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Cold temperature preference in bacterially infected *Drosophila melanogaster* improves survival but is remarkably suboptimal



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ABSTRACT

Altering one's temperature preference (e.g. behavioral fever or behavioral chill) is a common immune defense among ectotherms that is likely to be evolutionarily conserved. However, the temperature chosen by an infected host may not be optimal for pathogen defense, causing preference to be inefficient. Here we examined the efficiency of temperature preference in *Drosophila melanogaster* infected with an LD₅₀ of the gram negative bacteria *Pseudomonas aeruginosa*. To this end, we estimated the host's uninfected and infected temperature preferences as well as their optimal survival temperature. We found that flies decreased their preference from 26.3 °C to 25.2 °C when infected, and this preference was stable over 48 h. Furthermore, the decrease in temperature preference was associated with an increased chance of surviving the infection. Nevertheless, the infected temperature preference did not coincide with the optimum temperature for infection survival, which lies at or below 21.4 °C. These data suggest that the behavioral response to *P. aeruginosa* infection is considerably inefficient, and the mechanisms that may account for this pattern are discussed. Future studies of infected temperature preferences should document its efficiency, as this understudied aspect of behavioral immunity can provide important insight into preference evolution.

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1. Introduction

Fever in endotherms is a highly conserved, metabolically-generated increase in host body temperature that improves immune defense (Kluger 1978; Kluger et al. 1998). Ectotherms can also alter their body temperature adaptively in response to infection. However, this is accomplished by seeking out warmer (behavioral fever) or cooler (behavioral chill) temperatures, not by altering metabolic activity. For instance, invertebrate house flies (*Musca domestica*) and grasshoppers (*Melanoplus sanguinipes*) improve their chance of surviving fungal infections by relocating to warmer environments (Watson et al. 1993; Inglis et al. 1996). Infected vertebrate zebrafish (*Danio rerio*) likewise improve immune defense by seeking out warmer waters (Boltana et al. 2013). Such behavioral alterations to infection have been reported across a wide variety of ectothermic taxa and the phenomenon is likely to be evolutionarily conserved in animals (Kluger et al. 1998). Still, numerous studies have failed to detect changes in

the thermal preferences of infected ectothermic hosts, even when fitness would be increased by such a response (Stahlschmidt and Adamo 2013), suggesting that the expression and/or evolution of the behavior is complex.

Assuming that the host is capable of the behavior, there are several reasons why altered temperature preferences might not be elicited upon infection with a virulent pathogen. First, a change in temperature preference does not improve host fitness. This may occur if the host's temperature–fitness function is flat for the pathogen in question, or if the host is already at its thermal optimum. Second, the cost of the behavioral response outweighs the benefit for a given host. This may occur when an individual host has little remaining residual reproductive value (e.g. older hosts or hosts infected with sterilizing pathogens), causing it to forgo an immune investment and instead invest in reproduction (e.g. terminal investment; Fedorka et al. 2013; Fedorka 2014). Third, there is a lack of coevolutionary history between the host and pathogen, which could result in the host not recognizing an appropriate Pathogen Associated Molecular Pattern (PAMP) to initiate the behavior. Fourth, the behavior is inhibited by the invading pathogen. Behavioral inhibition is plausible when one considers that pathogen manipulation of host behavior is a common occurrence (Moore 2002). Unfortunately, the causes underlying the lack of behavior are difficult to assess and are generally not explored.

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Even if an infected host exhibits an adaptive shift in thermal preference, it does not mean the response is efficient. That is to say, the temperature chosen by a host when infected may not be the optimal temperature to maximize fitness. Inefficient temperature preference is an understudied aspect of ectothermic immune function that can provide important insights into the behavior's evolution. One potential reason for an inefficient preference is the aforementioned lack of host-pathogen coevolutionary history. This can be caused by (i) weak selection for the optimal infected temperature preference due to infrequent host-pathogen interactions, or (ii) a lack of evolutionary time to allow selection to shape the preference, even if selection is relatively strong (Fig. 1A). A second potential reason for an inefficient preference is pathogen inhibition. In order to maximize its own fitness, a pathogen might manipulate the infected host's temperature preference (IT_P) that results in a perpetual tug-of-war that keeps the host away from its temperature optimum (Fig. 1B). It is important to note that a "weaker" response by a certain class of host (e.g. older hosts) due

