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ESF ThermAdapt project report for Exchange Grant 2570

Project title: Adaptation of performance curves to a warmer world: Consequences of local adaptation, asymmetry and generalist-specialist trade-offs.

Host: Prof. Dr. Wolf Blanckenhorn, Institute of Evolutionary Biology and Environmental Studies
University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich

Purpose of visit

- 1) Joint experimental design and data collection to parameterise existing agent-based model
- 2) Extension of modelling framework to bridge enzyme kinetics and population dynamics

Background

Mounting evidence suggests that if global warming continues unabated, humans risk causing a sixth mass species extinction event (Thomas et al. 2004; IPCC 2007); for many species adaptive responses to global warming and land-use change are necessary for survival (Hannah et al. 2002; Botkin 2007). Evidence for rapid evolutionary change is widespread (Stockwell et al. 2003; Parmesan 2006; Kinnison & Hairston 2007), though it remains to be seen whether such responses are adequate to cope with both the extent and rate of climate change predicted for this century (Blows & Hoffmann 2005). Given sufficient adaptive genetic variance a population is expected to evolve a shift in its thermal optimum (Lynch & Lande 1993; Skelly et al. 2007) and/or a change in thermal specialisation (Huey & Kingsolver 1993). This is evidenced by latitudinal clines seen for many organisms, ranging from protists (Boegnigk et al. 2007) to fruitflies (Hoffmann et al. 2002) and pine trees (Rehfeldt 1999). Such clines are known to evolve quickly, as demonstrated by the invasion of the Cabbage White Butterfly *Pieris rapae* in North America (Kingsolver et al. 2007) or that of the fruitfly *Drosophila melanogaster* in eastern Australia (Hoffmann & Weeks 2007). Intra-specific adaptive clines in heat and cold resistance may be common (Hoffmann et al. 2002) and can develop over distances as short as 100-400m (Rashkovetsky et al. 2006). Despite this, adaptation may be limited by low heritability, which can arise in small populations due to the eroding effects of genetic drift (Willi & Hoffmann 2009) or which, in some cases, may reflect a genuine lack of adaptive genetic variation available for selection, as appears to be the case for desiccation resistance in populations of *D. birchii* at the edge of the range (Hoffmann et al. 2003).

Analytical models confirm the expectation that a high heritability for the thermal optimum increases the ability of organisms to track evolutionary change and avoid extinction (Lynch & Lande 1993; Bürger & Lynch 1995) while the role of thermal specialisation appears more complex. Huey and Kingsolver (1993) used the analytical model of Lynch and Lande (1993) to investigate the relationship between maximum performance and breadth of performance. They found that, in the case where genetic variance for the thermal optimum and performance breadth are assumed independent, an organism with intermediate thermal specialisation will tolerate the greatest rates of climate change. However, if maximal performance and performance breadth are subject to a trade-off, specialists will be best placed to deal with such changes while the opposite will be true if genetic variance in the thermal optimum is positively related to performance breadth. These conflicting responses depend

crucially upon the costs of being a generalist and on the demographic feedback processes determining genetic variance via mutation-selection-drift balance. In reality performance curves are typically asymmetric (Martin & Huey 2008). This can have important consequences for fitness in variable environments. The interaction between demography and asymmetry underlies the seemingly non-adaptive mismatch between thermal optima and median body temperatures (Huey & Berrigan 2001) but exactly how thermal specialisation and asymmetry affect the maintenance of genetic variance for performance curve traits, and ultimately population dynamics, remains unexplored (Kingsolver 2009).

Data collection

Experiment 1: Genetic differentiation. Drs David Berger and Richard Walters scored thermal reaction norms for various life history traits (growth rate, development time, body size and fecundity) for each of ten isofemale lines for four European populations in the dung fly *Sepsis punctum*. A 5 temperature x 2 food quantity factorial design was used. Each treatment consisting of two replicates of 20 individuals, giving trait mean thermal clines for isofemale lines based upon 200 individuals. In total, approximately 16,000 individuals will be measured. This work is to be extended to six populations to complete a latitudinal cline from North Sweden to southern Italy during the spring of 2010. The aim is to quantify genetic variation evident as genetic differentiation between populations and assess local adaptation in respect to temperature. State-dependent (temperature) genetic variance estimates will be used to parameterize enzyme-kinetic (Sharpe-Schoolfield equation) based environmental tolerance curves for an allelic simulation model. The work is complemented by molecular work (D. Berger) on neutral genetic markers (Fst estimates). Individuals are in the process of being measured therefore results are forthcoming.

Experiment 2: Laboratory evolution. Drs David Berger and Richard Walters started a selection experiment on *S. punctum* to investigate potential for future thermal adaptation to both a change in mean temperature (4 x warm lines 4 x cold lines) and variance in temperature (4 x warm/cold *within* generation lines vs. 4 x warm/cold *between* generation lines). Changes to thermal reaction norms will be scored again after five and ten generations of laboratory evolution.

Together these results will be used in conjunction with life-history and allelic simulation models to understand responses to climate change by inferring selection gradients, genetic variance for potential adaptation and possible constraints on responses to selection.

