

GUEST EDITORIAL

Looking for answers to questions about heat stress: researchers are getting warmer

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While the public continues to debate the reality of global warming, scientists should prepare to deal with the consequences of this very real phenomenon. Our planet has warmed by 0.13 °C per decade since 1956, and will likely warm more rapidly in the decades to come (Intergovernmental Panel on Climate Change 2007). This global measure of thermal change belies the more pronounced and less predictable changes that are occurring on smaller scales (Walther *et al.* 2002). For example, the greater frequency and intensity of heat waves in many areas ranks among the more threatening aspects of anthropogenic climate change. Will acclimation or adaptation enable the persistence of populations that face such thermal stresses? And, if populations do persist, will their densities and compositions change radically? To answer these questions, we must understand a suite of phenomena, ranging from the mechanistic basis of thermotolerance to the demographic and ecological consequences of thermal plasticity (Angilletta 2009). This issue of *Functional Ecology* contains four papers that improve our understanding of these phenomena. To enhance your appreciation of this collection, I briefly highlight the significance of each paper while laying out the broader issues concerning the biological impacts of heat stress.

During rapid warming, the performance of an organism depends on its capacity to protect and modify its cellular structures. Brief exposure to extreme heat often causes greater thermotolerance within hours, a phenomenon referred to as hardening (Hoffmann *et al.* 2003). This process depends on the up-regulation of heat-shock proteins, which prevent other proteins from aggregating during stress (Feder & Hofmann 1999). Despite the ubiquity of this view, we do not know whether heat-shock proteins are the primary cause of the thermotolerance acquired after heat stress. In some experiments, the expression of heat-shock proteins correlated strongly with the acquisition of thermotolerance, but in other experiments it did not (see references in Bahrndorff *et al.* 2009). In this issue, Bahrndorff *et al.* (2009) report a strong correlation between the acquisition of thermotolerance and the expression of *hsp70* in springtails (*Orchesella cincta*). Both the concentration of *hsp70* and the thermotolerance of springtails peaked more than 20 h after an initial heat shock and remained high for at least 2 days. Interestingly, the concentration of mRNA for *hsp70* peaked within 4 h of heat

shock, suggesting that a substantial lag exists between the transcription of mRNA and the production of heat-shock proteins. In a changing environment, this lag would play an important role in the evolution of constitutive vs. induced thermotolerance (Shudo *et al.* 2003).

Although the up-regulation of heat-shock proteins can rapidly confer thermotolerance, we still do not know whether this thermal plasticity enhances the fitness of genotypes in natural environments. To address this problem, researchers have recently begun to conduct field experiments with fruit flies (*Drosophila melanogaster*) whose thermotolerances were enhanced by hardening or selection (Kristensen *et al.* 2007; Loeschcke & Hoffmann 2007; Kristensen *et al.* 2008). Extending this line of investigation, Sørensen *et al.* (2009) compared the activity of mutant flies that fail to up-regulate heat-shock proteins during thermal stress with the activity of rescued mutants and control flies that can up-regulate these proteins. The researchers released these flies on warm days and recorded the number of individuals that reached nearby bait stations. Relative to control flies, neither mutants nor rescued mutants had much success in reaching a bait station. The poor performance of genetically modified lines was surprising considering that these lines performed as well as the control line in a laboratory study of activity at a high temperature (i.e. completion of a food maze at 36 °C). These results contradict those of previous experiments in which induced or selected increments in thermotolerance enhanced activity on warm days. Field experiments that quantify the performances of genetically modified lines can reveal selective pressures on thermal plasticity, as long as they include the appropriate controls (e.g. both wild type and mutant rescued lines).

Perhaps the biggest challenge in understanding the ecological impacts of climate change arises from the variation in thermotolerance among organisms. The magnitudes of geographic and phenological shifts during recent climate change have varied greatly among species (Parmesan 2006, 2007), potentially reflecting different thermotolerances. Peck *et al.* (2009) quantified variation in thermotolerance within and among 14 species of marine invertebrates from the Antarctic. By raising water temperatures by 1 °C/day, they observed several patterns. First, large individuals of each species became unresponsive before small individuals did. This intraspecific variation would make populations more sensitive to warming because the largest individuals likely contribute the most to population growth. Second, sedentary species succumbed

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earlier than active species. This interspecific variation could disrupt ecological processes during environmental warming (Visser & Both 2005). Finally, all species persisted longer in this experiment than they did in previous experiments involving slower warming. This result underscores the need to use relevant rates of environmental change when estimating thermotolerance (see also Chown *et al.* 2009).

Much debate has focused on whether species will persist by adapting genetically to our changing climate (Berteaux *et al.* 2004; Skelly *et al.* 2007; Visser 2008). Thermotolerance can evolve during climate change but what about the demographic costs? Will adaptation restore fitness before selective and stochastic processes drive populations to extinction? Current models assume that adaptation to high temperatures causes maladaptation to low temperatures, limiting the thermal breadth of performance (Angilletta *et al.* 2002). Yet, empirical data often contradict this assumption (Angilletta *et al.* 2003). This discrepancy deserves our attention because the thermal breadth of performance should limit the rate of adaptation in a warming environment (Lynch & Lande 1993; Huey & Kingsolver 1993). Through a meta-analysis of experiments, Dixon *et al.* (2009) found that species of insects that develop most rapidly at a relatively high temperature usually cannot develop at relatively low temperatures. If this interspecific phenotypic correlation reflects intraspecific genetic correlations, some physical or genetic factor must constrain the evolution of thermal breadth. Nonetheless, the breadth of development ranged from 13 to 29 °C among species, indicating substantial potential for the evolution of specialists or generalists. Furthermore, many species of plants and animals exhibit variation in the thermal breadth of performance throughout their range (reviewed by Angilletta 2009). We need to know how certain genotypes extend the thermal breadth of performance and what costs they pay to do so. That way, we might theorize whether the benefits of generalization outweigh the costs in changing environments.

