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Thermal plasticity is related to the hardening response of heat shock protein expression in two *Bactrocera* fruit flies

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ABSTRACT

It is generally believed that widely distributed species differ in their thermal plasticity from narrowly distributed species, but how differences in thermal plasticity are regulated at the molecular level remains largely unknown. Here, we conducted a comparative study of two closely related invasive fruit fly species, *Bactrocera correcta* and *Bactrocera dorsalis*, in China. The two species had overlapping distributions, but *B. dorsalis* had a much wider range throughout the country and a longer invasive history than *B. correcta*. We first examined the effects of thermal acclimation on the ability of the two fruit flies to survive heat stress. The heat shock tolerance of *B. dorsalis* was significantly enhanced by heat hardening at 35, 37, 39 and 41 °C, but that of *B. correcta* was only enhanced by heat hardening at 39 °C and 41 °C. Thus, the more widespread species has a higher thermal plasticity than the narrowly distributed species. We then determined the expression of Hsp70 and Hsp90 during different developmental stages and their responses to thermal hardening. The expression of both Hsp70 and Hsp90 in larvae was upregulated in response to heat hardening, starting at 35 °C for *B. dorsalis* and at 39 °C for *B. correcta*. The two species exhibited a highly consistent pattern of thermal response in terms of their heat shock survival rates and levels of Hsp gene expression. The results suggest that the difference in thermal plasticity may be responsible for the different distributions of the two species and that Hsp expression may be involved in the regulation of thermal plasticity. Our findings have important implications for the prediction of the thermal limits and ecological responses of related species in nature.

1. Introduction

Invasive species constitute a major threat to biodiversity, ecosystem function and agricultural production (Mack et al., 2000; Ricciardi, 2007; Kang et al., 2009). The natural range expansion of ectothermic invasive species are constrained primarily by their capacity to tolerate unfavorable environmental conditions, such as temperature extremes and fluctuations (Bale and Walters, 2001; Chen and Kang, 2005a; Somero, 2005; Bowler and Terblanche, 2008; Gaston, 2009), although biotic interactions can also pose further constraints (Davis et al., 1998; Van der Putten et al., 2010). The thermal plasticity by which organisms adjust their physiological performance in response to changing thermal environments has been identified as an important strategy for coping with thermal stress for many species (Mitchell et al., 2011). Species with a high thermal plasticity not only will have an advantage in terms of range expansion but will also perform better, for example, in terms of their feeding and reproduction capabilities during severe and frequent extreme temperature events (Huang et al., 2007; Bürgi and Mills, 2010). Thermal plasticity has been found to differ between tropical and temperate populations of *Drosophila melanogaster*, particularly under thermal stress. Compared with temperate flies, tropical flies performed better in terms of their productivity in warm environments but worse in cold environments (Trotta et al., 2006). Heat acclimation and hardening at moderate levels of temperature stress represent examples of thermal plasticity. Acclimation to low temperatures can enhance cold tolerance, but the extent of this enhancement varies among populations and species (Chen and Kang, 2004, 2005b). Recently, increased attention has been devoted to the application of laboratory-derived measures of thermal plasticity to the prediction of the thermal limits for a variety of taxa, as well as to the estimation of the ecological responses of individual species in nature (Chen and Kang, 2005b; Terblanche et al., 2007; Chown et al., 2010; Calosi et al., 2008; Helmuth et al., 2010; Hoffmann, 2010; Sunday et al., 2011). Thus, an understanding of

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the mechanisms underlying thermal plasticity is important, particularly in the context of the more pronounced temperature extremes predicted to occur as a result of global climate change (Easterling et al., 2000; Karl and Trenberth, 2003).

It is generally believed that the thermal plasticities of widely distributed species differ from those of narrowly distributed species, but this belief has not yet been tested for numerous species (Mitchell et al., 2011). For this study, we examined two fruit fly species, *Bactrocera correcta* and *Bactrocera dorsalis*, that are invasive in China. *B. correcta* was first reported in China in 1989 (Wang and Zhao, 1989; Liu et al., 2009), and its distribution is mainly limited to one province in southwestern China (Fig. 1). In contrast, the congeneric species *B. dorsalis*, which was first reported in China in 1912 (Hsu, 1973), has a wide distribution across 17 provinces, ranging from 14 °N to 30 °N in latitude (Wang et al., 2009; Wan et al., 2011; Li et al., 2012; Crop Protection Compendium, 2014) (Fig. 1). Previous studies have demonstrated that the two species differ in their resistance to temperature stress (Yang et al., 1994; Liu and Ye, 2009). Still, both of these fruit fly species feed on fruits such as oranges, guavas, and mangos, which are all planted in southern China (Li et al., 2012; Jiang et al., 2013). Thus, the history of expansion, basal thermal tolerance, and selection of host plants should not be critical factors that have determined the current distribution of the two species in southern China. Instead, we postulate that the difference in thermal plasticity between the two species may be a reason for their differing distribution patterns, but this hypothesis has not yet been validated by empirical evidence.

