



**ESF Scientific Programme**  
"Thermal adaptation in ectotherms:  
Linking life history, physiology and behaviour"

<http://www.esf.org/thermadapt>

**Report on:**

ESF Science Meeting

Barcelona 15<sup>th</sup> – 17<sup>th</sup> March 2007

*Institut d'Estudis Catalans (Sala Prat de la Riba)*  
*Carrer del Carme 47. Barcelona*

2<sup>nd</sup> Steering Committee Meeting

Barcelona 18<sup>th</sup> March 2007

*Amphitheatre of the "Residència d'Investigadors"*

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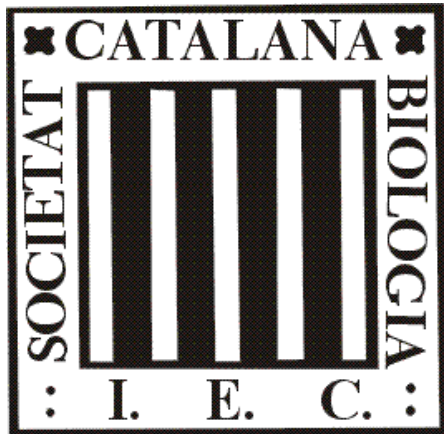


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"Thermal adaptation in ectotherms:  
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ESF Science Meeting  
Barcelona 15<sup>th</sup> – 17<sup>th</sup> March 2007  
*Institut d'Estudis Catalans (Sala Prat de la Riba)*  
*Carrer del Carme 47. Barcelona*

**Organizer:** Mauro Santos, *Vice Chair* of the Programme



**Sponsor:**

*Societat Catalana de Biologia*

## Steering Committee

Wolf Blanckenhorn – *Chair*, Zürich [wolfman@zoolmus.unizh.ch](mailto:wolfman@zoolmus.unizh.ch)  
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Hans van Dyck – Louvain-la-Neuve [vandyck@ecol.ucl.ac.be](mailto:vandyck@ecol.ucl.ac.be)

## Invited Speakers

Linda Partridge – London [l.partridge@ucl.ac.uk](mailto:l.partridge@ucl.ac.uk)  
Raymond B. Huey – Seattle, WA [hueyrb@u.washington.edu](mailto:hueyrb@u.washington.edu)  
Ary A. Hoffmann – Melbourne [ary@unimelb.edu.au](mailto:ary@unimelb.edu.au)  
Luis Serra – Barcelona [lserra@ub.edu](mailto:lserra@ub.edu)  
Steven L. Chown – Matieland [slchown@sun.ac.za](mailto:slchown@sun.ac.za)  
Goggy Davidowitz – Tucson, AZ [goggy@email.arizona.edu](mailto:goggy@email.arizona.edu)  
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Joel G. Kingsolver – Chapel Hill, North Carolina [jgking@bio.unc.edu](mailto:jgking@bio.unc.edu)  
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Kuke Bijlsma – Haren [r.bijlsma@rug.nl](mailto:r.bijlsma@rug.nl)  
Michael Kearney – Victoria [mrke@unimelb.edu.au](mailto:mrke@unimelb.edu.au)  
José M. Cano – Helsinki [jose.canoarias@helsinki.fi](mailto:jose.canoarias@helsinki.fi)  
Robby Stoks – Leuven [Robby.stoks@bio.kuleuven.be](mailto:Robby.stoks@bio.kuleuven.be)

## Scope

Climatic change is altering the geographic ranges, abundances, phenologies and biotic interactions of organisms, and may also alter the genetic composition of species. The proposed Science Meeting will be the first to be organized within the above ESF Scientific Programme and will address a number of 'hot' questions on thermal adaptation:

- 1 Is thermal adaptation comparable / similar / identical over all ectotherms?
  - 1.1 What aspects have to be identical?
  - 1.2 Where are the differences? Can any differences be classified?
- 2 Thermal adaptation
  - 2.1 Direct effects – c.f. biophysical, biochemical, physiological
    - 2.1.1 Biophysical (Sharpe-Schoolfield model)
    - 2.1.2 Biochemical (metabolic control)
    - 2.1.3 Integration of effects
    - 2.1.4 Any predictions from biophysics / biochemistry to morphology?
  - 2.2 Indirect effects – environmental change
    - 2.2.1 Adaptation to prevailing environment
    - 2.2.2 Counter-effect selection
  - 2.3 How do direct and indirect effects interact?
- 3 Plasticity *vs.* genetics; i.e., acclimation *vs.* adaptation
  - 3.1 Identical mechanisms?
- 4 Clinal patterns
  - 4.1 Morphological clines: morphology not selected but correlated response to selection targeted on lower level?
  - 4.2 Counter-gradient morphology: result of selection targeted on morphology accompanied by correlated response at lower level?
- 5 Latitudinal shifts in genetic biomarkers: local adaptation or progressive invasion?

These questions are challenging and ambitious, and the list of proposed participants includes some of the European leaders in the field. A number of experts outside Europe will be also incorporated. The exchange of ideas and know-how is guaranteed, and the proposed Meeting could have an important and lasting impact in the field of thermal adaptation.

## Venue

The sessions will take place at the *Institut d'estudis Catalans* (IEC, *Carrer del Carme 47, Sala Prat de la Riba* <http://www.iecat.net/serveis/Sales/SalesA.htm#SPratR>), located in a remarkable building at the historic centre of the city.



To get to the city centre from the International Airport of Barcelona you can take a bus, train or taxi (around €25).

- Bus: the bus stop is located at the exit of each Terminal (you will probably leave the airport by Terminal A or B). Take the blue bus (frequency 15') with the yellow logo *Aerobus* and go to the final stop (*Plaça Catalunya* – Catalunya square). The *Residència d'Investigadors* (lodging) is about 10-15' walking distance from the final bus station. Go to *La Rambla* (a famous street with many flower shops) in direction to the harbour. *Carrer del Carme* (Carme street) and *Carrer Hospital* (Hospital street, lodging) are perpendicular to *La Rambla* at the right side looking towards the harbour (see map below).
- Train: the train station is well indicated (frequency 30'). As before, go to *Plaça Catalunya*.

Participants arriving at Girona airport (around 90 Km North from Barcelona) need to take the bus to Barcelona. The final stop is not at walking distance and they have to take the metro and arrive to *Liceu* station (located in *La Rambla*, see map).

Public city transportation (not the *Aerobus*) works with unitary tickets (metro+bus+tram) allowing change of line during 1½ hours but only in one direction: validation must be done if you change from metro to bus or vice versa. T10 cards (valid for 10 travels) can be bought at the stations with

cash (EURO) or any commonplace credit card. If you plan to travel around the city, “T10-1zone” (€6.90) is your choice.



## Lodging

*Residència d'Investigadors* (Residence for Researches <http://www.residencia-investigadors.es/english/english.html>), *Carrer Hospital 64*.  
Two minutes walking distance from the meeting venue (see map).

# RESIDÈNCIA D'INVESTIGADORS

Carrer Hospital, 64  
08001 – Barcelona  
Tel.: +34 93 443 86 10  
Fax: +34 93 442 82 02  
e-mail: [investigadors@resa.es](mailto:investigadors@resa.es)

## General information:

- Reception opens from 7:30 to 22:00 Monday to Friday and from 8:00 to 20:00 on weekends. You should pay within this time.
- The night watchman is from 22:00 to 7:30 Monday to Friday and from 20:00 to 8:00 on weekends.
- Breakfasts are served from 7:30 to 9:30 Monday to Friday and from 8:30 to 10:30 on the weekends and public holidays. The dining room is located in 'entresol' floor (letter E in the lift).
- Rooms are cleaned daily as long as they are left before 12:00 noon. From that hour on cleaning cannot be guaranteed.
- The TV hall is located besides the dining room. There is also a HiFi equipment and newspapers.
- We have wireless internet in all the Residence. For more information please ask at the Reception desk.
- From your room you can call Reception by dialing 9. For outside calls you have to dial number 0. For international calls you should dial 00 (international) + country code + phone number.
- On departure rooms should be left before 12 noon. We request that you bring your luggage to the reception before this time.
- If you decide to extend your stay, please inform us as soon as possible.
- **We do not accept American Express.**

We wish you a pleasant stay with us.

