EUROPEAN SCIENCE FOUNDATION
SETTING SCIENCE AGENDAS FOR EUROPE

RESEARCH NETWORKING PROGRAMME

THERMAL ADAPTATION IN ECTOTHERMS: LINKING LIFE HISTORY, PHYSIOLOGY, BEHAVIOUR AND GENETICS (ThermAdapt)

Standing Committee for Life, Earth and Environmental Sciences (LESC)

The European Science Foundation (ESF) was established in 1974 to create a common European platform for cross-border cooperation in all aspects of scientific research.
With its emphasis on a multidisciplinary and pan-European approach, the Foundation provides the leadership necessary to open new frontiers in European science.
Its activities include providing science policy advice (Science Strategy); stimulating cooperation between researchers and organisations to explore new directions (Science Synergy); and the administration of externally funded programmes (Science Management). These take place in the following areas: Physical and engineering sciences; Medical sciences; Life, earth and environmental sciences; Humanities; Social sciences; Polar; Marine; Space; Radio astronomy frequencies; Nuclear physics.
Headquartered in Strasbourg with offices in Brussels, the ESF's membership comprises 75 national funding agencies, research-performing agencies and academies from 30 European countries.
The Foundation's independence allows the ESF to objectively represent the priorities of all these members.

Cover images:
Zigzag (top) and melanistic (bottom) form of the same snake species in Europe (adder: *Vipera berus*). Melanistic snakes are known to heat up faster, hence they might have higher performance under restricted thermal conditions. This ability can be especially beneficial in the cooler regions of their distribution, where the melanistic form occurs frequently.
Photos: Gábor Herczeg

Summary

Climate crucially affects all organisms. Particularly cold-blooded (ecto- or poikolothermic) organisms respond readily to changes in their thermal environment. In the simplest case, animals can leave unsuitable (hot or cold) habitats. They can also acclimate (a short-term physiological and behavioural response) to the conditions, for example by adjusting their metabolic rate. In the long-term, metabolism, thermal tolerance and heat or cold resistance can evolve, resulting in differences between species or geographic populations of a single species. Organisms may also be constrained in adapting to a changing environment, in which case they can die out. Adaptation at the physiological level, or lack thereof, affects the dispersal, migration, diapause and, ultimately, the distribution of species. As a result, prominent within-species temperature-size effects (larger at cooler temperatures), Bergmann (larger at higher latitudes), and converse Bergmann clines (larger at lower latitudes) occur in all major animal groups but remain largely unexplained. The genetic, physiological, life history and behavioural mechanisms by which temperature acclimation and adaptation is achieved are not well understood and therefore of central interest for ecologists and evolutionary biologists, particularly in the face of recent rapid human-made environmental and climate changes. How will species, and ultimately the human environment, cope with rapid global warming? We have launched a cross-disciplinary, cross-taxonomic European effort to promote interactions between researchers working on thermal adaptation at different levels of biological organisation to integrate various approaches, from molecular biology to systems ecology, to link micro-evolutionary processes to macro-evolutionary patterns.

The running period of the ESF ThermAdapt Research Networking Programme is for five years from October 2006 to October 2011.

