant than those reared in 25 °C (Bubliy and Loeschcke, 2002), and flies reared in 31 °C were more heat tolerant than flies reared in 25 °C (Colinet et al., 2013). Most research in this area is focused on acclimation to high or low temperatures, whereas fewer studies have examined the effect of temperature variation, which may however also influence thermal adaptation (Arias et al., 2011; Fischer et al., 2011; Pertoldi and Bach, 2007). Here, we have examined how adult acclimation to temperature variation may affect thermal tolerance to extreme temperatures.

Many heat shock proteins (HSPs) function as "molecular chaperones" to maintain correct protein folding (Parsell and Lindquist, 1993). The transcriptional induction of genes encoding *hsp*, especially *hsp70*, is commonly known to respond to stresses such as heat shock (Hoffmann et al., 2003), mechanical damage (Luna et al., 2009), hypoxia (Azad et al., 2009), lowered pH (Huesca et al., 1998), chemical exposure (Nazir et al., 2003), oxidative stress (Menoret et al., 2002), and UV radiation (Bonaventura et al., 2006). *hsp70s* are known to be important in coping with extreme temperatures and have been frequently studied in the context of thermal adaptation in many insects (Dahlhoff and Rank, 2000; Karl et al., 2009; Sørensen et al., 2003; Wang and Kang, 2005).

Apart from phenotypic plasticity, adaptation to dissimilar thermal environments may involve genetic factors, for instance allozyme polymorphism in the metabolic enzymes. The *D. melanogaster* study by Sezgin et al. (2004) revealed SNPs in three metabolic genes that appeared to be related to thermal adaptation.

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The gene *phosphoglucose isomerase* (*Pgi*, systematic name *glucose-6-phosphate isomerase, Gpi*, EC 5.3.1.9) is highly polymorphic in most species and the allozymes have been shown to be related to thermal tolerance (Riddoch, 1993). *Pgi* catalyzes the conversion of glucose-6-phosphate to fructose-6-phosphate in glycolysis, and it is one of the key enzymes in glucose metabolism. In *Colias* butterflies, PGI allozyme alleles have been suggested to differ in thermal stability and to be related to flight performance and fecundity (Watt, 1983, 1992; Watt et al., 1996). PGI allozymes have been related to flight ability in low temperature in *Danaus plexippus* (Hughes and Zalucki, 1993), and allelic variation in PGI has been associated with thermal tolerance in the leaf beetle *Chrysomela aeneicollis* (Neargarder et al., 2003) and related to chill-coma recovery time in the copper butterfly *Lycaena tityrus* (Karl et al., 2008). It is also commonly known that many glycolysis enzymes are induced by heat shock, which has been suggested to be related to higher energy demands during stress (Hohmann and Mager, 2003), and indeed, many glycolysis pathway genes are among the regulatory targets of HSPs (Sato et al., 1999; Schmitt and McEntee, 1996). In the study by Wang et al. (2012), activities of measured glycolytic enzymes were increased after upregulation of HSP70 in order to compensate ATP balance.

Here, we acclimated adult Glanville fritillary butterflies (*Melitaea cinxia*) at dissimilar conditions of variable temperature to examine responses to extreme temperature differences. The Glanville fritillary butterfly is widely distributed across Eurasia, and it has become a model species in population and evolutionary biology (Ehrlich and Hanski, 2004; Hanski, 1999). We compared differences in thermal tolerance of butterflies originating from two contrasting environments in Finland and China. Xinjiang in China has a very continental climate with extremely high summer temperatures, very low winter temperatures, and very marked diel fluctuation in temperature. The Åland Islands in Finland have a North European climate with moderate variation in thermal conditions. We also analyzed the associations between *hsp70* expression and allelic variation in *Pgi* with thermal tolerance.

2. Material and methods

The Chinese Glanville fritillary population originates from Nantaizi (40°24'N, 87°12'E), the Tianshan Mountains, Xinjiang, in northwest China. The Finnish population is from the Åland Islands (60°07'N, 19°54'E) in SW Finland. Larvae were reared in the laboratory in common garden conditions and fed with *Veronica spicata*, the natural host plant in both populations.

One-day-old adult butterflies were acclimated in two different temperature regimes for 2 days (Fig. 1). The small-amplitude acclimation condition (SA) mimics moderate temperature variation, such as occurs naturally in Finland. The large-amplitude acclimation condition (LA) reflects the thermal conditions in China. The mean daytime temperature in June is around 25 °C in Åland Islands, and the daily temperature variation is 10–15 °C. In Nantaizi in China, the daytime temperature in June is 35–40 °C, and the daily temperature variation reaches 30 °C. We used the common photoperiod of 12 h light followed by 12 h of dark. Butterflies were fed daily with 20% honey water solution.