Modelling

It has been suggested that tropical species of ectotherms are at a greater risk of extinction under climate warming than their temperate equivalents (Tewksbury et al. 2008). Tropical species tend to be thermal specialists, which maintain internal body temperatures closer to their lethal thermal limits (Deutsch et al. 2008). This physiological adaptation is associated with limited warming tolerance, making tropical species more vulnerable to climate warming despite predicted exposure to lower regional increases in temperature. Recent efforts to assess genetic variance in relevant ecological traits, such as desiccation resistance and cold tolerance, reveal that tropical species might also have less potential to adapt to climate warming (Kellermann et al. 2009). Kellermann and colleagues analysed heritabilities for a number of species of *Drosophila*, from widely distributed, thermal generalist species to thermal specialists with restricted distributions. Additive genetic variance is critical to a species ability to adapt and avoid extinction (Lynch & Lande 1993). However, environmental tolerance, in this case thermal specialisation, is also predicted to be critical in determining extinction risk (Huey and Kingsolver 1993; Bürger & Lynch 1995).

To quantitatively evaluate extinction risk for tropical vs. temperate areas we applied the Stochastic House of Cards approximation (SHC) to available data on the thermal reaction norms of insect species as a means to predict additive genetic variance for a change in thermal optima as a function of effective population size (Bürger et al. 1989). For heuristic purposes, we applied the SHC approximation to the species pair chosen by Deutsch et al. (2008) to illustrate predicted responses to climate warming for a temperate generalist vs. a tropical specialist species (from figure 1: *Acyrtosiphon pisum* (Hemiptera; 52°N) and *Clavigralla shadabi* (Hemiptera; 6°N)). Gaussian distributions were fitted to the two fitness curves to estimate its breadth ($\omega \approx 7.5$ and ≈ 2.5 , respectively) and by taking recommended values for the remaining genetic parameters heritability was calculated as a function of effective population size (Bürger & Lynch 1995: loci number $n=50$; mutational effect $\alpha^2=0.05$; mutation rate $\mu=0.002$; environmental component of phenotypic variance $\sigma_e^2=1$). The SHC

approximation suggests stabilising natural selection associated with thermal specialism could alone account for differences in heritability between tropical and temperate species of the magnitude observed by Kellermann et al. (2009), even assuming small to moderate population sizes. Consequently, low heritability may reflect greater stabilising selection pressure rather than an absolute genetic constraint.

Using the quantitative genetics modelling framework of Bürger and Lynch (1995) we extended the analysis to include effects of temperature on potential fitness per se via fecundity vs. generation time ('Hotter is Better' hypothesis: Frazier et al. 2006; Knies et al. 2009; Angilletta et al. 2010) and the purported effect of temperature on mutation rates, as predicted by metabolic theory (Davies et al. 2004; Gillooly et al. 2007; Gillman et al. 2009). In doing so, we found that these additional advantages of tropical temperatures could be sufficient to overcome low heritabilities for ecological traits resulting from thermal specialisation. The full model analysis has been submitted to *Science* as a Technical Comment in response to Kellermann et al. (2009).

Other activities

- Presented a talk during the Behaviour, Ecology and Evolution Seminar (BEES) series, entitled: 'Forecasting evolutionary responses and extinction risk under environmental change'.
- Regular attendee of the BEES series.

Skills learnt

Practical details of two experimental systems: dung fly species *Sepsis punctum* and *Scathophaga stercoraria*.

Further collaboration

Richard Walters has extended his time at the University of Zurich until May 2010 in order to finish planned experiments, modelling and manuscript preparation, and to conduct further experiments on body size plasticity in respect to thermal and food conditions on the yellow dung fly *Scathophaga stercoraria*. These results will be used as a basis to parameterise an extended version of a spatially-explicit allelic simulation model of environmental tolerance curves based upon biophysics (de Jong & van der Have 2008).

Publications

Walters RJ, Berger D and Blanckenhorn W. Thermal specialisation, genetic variance and extinction risk under climate warming (submitted to *Science*).

Walters RJ and Berger D (2010) Thermal games: putting temperature back on the evolutionary agenda. *Evolution* DOI: 10.1111/j.1558-5646.2009.00878.x (book review)

Berger D and **Walters RJ** (2009) Thermal Adaptations: A Theoretical and Empirical Synthesis," by Michael J. Angilletta, Jr. *The Quarterly Review of Biology* **84**: 410. (book review)

Manuscripts in preparation

Walters RJ, Berger D and Blanckenhorn W. Genetic variance and thermal plasticity in a species of dung fly: model predictions and empirical tests.

Walters RJ, Berger D, Schäfer M and Blanckenhorn W. Body size plasticity in the Yellow dung fly: selection, adaptation and constraints.

Berger D, **Walters RJ** and Blanckenhorn W. Genetic differentiation and thermal adaptation in the dung fly *Sepsis punctum*.

Berger D, **Walters RJ** and Blanckenhorn W. Laboratory evolution of thermal reaction norms.

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