Marta Baldé Auladell  
Manager



## Lunch

Lunches on Friday 16<sup>th</sup> and Saturday 17<sup>th</sup> of March will be organized in a restaurant very close to the venue. As for other days, there are many places to eat around the *Institut d'Estudis Catalans* at a reasonable good price. Suggestions will be made on arrival to the venue. If you do not want to have lunch at a restaurant there are also many choices. Quite close to the venue there is a famous market called *La Boqueria* where you can buy almost anything you can imagine.

On Saturday 17<sup>th</sup> there will be a Conference Dinner at 21:00.

## Safety in Barcelona

Generally speaking, Barcelona is a safe city and the chances of being the victim of crime are low or almost nil. But please be aware of pickpockets! Don't advertise cameras, mp3 players, laptops or fancy mobile phones. In addition, leave the original documents (passport, etc.) in your room and carry a photocopy: this can always solve an unwanted nightmare!

## Reimbursement Rules

Concerning the reimbursement procedure in the case of a science meeting organized within the framework of an ESF programme, it should be based on ESF's financial rules for reimbursement.

- Steering Committee members: The *ESF Travel Claim Form* should be sent to ESF within one month following the meeting.
- Invited Speakers: If you are planning to travel by plane we would like you to obtain, if possible, an APEX ticket. A standard meal allowance of €1 can be paid for any lunch or dinner not provided by an airline or during the meeting. Accommodation will be paid for directly by the programme and covers the cost of a single room and breakfast; all extras such as mini-bar, telephone, supplement for double room etc. should be paid for by you on departure. Travel expenses will be reimbursed after the meeting upon reception of original receipts and invoices. The *Travel Claim Form* you have to fill is at the end of this document and has to be sent to:

Mauro Santos  
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Facultat de Biociències, Edifici C  
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Spain

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## Power Point Presentations

There should be no problems for PC or Mac users. But it is always a good idea to bring a PDF copy of your Power Point presentation.



## Thermal adaptation in ectotherms

Barcelona 15<sup>th</sup> – 17<sup>th</sup> March 2007

*Institut d'Estudis Catalans (Sala Prat de la Riba)*

*Carrer del Carme 47, Barcelona*

### Programme

#### Thursday, 15<sup>th</sup> of March

Registration will be open from 11:00 – 15:00 at the *Institut d'Estudis Catalans*.

15:15 – 15:30 Opening of the conference by **Wolf Blanckenhorn**, Chair of the Programme

#### **Session 1: “Integrative Physiology of Thermal Adaptation”** chaired by **Wolf Blanckenhorn**

15:30 – 16:15 **Joel G. Kingsolver**, Chapel Hill, North Carolina, (US):  
*Evolutionary responses of insects to rapid climate change: development time, size and thermal sensitivity*

16:15 – 17:00 **Hans O. Pörtner**, Bremerhaven, (DE):  
*Physiological mechanisms linking climate to ecosystem change*

17:00 – 17:30 Coffee break

17:30 – 18:15 **Goggy Davidowitz**, Tucson, Arizona, (US):  
*Deconstructing the physiology of thermal reaction norms*

18:15 – 19:00 **David Atkinson**, Liverpool, (UK):  
*Integrated thermal adaptation across levels of body organization*

19:00 – 19:45 **Steven L. Chown**, Matieland, (ZA):  
*Evolutionary physiology of thermal responses: challenges in linking molecular mechanisms to population dynamics*