Introduction

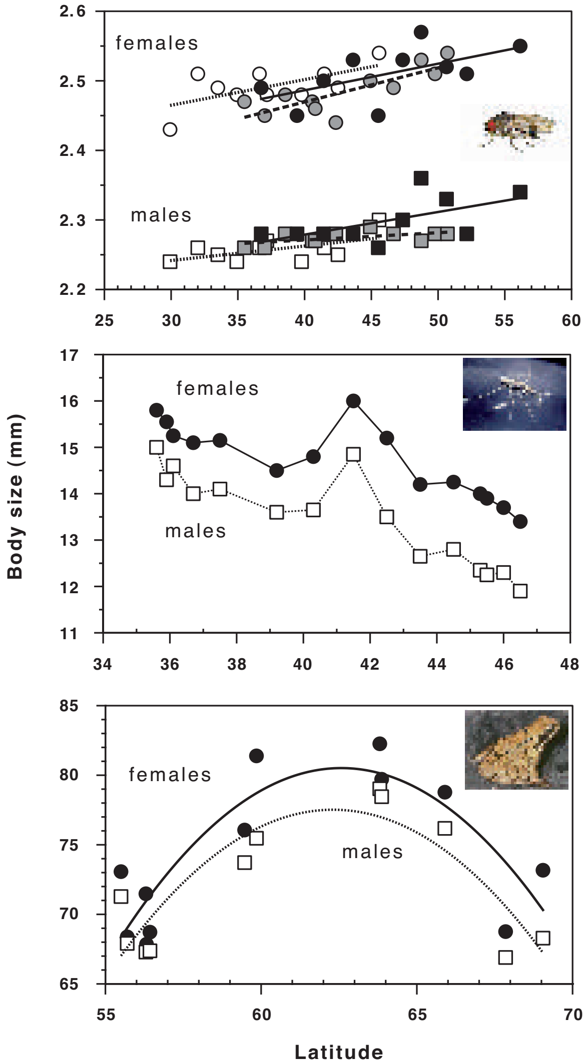
Living organisms typically encounter a wide range of temperatures, both within and across populations. Physiologists have long known that each organism has a thermal tolerance range at which it lives comfortably and functions properly, and beyond which it experiences stress. Within these limits, organisms can respond to temperature by behavioural, biochemical, physiological or morphological adjustments that often have a genetic component. However, when temperatures become too cold or too hot, fitness, as measured primarily by survival, growth and reproduction, is typically and often drastically curtailed. The thermal tolerance range differs between species, and also sometimes between populations within a species. For example, temperate insect species typically have a broader thermal tolerance range than tropical species, with low upper as well as lower temperature boundaries. Which mechanisms increase this tolerance, as well as the resistance to heat and cold, and what are the constraints?

In any case, the fact that species and populations differ in their thermal tolerances indicates that organisms regularly acclimate (a physiological response, often coupled with a behavioural response) or adapt (a genetic response) to climate changes. This affects the dispersal, migration, diapause and, ultimately, the distribution of species as well as populations of particular species. The mechanisms by which this is achieved are not well understood but of central interest to ecologists and evolutionary biologists, as are the mechanisms limiting adaptive evolution of natural populations. Certain traits of some species can be highly constrained. For example, the upper boundary at which *Drosophila melanogaster* become sterile is the same for all populations, be they temperate or tropical. Particularly in the face of the recent rapid human-made environmental and climate changes it is becoming increasingly important to investigate thermal adaptation on a concerted, global scale. How will species cope with this rapid global warming? And how will this affect ecological communities, the environment and, ultimately, humankind?

There already exists a rich literature on thermal responses in ectotherms (cold-blooded organisms) starting with the long-described clinal pattern correlating with temperature known as Bergmann's rule (i.e. organisms grow bigger towards the poles, typically reflecting genetic differences) and the presumably related temperature-size rule (i.e. organisms grow bigger at cooler temperatures, largely a plastic developmental effect). Within-species temperature-size effects and Bergmann clines have been described in all major taxa ranging from vertebrates to unicellular organisms, and phylogenetically controlled comparative studies suggest patterns common to a wide variety of taxa. The adaptive explanation for such clines in endotherms (warm-blooded birds and mammals) has long seemed clear, although there is still some controversy: larger individuals have smaller surface-to-volume ratios more conducive to conserving heat in cold climates. In contrast, for ectotherms the cause must be different, as small ectotherms such as insects can acclimate to ambient temperature almost instantly. A unifying explanation for this prevalence of systematic temperature effects on body size is still lacking. Actually, Berrigan and Charnov (1994: *Oikos* 70:474-8) noted that these phenomena are a puzzle for life historians, and there is continuing debate about whether clines and plasticity have similar causes, whether ectothermic Bergmann clines are adaptive, or whether plasticity is a mere consequence of physiological processes or constraints at the cellular and, ultimately, energetic (ATP) level. Any proposed theory seems to apply in some species but not others, so there is only spotty evidence, but no general support for either class of hypotheses, and the role of physiological constraints limiting responses remains unclear. Importantly, there is hardly any direct support for adaptive explanations that involve demonstrating greater benefits and/or lesser costs (i.e. trade-offs) of larger size or delayed