On the third morning of their life, butterflies from both acclimation conditions were used in heat and cold tolerance experiments. Every butterfly was transferred into a plastic cylinder box (100 ml). In the heat shock treatment, the butterfly was transferred to a pre-heated cylinder box in water bath at 53 °C. We measured the heat knock-down time. The experiments took place in the morning between 10 and 11 am. In the cold shock treatment, plastic cylinder boxes with one butterfly in each were placed in a climate chamber and exposed to −5 °C for 2 h, after

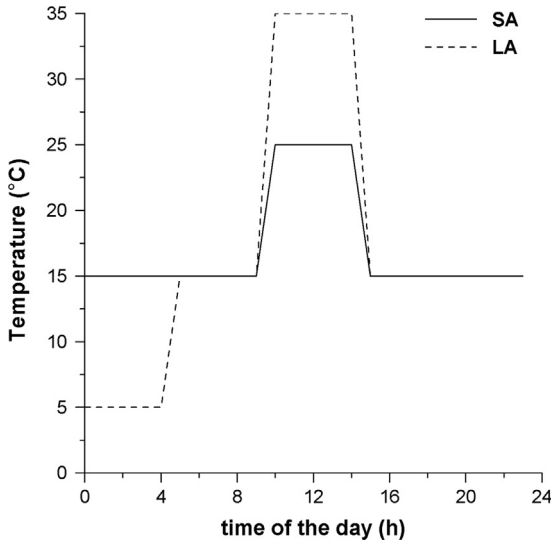

Fig. 1. Acclimation conditions of butterflies before the heat/cold shock. SA: small-amplitude acclimation; LA large-amplitude acclimation.

which they were moved to room temperature (21 °C). All cold shock treatments were conducted starting at 10 am. In a pilot experiment, cold exposure at −5 °C for 2 h did not cause the death of butterflies, while many butterflies died at −8 °C. Chill-coma recovery time was recorded at room temperature (21 °C) as the time from the end of the chill exposure to the time when the butterfly was standing on its feet.

We used 41 Chinese butterflies from 8 families and 60 Finnish butterflies from 8 families in the comparison of heat tolerance between the two populations, and 45 Chinese butterflies from 5 families and 107 Finnish butterflies from 20 families in the comparison of cold tolerance. The butterfly families used in the experiments consisted of 1 to 9 siblings. The pedigree of the butterflies was taken explicitly into account in the analyses.

To test the effect of the acclimation condition on *hsp70* expression, we collected samples of Finnish and Chinese butterflies prior to thermal stress. Following acclimation in LA and SA for 2 days, butterflies were snap-freezed in liquid nitrogen for DNA/RNA extraction and downstream *hsp70* expression measurements. *hsp70* expression was measured at the mRNA level with quantitative PCR (qPCR). *18S rRNA* gene was used as a reference gene. Several *hsp70* candidates were found from the Glanville fritillary draft genome assembly v1.0 (Ahola et al., in preparation). We selected two *hsp70* genes, referred to as *hsp70-1* (GenBank JX548526) and *hsp70-2* (GenBank JX548528), which shared the highest identity with the published *Bombyx mori hsp70* (NP_001037396) reference gene. Altogether 55 Finnish butterflies from 18 families and 31 Chinese butterflies from 5 families were available for the *hsp70* gene expression study.

To test the relationship between *Pgi* and thermal tolerance, we genotyped the *Pgi* SNP EU888473.1 (*Pgi*):c.331A > C), which is referred to as *Pgi* AA111 (Orsini et al., 2009). *Pgi:c.331AA* and *Pgi:c.331AC* genotypes are common in the Finnish population, while *Pgi:c.331CC* is rare (in China *Pgi:c.331CC* is common). To increase the sample size of the Finnish butterflies for the *Pgi* study, we performed an additional heat tolerance treatment with another set of 112 Finnish butterflies from 20 families. DNA was extracted from butterfly abdomen with NucleoSpin 96 tissue kit (Macherey-Nagel, Düren, Germany). The PCR reaction system (20 μl) of (*Pgi*): c.331A > C genotyping consisted of 20–30 ng of genomic DNA, 0.4 μM of the primer pair (Table 1), 200 μM of dNTPs mix and 0.5 U of KAPA Taq polymerase (KAPA Biosystems, MA, USA). The PCR amplification condition included denaturing at 95 °C for 3 min,

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