## Friday, 16<sup>th</sup> of March

### **Session 2: “Evolutionary Adaptation to Temperature: Global Patterns”** chaired by **Juha Merilä**

- 09:00 – 09:45 **Raymond B. Huey**, Washington, (US):  
*Latitudinal impacts of climate warming on terrestrial ectotherms*
- 09:45 – 10:15 **Hans Van Dyck**, Louvain-la-Neuve, (BE):  
*Flying heliotherms in changing landscapes: behaviour, life-history and thermal environment in speckled wood butterflies*
- 10:15 – 11:00 **Warren P. Porter**, Madison, (US):  
*Mechanistically modeling the impact of past and future air temperature changes on ectotherms across a continent: the effect of body size, activity thresholds and diurnal vs. nocturnal activity patterns*
- 11:00 – 11:30 Coffee break
- 11:30 – 12:15 **Michael Kearney**, Victoria, (AU):  
*A trait-based approach to predicting species distributions: integrating mechanistic thermal niche modelling with GIS data*
- 12:15 – 12:45 **Robby Stoks**, Leuven, (BE):  
*Genetic adaptation to temperature increase: first results on a mesocosm experiment*
- 13:00 – 15:00 Lunch

### **Session 3: “Theoretical Aspects of Thermal Adaptation”** chaired by **Christian Schlötterer**

- 15:00 – 15:45 **Jan Kozłowski**, Kraków, (PL):  
*Cell size, temperature, and body size optimization in ectotherms*
- 15:45 – 16:15 **Gerdien de Jong**, Utrecht, (NL):  
*Temperature dependence of body size: from biophysics to adaptation*

### **Session 4: “Evolutionary Adaptation to Temperature: Growth and Development”** chaired by **Gerdien de Jong**

- 16:15 – 17:00 **Paul M. Brakefield**, Leiden, (NL):  
*Evolution of plasticity in *Bicyclus* butterflies and seasonal temperatures*
- 17:00 – 17:30 Coffee break
- 17:30 – 18:15 **Christian P. Klingenberg**, Manchester, (UK):  
*Using shape analysis to gauge the effects of temperature and thermal adaptation*

18:15 – 19:00 **Sandro Cavicchi**, Bologna, (IT):  
*The evolution of body size and shape: the evolutionary and developmental genetics approach*

19:00 – 19:45 **Jean R. David**, Gif-sur-Yvette Cedex, (FR):  
*Phenotypic thermal plasticity: various adaptive aspects in *Drosophila**

## **Saturday, 17<sup>th</sup> of March**

### **Session 5: “Evolutionary Adaptation to Temperature: Latitudinal/Altitudinal Gradients”** chaired by **Luc De Meester**

09:00 – 09:30 **Juha Merilä**, Helsinki, (FI):  
*Thermal adaptation along a latitudinal gradient*

09:30 – 10:00 **Klaus Fischer**, Bayreuth, (DE):  
*Genetic and environmental effects on thermal adaptation in butterflies*

10:00 – 10:30 **Wolf Blanckenhorn**, Zurich, (CH):  
*Bergmann and converse Bergmann clines: thermal adaptation?*

10:30 – 11:00 **Toomas Tammaru**, Tartu, (EE):  
*Growth allometry of lepidopteran larvae: a life-history perspective*

11:00 – 11:30 Coffee break

### **Session 6: “Evolutionary Adaptation to Temperature: Genetic Markers”** chaired by **Volker Loeschcke**

11:30 – 12:15 **Linda Partridge**, London, (UK):  
*Latitudinal variation in body size of the fruit fly *Drosophila**

12:15 – 13:00 **Ary A. Hoffmann**, Parkville, (AU):  
*Linking field fitness with genetic polymorphisms under thermal selection in *Drosophila**

13:00 – 15:00 Lunch

15:00 – 15:45 **Luis Serra**, Barcelona, (ES):  
*Chromosomal variability and thermal adaptation in *Drosophila subobscura**

15:45 – 16:15 **Mauro Santos**, Barcelona, (ES):  
*Net fitness evolution in a warming world: the case of *Drosophila subobscura**

**Session 7: “Evolutionary Adaptation to Temperature: Genetics and Behaviour”** chaired by **Mauro Santos**

16:15 – 17:00 **Kuke Bijlsma**, Haren, (NL):

*The interplay between genetic and thermal stress*

17:00 – 17:30 Coffee break

17:30 – 18:00 **Volker Loeschke**, Aarhus, (DK):

*Thermal adaptation and environmental stress: from selection experiments to gene expression studies and field releases*