The same butterfly species (Map butterfly: *Araschnia levana*) looks different depending on the thermal and photoperiodic environment (so-called polyphenism). Photos: Holger Gröschl maturation in colder environments. This remains true despite increased experimental efforts in recent years, including quantitative genetic analyses of population differences, comparative studies, and occasional studies of experimental thermal evolution in the laboratory. Furthermore, at least in arthropods so-called converse Bergmann clines, which are mediated by season length rather than temperature, and which confound latitudinal patterns, are also common in nature.

At the whole organism level, animal migration, dispersal and distribution have also been widely studied by ecologists. It is obvious that patterns often relate to microclimate, but again, the underlying physiological mechanisms are generally not well understood. While temperature-size and dispersal patterns are well known and widespread taxonomically, a major problem with current research on thermal adaptation is that it is patchy and little integrated with regard to biological subdisciplines, species investigated, and methods used. Physiological research on thermal adaptation (understandably) concentrates on commercial fish, plant and insect species, while there is little such work on other taxa. Similarly, genetic research concentrates almost entirely on *Drosophila*, for obvious reasons. In recent years, molecular and evolutionary geneticists have identified important elements of the genetic (and physiological) basis of thermal resistance and defence mechanisms against temperature stress, such as cold and heat shock proteins, and of molecular chaperones, which are proteins involved in 'house-keeping' functions of the cell. Stress-induced heat shock proteins have important effects on life-history traits such as development time, life span and fecundity. However, detailed information on the genes underlying species differences in temperature boundaries and stress resistance, or genes mediated intra-specific differences in thermal adaptation, is still lacking. For example, it would be beneficial and might be feasible to apply genetic know-how from *Drosophila* research to other species that are ecologically well characterised in their natural habitat, such as, for instance, the well-researched yellow dung fly. Current technological advances make it possible to investigate on a large scale the candidate genes by looking at expression patterns. Furthermore, the current capacities of sequencing will lead to a fast accumulation of genomes from phylogenetically closer species than the ones so far sequenced, which will allow fine-scale comparative analyses. Probably a major problem will be the establishment of causal associations between expression profiles and adaptive variation at the population and species levels, and for this reason exhaustive information from carefully controlled laboratory experiments will be essential.



Bergmann (larger at higher latitudes; top), converse Bergmann (larger at lower latitudes; centre), and a composite, hump-shaped latitudinal cline in body size in three species of ectothermic (cold-blooded) organisms: wing length of the fruit fly *Drosophila subobscura* in Europe (black), North America (grey) and South America (white); total body length of the North American water strider *Aquarius remigis*; and snout-vent length for the grass frog *Rana temporaria* in Scandinavia (respectively).
References (respectively): Huey et al. 2000 (*Science*); Brennan and Fairbairn 1995 (*Biol. J. Linn. Soc.*); Laugen et al. 2005 (*Evol. Ecol. Res.*).