As poikilotherms, insect species have a poor ability to adjust and maintain their body temperature. Hence, environmental temperature is an important regulating factor of their metabolisms. One important mechanism for resisting the stress caused by an external temperature change is the production of heat shock proteins, which allow insects to adapt to different habitats. Heat shock proteins (Hsps) were first identified as gene products for which expression is induced by heat and other stresses (Lindquist, 1986; Ritossa, 1996; Roberts et al., 2010). Subsequently, their roles as molecular chaperones were gradually elucidated (Gething and Sambrook, 1992; Morimoto et al., 1994; Hartl, 1996). Hsps are now known to play various roles in the successful folding, assembly, intracellular localization, secretion, regulation, and degradation of other proteins (Gething, 1997). Specifically, many stress factors can induce the rapid upregulation of Hsp70 expression and the level of this upregulated expression can be correlated with the level of thermal stress resistance of a species (Feder and Hofmann, 1999). Hsp90 is a key regulator of numerous signal pathways (Rutherford et al., 2007) and has the capacity to buffer the expression of hidden genetic variation that can be caused by stressful conditions (Rutherford and Lindquist, 1998; Chen and Wagner, 2012). Thus, the natural variation in Hsp gene expression can be of consequence in determining phenotypes (Chen et al., 2007b; Chen and Wagner, 2012) and can confer adaptations to changing environments (Walser et al., 2006; Hoffmann and Willi, 2008). The onset temperature of Hsp expression is related to a species' overwintering isotherm, suggesting that Hsp expression is crucial for survival during periods of thermal stress and influences a the range expansion of species in nature (Huang et al., 2007; Kang et al., 2009). However, the question of how the induction of Hsp expression is related to the thermal plasticity of species, thus promoting insect adaptations to temperature changes, has not been well explored.

In this study, we tested the hypothesis that the divergence in thermal plasticity in two congeneric fruit flies is associated with differences in their expression of Hsp genes in response to thermal hardening, which, in turn, has defined the present habitation conditions of the two *Bactrocera* species examined. A comparative study was conducted to examine the effect of thermal acclimation on the ability of the two fruit flies to survive heat stress. The expression levels of Hsp70 and Hsp90 were quantified during different developmental stages and during the species' responses to thermal hardening. The widely distributed species has a higher thermal plasticity than the narrowly distributed species. Our

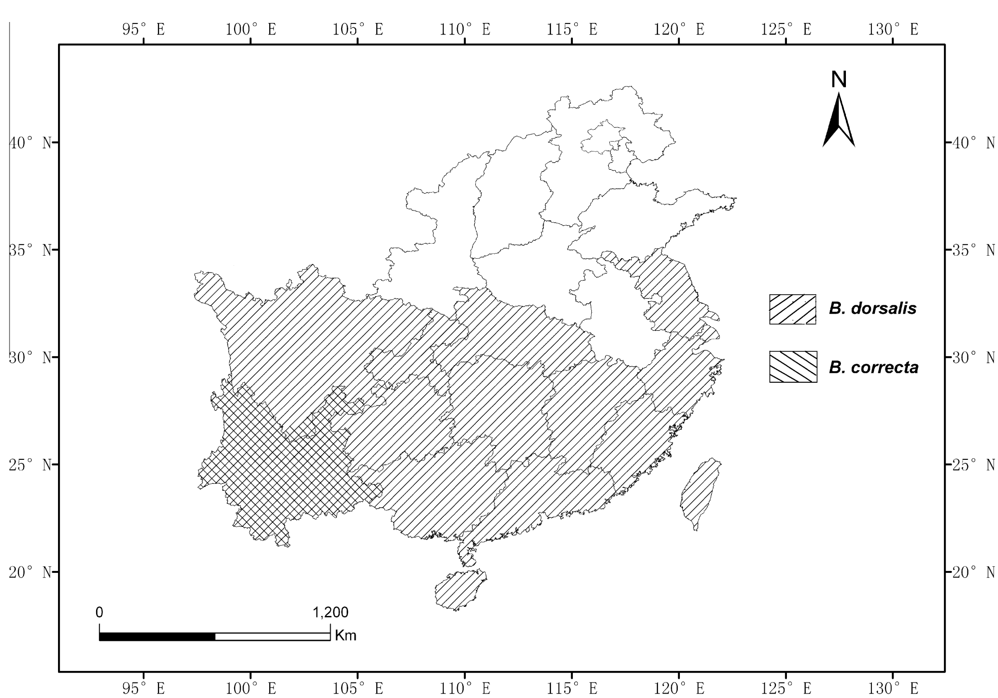

Fig. 1. Current distributions of *B. dorsalis* and *B. correcta* in southern China. The map shows the provincial regions in which the occurrence of the indicated species has been reported.