These four papers remind us that we have much to discover about the responses of organisms to heat stress and the ecological and evolutionary implications of these responses. Advances in this area of research will undoubtedly help us interpret the recent impacts of climate change and predict the future impacts. Already, biologists have developed mechanistic models that focus on the role of thermotolerance in defining population dynamics or geographic ranges (Buckley 2008; Crozier & Dwyer 2006; Kearney *et al.* 2008). Ultimately, the value of these models depends on our ability to quantify thermotolerances and their potential to acclimate or adapt to environmental change.

References

- Angilletta, M.J. (2009) *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford University Press, Oxford.
- Angilletta, M.J., Niewiarowski, P.H. & Navas, C.A. (2002) The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology*, **27**, 249–268.
- Angilletta, M.J., Wilson, R.S., Navas, C.A. & James, R.S. (2003) Tradeoffs and the evolution of thermal reaction norms. *Trends in Ecology and Evolution*, **18**, 234–240.
- Bahrndorff, S., Marien, J., Loeschcke, V. & Ellers, J. (2009) Dynamics of heat-induced thermal stress resistance and Hsp70 expression in the springtail, *Orchesella cincta*. *Functional Ecology*, **23**, 233–239.
- Berteaux, D., Réale, D., McAdam, A.G. & Boutin, S. (2004) Keeping pace with fast climate change: can Arctic life count on evolution? *Integrative and Comparative Biology*, **44**, 140–151.
- Buckley, L.B. (2008) Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. *American Naturalist*, **171**, E1–E19.
- Chown, S.L., Jumbam, K.R., Sørensen, J.G. & Terblanche, J.S. (2009) Phenotypic variance, plasticity and heritability estimates of critical thermal limits depend on methodological context. *Functional Ecology*, **23**, 133–140.
- Crozier, L. & Dwyer, G. (2006) Combining population-dynamic and ecophysiological models to predict climate-induced insect range shifts. *American Naturalist*, **167**, 853–866.
- Dixon, A.F.G., Honěk, A., Keil, P., Kotela, M.A.A., Šizling, A.L. & Jarošík, V. (2009) Relationship between the minimum and maximum temperature thresholds for development in insects. *Functional Ecology*, **23**, 258–265.
- Feder, M.E. & Hofmann, G.E. (1999) Heat-shock proteins, molecular chaperones, and the stress response: evolutionary and ecological physiology. *Annual Review of Physiology*, **61**, 243–282.
- Hoffmann, A.A., Sørensen, J.G. & Loeschcke, V. (2003) Adaptation of *Drosophila* to temperature extremes: bringing together quantitative and molecular approaches. *Journal of Thermal Biology*, **28**, 175–216.
- Huey, R.B. & Kingsolver, J.G. (1993) Evolution of resistance to high temperature in ectotherms. *American Naturalist*, **142**, S21–S46.
- Intergovernmental Panel on Climate Change (2007) Climate Change 2007: Synthesis Report. Fourth Assessment Report of the Intergovernmental Panel on Climate Change.
- Kearney, M., Phillips, B.L., Tracy, C.R., Christian, K.A., Betts, G. & Porter, W.P. (2008) Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates. *Ecography*, **31**, 423–434.
- Kristensen, T.N., Loeschcke, V. & Hoffmann, A.A. (2007) Can artificially selected phenotypes influence a component of field fitness? Thermal selection and fly performance under thermal extremes. *Proceedings of the Royal Society B*, **274**, 771–778.
- Kristensen, T.N., Hoffmann, A.A., Overgaard, J., Sørensen, J.G., Hallas, R. & Loeschcke, V. (2008) Costs and benefits of cold acclimation in field-released *Drosophila*. *Proceedings of the National Academy of Sciences USA*, **105**, 216–221.
- Loeschcke, V. & Hoffmann, A.A. (2007) Consequences of heat hardening on a field fitness component in *Drosophila* depend on environmental temperature. *American Naturalist*, **169**, 175–183.
- Lynch, M. & Lande, R. (1993) Evolution and extinction in response to environmental change. *Biotic Interactions and Global Change* (eds P. Kareiva, J. Kingsolver & R. Huey), pp. 234–250. Sinauer Associates, Inc., Sunderland.
- Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, **37**, 637–669.
- Parmesan, C. (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, **13**, 1860–1872.
- Peck, L.S., Clark, M.S., Morley, S.A., Massey, A. & Rossetti, H. (2009) Animal temperature limits and ecological relevance: effects of size, activity and rates of change. *Functional Ecology*, **23**, 249–257.
- Shudo, E., Haccou, P. & Iwasa, Y. (2003) Optimal choice between feedforward and feedback control in gene expression to cope with unpredictable danger. *Journal of Theoretical Biology*, **223**, 149–160.
- Skelly, D.K., Joseph, L.N., Possingham, H.P., Freidenburg, L.K., Farrugia, T.J., Kinnison, M.T. & Hendry, A.P. (2007) Evolutionary responses to climate change. *Conservation Biology*, **21**, 1353–1355.
- Sørensen, J.G., Loeschcke, V. & Kristensen, T.N. (2009) Lessons from the use of genetically modified *Drosophila melanogaster* in ecological studies: Hsf mutant lines show highly trait-specific performance in field and laboratory thermal assays. *Functional Ecology*, **23**, 241–248.
- Visser, M.E. (2008) Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B*, 649–659.
- Visser, M.E. & Both, C. (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B*, **272**, 2561–2569.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.