Scope

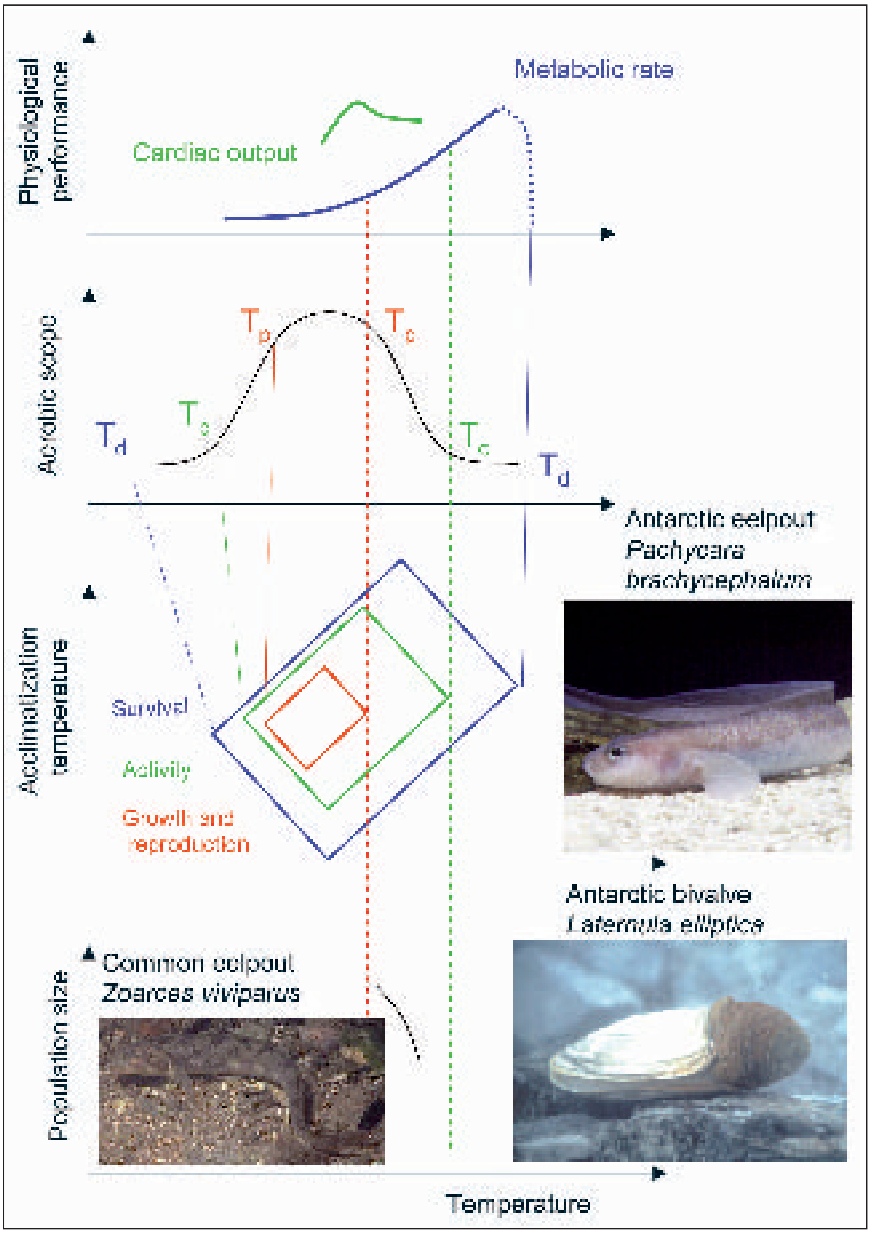
The scope of this programme is to launch a cross-disciplinary, cross-taxonomic European network of scientists currently working on thermal adaptation and resistance in ectothermic organisms. This includes cooperation with extra-European researchers and institutions to maintain a global perspective. To integrate the various approaches, we like to promote interactions between life historians, physiologists, geneticists, behavioural and comparative biologists, which typically work at different levels of biological organisation. Crucially, we want to involve scientists working in molecular and cell biology to promote the use of new genetic and genomic techniques, such as gene profiling to study genomic responses associated with thermal adaptation and exposure to temperature extremes, or protein-level responses to identify post-transcriptional mechanisms. Broad use of these costly and know-how-intensive methods is best and most efficiently facilitated through a concerted effort on a European scale, involving training, exchange of personnel, specimens and selection lines, and sharing of facilities.