18:00 – 18:30 **Gábor Herczeg**, Budapest, (HU):

*Behavioural regulation of body temperature: current views and future perspectives*

18:30 – 19:00 **José M. Cano**, Helsinki, (FI):

*Apparent trade-off between standard metabolic rate and locomotor performance in resident populations of brown trout (*Salmo trutta*) across a thermal gradient*

19:00 – 20:00 *Debate for General Conclusions and New Avenues for Thermal Research*, chaired by **Wolf Blanckenhorn**

21:00 Conference dinner

**Sunday, 18<sup>th</sup> of March**

*Amphitheatre of the "Residència d'Investigadors"*

09:30 – 13:30 Steering Committee Meeting (only for SC members)

**Summary ESF *ThermAdapt* Barcelona Expert Meeting 15 – 17 March 2007**  
***Thermal adaptation in ectotherms: Linking life history, physiology, behaviour***  
***and genetics***

After the initial Steering Committee meeting in Zurich in October 2006, our 5-year ESF ThermAdapt Programme was essentially launched by the expert meeting that took place from 15 – 17 March 2007 in Barcelona, in the beautiful downtown building of the *Institut d'Estudis Catalans*. Vice-chair Mauro Santos aptly organized the meeting together with a consortium of helpers of his local universities.

The main purpose of the expert meeting was to gather *the* topmost European and overseas experts in the field of thermal adaptation, in addition to the Steering Committee members of the *ThermAdapt* programme, to review the current status of the field and possibly come up with a list of topics and questions on which the programme might want to focus in the years to come. The list of invited speakers at the meeting is illustrious (see page 4). The dense program covered all topics of our initial scope list (see pages 10-13), and was subdivided into 7 sessions on physiology, global patterns, theory, growth & development, latitudinal gradients, genetic markers, and behaviour. In total 65 delegates, including guests, attended the meeting (see pages 48-49).

Lunches were taken in a nearby local restaurant, and in the evening the delegates could sample local food, drink and culture of their choice. All delegates stayed overnight in the nearby *Residencia d'Investigadors*. The expert meeting was concluded with an opulent meal at the Hotel 1898 on Saturday evening.

All speakers submitted an abstract of their talk including their central points and suggestions of future avenues or questions to focus on. These are given below. A non-comprehensive list of additional research questions to focus on were gathered by e-mail after the meeting and is also given below.

At the end of the meeting, it was decided that a comprehensive review of the ideas presented and focus on only some of the many interesting areas, questions and (sub)topics for further study is premature at this point. Rather, the programme should be open to all topics for the moment to better integrate the field, and a narrowing-down of topics should, if at all, happen only during the later stages of the programme.



Thermal adaptation in ectotherms

**ESF – Science Meeting and Steering Committee Meeting**

Barcelona 15<sup>th</sup> – 18<sup>th</sup> March 2007  
*Institut d'Estudis Catalans (Sala Prat de la Riba)*  
*Carrer del Carme 47. Barcelona*

**Abstracts**

## **Integrated thermal adaptation across levels of body organization**

David Atkinson

*Population & Evolutionary Biology Division, School of Biological Sciences, The University of Liverpool, Biosciences Building, Crown Street, Liverpool L69 7BZ, U.K..*

[davida@liv.ac.uk](mailto:davida@liv.ac.uk)

Understanding the functional basis of plasticity or acclimation to temperature can help predict the evolutionary impacts of a change in thermal regime. But the effects of temperature on phenotypes are complex, differing between stages of ontogeny, organisms, and environments. A coherent understanding of this plasticity would need to account for the array of physiological and morphological responses at different levels of body organization. For example, in some studies the observation of similar size responses of cells and of whole bodies to developmental temperature requires an explanation that accounts for the effect at both these levels of organization.

