



Artificial selection on chill-coma recovery time in *Drosophila melanogaster*: Direct and correlated responses to selection



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ABSTRACT

Artificial selection can be used to create populations with extreme phenotypic responses to environmental stressors. When artificial selection is applied to a single component of a stress response, this selection may result in correlated responses in other stress responses, a phenomenon called cross-tolerance, which is ultimately controlled by the genetic correlations among traits. We selected for extreme responses to cold tolerance by selecting for chill-coma recovery time from a single temperate population of *Drosophila melanogaster*. Chill-coma recovery time is a common metric of low, but non-lethal, cold temperature tolerance. Replicated divergent artificial selection was applied to a genetically variable base population for 31 generations, resulting in two cold resistant, two cold susceptible, and two unselected control lines. To quantify the relationship between selection on chill-coma recovery and other metrics of thermal performance, we also measured survivorship after acute cold exposure, survivorship after chronic cold exposure, survivorship after cold exposure following a pre-treatment period (rapid cold hardening), starvation tolerance, and heat tolerance. We find that chill-coma recovery time is heritable within this population and that there is an asymmetric response to increased and decreased chill-coma recovery time. Surprisingly, we found no cross-tolerances between selection on chill-coma recovery time and the other environmental stress response traits. These results suggest that although artificial selection has dramatically altered chill-coma recovery time, the correlated response to selection on other stress response phenotypes has been negligible. The lack of a correlated response suggests that chill-coma recovery time in these selection lines is likely genetically independent from measures of cold survivorship tested here.

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1. Introduction

Daily and seasonal variation in climate, including temperature, is a stressful environmental factor to which organisms must respond (Harshman et al., 1999; Koehn and Bayne, 1989; Pidwirny, 2006; Sibly and Calow, 1989). For ectotherms, extreme temperatures directly influence most biochemical and physiological functions of the organism (Overgaard and Sorensen, 2008), inducing critical physiological processes required to maintain fitness (Brakefield, 2003; Hoffmann and Parsons, 1991). Low temperatures are particularly damaging as these temperatures will damage cell membranes and decrease overall cellular and physiological function and survivorship (Hazel, 1995; Overgaard et al., 2007; Rajamohan and Sinclair, 2008).

Understanding how organisms improve tolerance to cold stress has been a primary focus of physiological research both on short-term and long-term time scales (Gerken et al., 2015; Lee et al., 1987; Nyamukondiwa et al., 2011; Powell and Bale, 2006). General processes that may increase survivorship after cold stresses include within-generation *acclimation* responses caused via thermal pre-exposures to stress (Gerken et al., 2015; Lee et al., 1987; Rajamohan and Sinclair, 2008) or the across-generation genetic *adaptation* via shifts in allele frequency caused by the differential survivorship of natural genotypes after a stress exposure. These long-term and short-term cold tolerance mechanisms may be closely related physiologically or genetically, and selection pressures on a single component of cold tolerance may also change (via genetic correlations) other fitness or stress survivorship traits (Gibert et al., 2001; Hoffmann and Parsons, 1989; Leips and Mackay, 2000). Using artificial selection, it is possible to change the allele frequencies in genomic regions associated with a particular trait as well as to measure the magnitude and direction of genetic correlations between the trait under selection and other

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environmental stress response traits (Harshman et al., 1999; Košťál et al., 2012; Mackay et al., 2012; MacMillan et al., 2009, Overgaard and Sorensen, 2008, Service, 1987).

Cross-tolerance occurs when selection to a given environmental stressor results in a correlated response to tolerance in another environmental stressor (Harshman and Hoffmann, 2000; MacMillan et al., 2009). Cross-tolerance has been demonstrated in a variety of organisms, and is thought to be especially prevalent in insects (Bayley et al., 2001, Ring and Danks, 1994; Vermeulen and Loeschcke, 2007), although these cross-tolerances are inconsistent across all insects (Anderson et al., 2005; Bublly and Loeschcke, 2005; Kristensen et al., 2007; Norry et al., 2007; MacMillan et al., 2009; Phelan et al., 2003) which may be partly attributed to differences in selection methodology (i.e. cold shock treatment (Kristensen et al., 2007; MacMillan et al., 2009) versus chill coma treatment (Anderson et al., 2005)). Selection may contribute to the directionality of correlation and cross-tolerance to other traits (MacMillan et al., 2009). For example, correlations have been observed when selection drives an increased heat tolerance which is positively correlated to an increase in cold tolerance, but selection to tolerance to cold does not necessarily carry a correlated response of tolerance to heat (Bublly and Loeschcke, 2005). Furthermore, studies have examined correlations between stress metrics such as cold tolerance and starvation resistance (Bublly and Loeschcke, 2005; Le Bourg, 2013; Le Bourg and Massou, 2015; Sinclair et al., 2007; Scharf et al., 2016), cold selection and heat tolerance capacity (Anderson et al., 2005; Kristensen et al., 2007), diet manipulations and metabolic mechanisms (Clark et al., 2015; Harshman et al., 1999; Sisodia et al., 2015), response to hypoxia and cold tolerance (Benasayag-Meszaros et al., 2015, Boardman et al., 2015), and cold survivorship, desiccation resistance, and body size (Benoit et al., 2009; Gantz and Lee, 2015; Jumbo-Lucioni et al., 2010, Terhzaz et al., 2015).