Key aims of the programme

- Conduct concerted comparative studies (among and within species)
- Relate dispersal behaviour and organism distribution to physiology and temperature variation within species
- Develop and test theory (e.g. biophysical model parameters)
- Link: genes → proteins → physiological activity → performance → fitness
- Transfer genetic expertise (West → East; bottom → top)
  Transfer organismic expertise (East → West; top → bottom)
- Transfer Drosophila expertise to other species (insects)
- Test for particular candidate genes (e.g. HSP) in other species.

Outdoor (top; England) and indoor (bottom; Belgium) artificial tank systems for experiments with multiple heated aquatic ecosystems provide a powerful way to investigate short-term evolutionary responses to environmental warming under realistic field conditions. This collaborative research between Belgian and UK researchers includes investigations of the evolutionary responses to warming of water fleas (*Daphnia* spp.; insert), which are central to maintaining the quality of shallow freshwaters (Photos: H. Feuchtmayr & Wendy Van Doorslaer).

Programme Activities



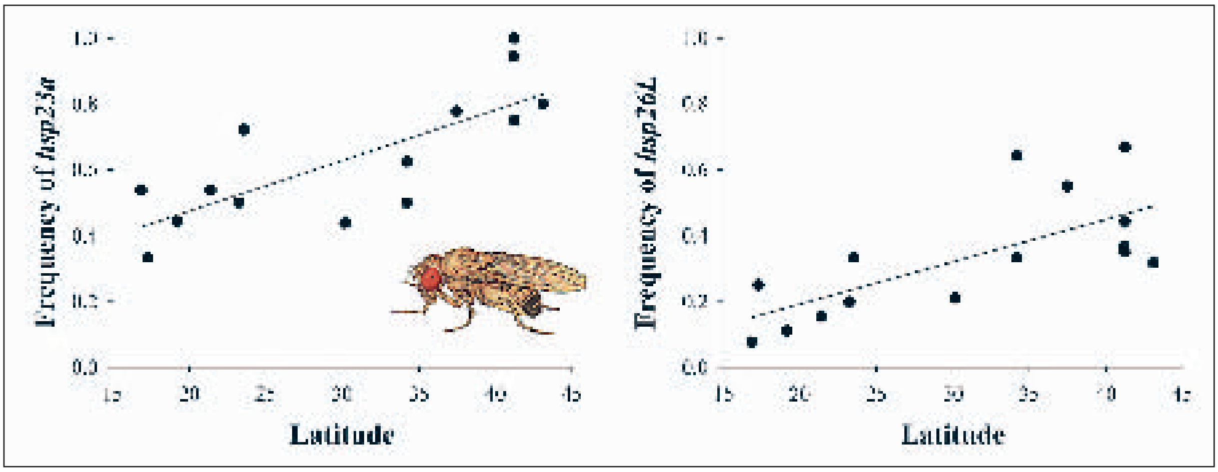
Elements of the concept of oxygen and capacity-limited thermal tolerance in aquatic metazoa and their ecological relevance (modified after Pörtner and Knust, 2007, Wang and Overgaard, 2007). The model builds on comparative physiological data obtained in eelpout from the Antarctic and the North Sea as well as in polar and temperate invertebrates. Beyond the upper 'pejus' temperature (Tp) of the fish, the cardiorespiratory system can no longer ensure sufficient aerobic scope to sustain reproduction and growth; eventually, activity (Tc) and molecular structures (Td) as well as survival are also compromised. These thermal limits are plastic and amenable to the thermal history (acclimatisation) of the animals (top three panels). Pörtner and Kunst (2007) show that summer temperatures above the pejus limit cause the population of the European eelpout to decline, indicating that global warming may take effect well before the lethal thermal limits (Td) are reached (bottom panel).
References: Pörtner, H.O. and Knust R. 2007 *(Science)*; Wang T. and Overgaard J. 2007 *(Science)*.