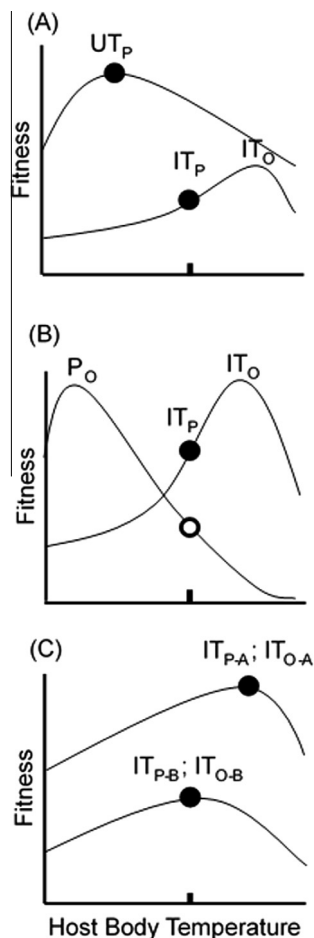


Fig. 1. The evolution and expression of behavioral fever. (A) When a lack of coevolutionary history exists between the host and pathogen, the infected host may not reach their infected temperature optimum (IT_O), resulting in a suboptimal/inefficient infected temperature preference (IT_P). UT_P represents the temperature preference of the uninfected host. (B) Pathogen manipulation may also result in a suboptimal IT_P due to selective pressure on the pathogen to reach its optimal host body temperature (P_O). (C) Multiple optima may exist for different groups of infected hosts within a species or population. Here, the fitness curves for two different hosts groups (A and B) are shown. For host B, a fully realized response may be too costly, and these hosts may exhibit a "weaker" infected temperature preference (IT_{P-B}) due to a decreased infected temperature optimum (IT_{O-B}) compared with host A's preference and optimum (IT_{P-A} and IT_{O-A}). Although this response would not be considered inefficient, it could appear as such if the experimental design did not account for host sampling bias.

to a higher behavioral cost does not represent an inefficient behavior, considering that the "weaker" response is still optimal for that class of host (Fig. 1C). It could be mistaken for inefficiency, however, if an experimental design suffered from sampling bias (e.g. not controlling for age, sex or reproductive history among treatments). Regrettably, most studies that document a host's altered temperature preferences when infected do not estimate the optimal temperature when infected (e.g. Boorstein and Ewald 1987; Adamo 1998; Karban 1998; Moore and Freehling 2002), making the prevalence of inefficient responses unknown among animals.

Here we examine the efficiency of temperature preference in *Drosophila melanogaster* infected with the gram negative bacterium *Pseudomonas aeruginosa*. We chose *D. melanogaster* as the host due to its prevalence as an invertebrate immunological model (Hoffmann 2003; Lemaitre and Hoffmann 2007) and *P. aeruginosa* as the pathogen because it is commonly used in invertebrate immunological studies (D'Argenio et al. 2001; Linder et al. 2008; Wittman and Fedorka 2015). *Pseudomonas* species exist naturally in wild populations of *D. melanogaster*, where oral-fecal transmission is the most likely route of infection, although infection via wounding may also occur (Corby-Harris et al. 2007; Chandler et al. 2011; Martins et al. 2013).

Once infected, *D. melanogaster* rely on a variety of immunological responses against gram-negative bacteria, including ROS production, lysozymes, phenoloxidase cascade, and IMD-related antimicrobial peptides (Vallet-Gely et al. 2008). No previous *D. melanogaster* study has found evidence of behavioral fever/chill (Ballabeni et al. 1995; Arnold et al. 2015). Still, the elicitation of a behavioral response is likely to be pathogen specific (Adamo 1998), and a response against bacterial pathogens has yet to be examined (previous work focused on nematodes and viruses). To examine the existence and efficiency of such a response in *D. melanogaster*, we estimated the host's uninfected (UT_P) and infected (IT_P) temperature preferences as well as their optimal body temperature when infected (IT_O). If a host's infected temperature preference (IT_P) coincides with its infected temperature optimum (IT_O), then the response would be deemed efficient. However, if IT_P fails to reach the optimum, then the behavior would be considered inefficient, and one of the above mechanisms would be involved in shaping this important immunological response.

2. Methods

2.1. Stock maintenance

Flies in this study originated from 40 gravid females collected in 2010 from a single location in Orlando Florida and maintained as a large outbred stock (~600 individuals per generation) to minimize the loss of genetic variation due to drift. Individuals were feed a cornmeal, yeast, sugar and agar food medium and kept in vertical incubators (Percival, Perry, IA, USA) at 25 °C with a 12 h:12 h light:dark photoperiod. Prior to all experiments, adult flies were collected upon eclosion and maintained in sex-specific vials at medium density (20 individuals per vial) to ensure virginity. All experimental flies were 5 ± 1 days old virgin females.

2.2. Experimental design

To determine if *D. melanogaster* exhibits a shift in thermal preference when infected with *P. aeruginosa*, and whether this preference is efficient, we estimated three key parameters: UT_P , IT_P , IT_O . These parameters were estimated using three separate treatments including an uninfected temperature-choice treatment (estimates UT_P), an infected temperature-choice treatment (estimates IT_P), and an infected no-choice temperature treatment

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