The goal in quantifying stress-related trait correlations is to identify genetic correlations among traits and to determine the capacity of selection on one trait to constrain or promote phenotypic evolution of another (Brakefield, 2003; Bublly and Loeschcke, 2005; MacMillan et al., 2009). As many organisms have shown a wide range of cross-tolerances, several hypotheses have emerged concerning the overlap of genomic regions influencing various stress responses. A lack of correlations between responses to various environmental stresses may suggest that there is no linkage between tolerances to such stresses—all stress responses are genetically independent of one another (Harshman and Hoffmann, 2000; Sinclair et al., 2007), or that the experiment is too small to detect a weak correlation caused by the low heritability of each trait. Cross-tolerances may also gradually weaken over time as fitness trade-offs occur or spurious associations (i.e., transient LD) are broken down (Phelan et al., 2003). However, strong cross-tolerances are likely to occur when the underlying quantitative trait loci controlling each environmental stress trait are shared (Bublly and Loeschcke, 2005; Norry et al., 2007).

In this study, we specifically examine the cross-tolerances between chill-coma recovery time and five other environmental stress response traits. Chill-coma recovery is a physiological response to non-lethal cold temperatures (David and Capy, 1988) that is a genetically variable and adaptive phenotype exhibiting significant clinal variation on multiple continents (Gibert et al., 2001; Kristensen et al., 2007; Rako and Hoffmann, 2006) as well as strong habitat associations among species (Gibert et al., 2001). At the end of 31 generations of replicated artificial selection, we measured five environmental stress responses traits on each of the selection and control lines. These stress responses included acute cold exposure (-6°C for one hour), chronic cold exposure (0°C for 16 h), a rapid cold hardening pre-treatment followed by cold exposure (two hours at 4°C followed by one hour at -6°C),

starvation tolerance, and survival after heat stress (38°C for one hour). Anderson et al. (2005) demonstrated that selection to chill-coma recovery time was mostly independent of stress response to other traits but Bublly and Loeschcke (2005) found correlations between selected traits and starvation and cold shock and heat shock survival. Indeed, artificial, direct selection can lead to a correlated response among traits (Hoffmann and Parsons, 1993; Partridge and Fowler, 1993). We predict that selection for increased resistance to cold stress via selection on chill-coma recovery time will result in an increased ability to survive multiple environmental stressors while lines selected for a susceptibility to cold tolerance will have decreased survivorship to other environmental stressors.

2. Methods

2.1. Experimental flies and chill-coma recovery time assay

Mated *Drosophila melanogaster* females were collected from a single population at the Raleigh, NC Farmer's Market using fruit bait and we established a population of 60 isofemale lines in 2004. This sample of isofemale lines was used to establish a genetically variable base population, by crossing the lines in a round robin design in separate culture vials, with four males and four females per vial. Three days after the crosses were initiated, a single inseminated female from each cross was placed in each of two culture bottles to initiate two replicate base populations. The progeny from these culture bottles were designated generation 0. To begin the first generation upon which selection was applied, approximately 25 virgin males and females per replicate base population were scored for cold tolerance and were used to initiate the three selection regimes (resistant, susceptible, and control) in each base population. Thus resistant line 1, susceptible line 1, and control line 1 were derived from base population 1, while resistant line 2, susceptible line 2, and control line 2 were derived from base population 2.

To measure chill-coma recovery time, the trait upon which selection was applied, we utilized the assay presented in Morgan and Mackay (2006). Specifically, 50 male and 50 female flies were transferred without anesthesia into empty vials and placed in chambers containing melting ice ($0^{\circ}\text{C} \pm 0.5$) for 3 h. After 3 h, individuals were removed from the cold treatment and returned to room temperature ($23^{\circ}\text{C} \pm 0.5$), and the chill-coma recovery time was measured by recording the amount of time until an individual was able to stand on its legs.

All of the individuals screened in this study were young flies (i.e., 5–7 days old), as previous studies have found that chill-coma recovery time changes as a function of age (David et al., 1998). Experimental individuals were maintained at 25°C and 60% humidity and a 12:12 h light/dark cycle until they were used in the experimental assay. We scored chill-coma recovery time every generation, rather than every other generation as we have been unable to detect any evidence of 'carry-over' effects, i.e., detrimental influence of the cold treatment on future success (Anderson et al., 2005; Harrison et al., 2011), for cold tolerance (data not shown). However, if 'carry over' effects do exist within these or other populations the result of these effects will be the underestimation of the genetic variation in the trait rather than the overestimation.

2.2. Artificial selection regime

Beginning at generation one, 50 virgin male and female progeny were collected from each of the six lines every generation. These individuals were assayed for chill-coma recovery time as

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