The programme's activities serve to combine and integrate research from different perspectives in the field of thermal adaptation and to actively promote exchange of knowledge and data. These include: an electronic *communication network and a web site* for exchanging information and pre-prints; regular organisation of *multidisciplinary workshops and conferences* on thermal adaptation and selected sub-topics, *training courses* for young scientists in the field and *exchange and travel grants* for scientific exchange.

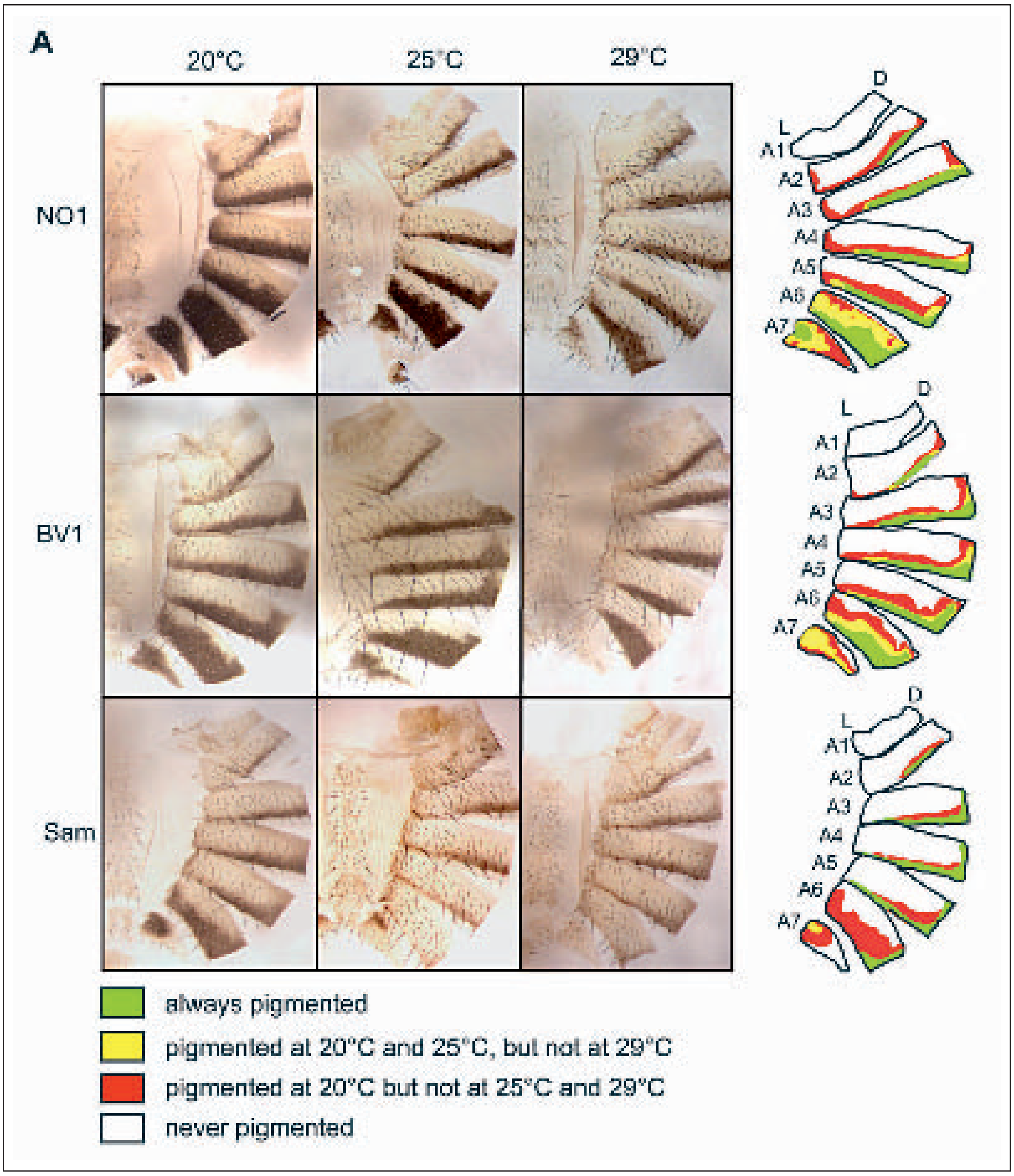
Funding

ESF Research Networking Programmes are principally funded by the Foundation's Member Organisations on an *à la carte* basis. ThermAdapt is supported by:

- **Fonds zur Förderung der Wissenschaftlichen Forschung (FWF)**
  Austrian Science Fund, Austria
- **Fonds National de la Recherche Scientifique (FNRS)**
  National Fund for Scientific Research, Belgium
- **Fonds voor Wetenschappelijk Onderzoek-Vlaanderen (FWO)**
  Research Foundation Flanders, Belgium
- **Akademie věd České republiky (ASČR)**
  Academy of Sciences of the Czech Republic, Czech Republic
- **Grantová agentura České republiky (GAČR)**
  Czech Science Foundation, Czech Republic
- **Forskningsrådet for Natur og Univers (FNU)**
  Natural Science Research Council, Denmark
- **Eesti Teadusfond (ETF)**
  Estonian Science Foundation, Estonia
- **Suomen Akatemia/Finlands Akademi**
  Academy of Finland, Finland
- **Deutsche Forschungsgemeinschaft (DFG)**
  German Research Foundation, Germany
- **Magyar Tudományos Akadémia (MTA)**
  Hungarian Academy of Sciences, Hungary
- **Országos Tudományos Kutatási Alapprogramok (OTKA)**
  Hungarian Scientific Research Fund, Hungary
- **Nederlandse Organisatie voor Wetenschappelijk Onderzoek (NWO) – Aard- en Levenswetenschappen (ALW)**
  Netherlands Organisation for Scientific Research – Earth and Life Sciences Council (NWO/ALW), Netherlands
- **Fundação para a Ciência e a Tecnologia (FCT)**
  Foundation for Science and Technology, Portugal
- **Slovenska Akademija Znanosti in Umetnosti (SAZU)**
  Slovenian Academy of Sciences and Arts, Slovenia
- **Ministerio de Educación y Ciencia (MEC)**
  Ministry of Education and Science, Spain
- **Consejo Superior de Investigaciones Científicas (CSIC)**
  Council for Scientific Research, Spain
- **Schweizerischer Nationalfonds (SNF)**
  Swiss National Science Foundation, Switzerland



Clinal variation in candidate genes in natural populations: Variation in allele frequencies in the heat shock proteins *Hsp23* and *Hsp26* in *Drosophila melanogaster* along a north-south gradient in East-Australia.
Reference: Frydenberg et al. 2003 *(Molecular Biology).*



Abdominal pigmentation plasticity in *Drosophila melanogaster* females from three different populations (NO1, BV1, Sam) grown at 20°C, 25°C, and 29°C. The drawings on the right summarise the plasticity of the different regions of the body according to the colour code. A1–A7, abdominal segment number; L, lateral region; D, dorsal region.
Reference: Gibert et al. 2007 (*Plos Genetics 3)*.

ThermAdapt Steering Committee

Wolf Blanckenhorn (Chair)
Zoologisches Museum
Universität Zürich-Irchel
Winterthurerstrasse 190
8057 Zürich
Switzerland
Tel: +41 44 635 4755
Fax: +41 44 635 4780
Email: wolf.blanckenhorn@zm.uzh.ch

Mauro Santos (Co-Chair)
Dept de Genètica y Microbiologia
Facultat de Ciències
Universidad Autonoma de Barcelona
Edifici Cn
Bellaterra 08193 Barcelona
Spain
Tel: +34 93 581 27 25
Fax: +34 93 581 23 87
Email: mauro.santos@uab.es

Anton Brancelj
National Institute of Biology
Vecna pot 111
1000 Ljubljana
Slovenia
Email: brancelj@nib.si
Tel: +386 61 123 33 88
Fax: +386 61 123 50 38

Gerdien De Jong
Department of Plant Ecology and Evolutionary
Population Biology
Utrecht University
Padualaan 8
Utrecht 3584 CH
Netherlands
Tel: +31 30 253 2246
Fax: +31 30 253 2837
Email: G.deJong@bio.uu.nl

Luc De Meester
Laboratory of Aquatic Ecology
Department of Biology
Faculty of Science
Katholieke Universiteit Leuven
Ch. De Bériotstraat 32
3000 Leuven
Belgium
Tel: +32 16 32 37 08
Fax: +32 16 32 45 75
Email: luc.demeester@bio.kuleuven.be

Klaus Fischer
Zoological Institute & Museum
Greifswald University
J.-S.-Bach-Str. 11/12
17489 Greifswald
Germany
Tel: +49 3834 864256
Fax: +49 3834 864252
Email: klaus.fischer@uni-greifswald.de

Gabor Herczeg
Departement of Systematic Zoology and Ecology
Eötvös Lorand University
1117 Budapest
Hungary
Email: gherc@freemail.hu

Alois Honek
Research institute of Crop Production
Drnovska 507
16106 6 Praha
Czech Republic
Tel: +420 233022269
Fax: +420 233310636
Email: honek@vurv.cz

Volker Loeschcke
Department of Biological Sciences
Section of Ecology and Genetics
University of Aarhus
Ny Munkegade – Bygning 1540
8000 Aarhus
Denmark
Tel: +45 89 42 32 68
Fax: +45 89 42 27 22
Email: volker.loeschcke@biology.au.dk

Margarida Matos
Centro de Biologia Ambiental
Dept Biologia Animal
Faculdade de Ciencias
Universidade de Lisboa
Bloco C2, Campo Grande
1749-016 Lisboa
Portugal
Tel: +351 21 750 00 00
Fax: +351 21 750 00 28
Email: mmmatos@fc.ul.pt

Juha Merilä
Department of Biological
and Environmental Sciences
University of Helsinki
PO Box 65
00014 Helsinki
Finland
Tel: +358 40 837 4165
Fax: +358 9 1915 7694
Email: juha.merila@helsinki.fi

Christian Schlötterer
Institut für Tierzucht und Genetik
Veterinärmedizinische Universität Wien
Josef Baumann Gasse 1
1210 Wien
Austria
Tel: +43 1 250775603
Fax: +43 1 250775693
Email: christian.schloetterer@vu-wien.ac.at

Toomas Tammaru
Institute of Ecology and Earth Sciences
University of Tartu
Vanemuise 46
51014 Tartu
Estonia
Tel: +372 5252420
Fax: + 372 7 383 013
Email: toomas.tammaru@ut.ee

Hans Van Dyck
Biodiversity Research Centre
Behavioural Ecology & Conservation Group
Catholic University of Louvain (UCL)
Croix du Sud 4
1348 Louvain-la-Neuve
Belgium
Tel: +32 10 479039
Fax: +32 10 473490
Email: vandyck@ecol.ucl.ac.be

ESF Liaison

Arja Kallio
Science

Ellen Degott-Rekowski
Administration

Life, Earth and Environmental Sciences Unit (LESC)
European Science Foundation
1 quai Lezay-Marnésia
BP 90015
67080 Strasbourg cedex
France
Tel: +33 (0)3 88 76 71 06
Fax: +33 (0)3 88 37 05 32
Email: thermadapt@esf.org

For the latest information on this Research Networking Programme consult the ThermAdapt website:
www.esf.org/thermadapt

EUROPEAN SCIENCE FOUNDATION
SETTING SCIENCE AGENDAS FOR EUROPE

1 quai Lezay-Marnésia | BP 90015
67080 Strasbourg cedex | France
Tel: +33 (0)3 88 76 71 00 | Fax: +33 (0)3 88 37 05 32
www.esf.org

Print run: 1500 by IREG Strasbourg – September 2007 -