I propose that a unifying framework can be built on Pörtner's hypothesis of oxygen- and capacity-limited thermal tolerance in animals [1,2]. When temperature is altered, I assume that maximizing aerobic scope, and hence the energy available to maximize fitness, involves phenotypic adjustments to counter the challenges posed by the changed temperature. Diverse evidence is supportive: temperature induces behavioural, morphological and physiological plasticity at different levels of body organization that is consistent with maintaining aerobic scope by regulating oxygen supply and consumption. However, rigorous quantitative tests are still required, and I propose a methodology to achieve this. Questions that still need answers include: in what situations (air- vs water-breathers? feeding mode? rapidity and predictability of environmental change? thermal biology of predator? body plan?) and which processes (ingestion? predation risk?) induce different functionally coherent clusters of plastic responses, and can these clusters be used to identify the mechanisms by which temperature affects particular populations or species?

- [1] Pörtner, H. O. 2002. Climate change and temperature dependent biogeography: systemic to molecular hierarchies of thermal tolerance in animals. *Comparative Biochemistry & Physiology* 132A: 739-761.
- [2] Atkinson, D., Morley, S. A. & Hughes, R. N. 2006. From cells to colonies: at what levels of body organization does the 'temperature-size rule' apply? *Evolution & Development* 8: 202-214.



## The interplay between genetic and thermal stress

Kuke Bijlsma

*Population & Conservation Genetics, Evolutionary Genetics,  
University of Groningen, P.O. Box 14, NL-9750 AA Haren, The Netherlands.*

[r.bijlsma@rug.nl](mailto:r.bijlsma@rug.nl)

From an evolutionary perspective, stress is generally defined as an environmental factor that impairs Darwinian fitness. This at first sight simple definition, however, conceals a complex matter as stress is not only an attribute of the external and internal environment, but also an attribute of the organism experiencing that environment. Consequently, an environment, and changes therein, can be perceived differently by different genotypes, while, on the other hand, changes in the genetic architecture of organisms can alter the perception of a constant environment. This results in a complex interaction between genotype and environment, often causing synergistic effects, and both should, therefore, be studied integrative. In a man-dominated world, many species have to cope with stressful deteriorating environmental conditions, e.g. thermal stress for ectotherms. At the same time species are subject to genetic stress due to small population sizes, resulting in fitness depression and changes in the genetic architecture.

By using *Drosophila* as a model organism, we are studying the complex interactions between genotype and thermal environment. On the one hand, we investigate changes in thermal tolerance brought about by changes in the genetic architecture of *Drosophila* by inbreeding. On the other hand, we investigate the fitness response of certain inbred lines in different thermal environments. By integrating the results of the different experiments we hope to get better insights into the genes involved in thermal tolerance, into how organisms cope with thermal stress, and how genetic drift affects the adaptive potential. I will discuss the findings particularly in relation to the persistence of small, inbreeding populations of endangered species.

## **Bergmann and converse Bergmann clines: Thermal adaptation?**

Wolf U. Blanckenhorn

*Zoological Museum, University of Zurich, Switzerland*

[wolfman@zoolmus.unizh.ch](mailto:wolfman@zoolmus.unizh.ch)

Large-scale clinal variation in quantitative and molecular genetic traits is presumably caused by climatic adaptation. Two seemingly opposite latitudinal trends in body size and associated life history traits exist in nature. According to Bergmann's rule, body size increases with latitude, presumably a temperature effect. According to the converse Bergmann rule, body size decreases with latitude, certainly a season length effect. Converse Bergmann clines are conceptually related to countergradient variation, whereby populations of a given species compensate seasonal limitations at higher latitudes by evolving faster growth and larger body sizes compared to their low latitude conspecifics. Furthermore, the optimal temperature (or beneficial acclimation) hypothesis states that all organisms have their optimal temperature range to which they are adapted, defining their thermal niche.

In my talk I shall discuss, compare and try to relate all these patterns to each other. Whereas converse Bergmann clines (and countergradient variation) are clearly adaptive because they are predicted by life history optimality models, the adaptive nature of Bergmann clines remains unclear to this day. In particular, recent comparative and experimental evidence indicates that Bergmann and converse Bergmann clines are not mutually exclusive because they are driven by different environmental causes and proximate mechanisms; they therefore can act in conjunction, resulting in any intermediate pattern. This compensates interpretation of any particular clinal pattern in light of thermal adaptation.

*Avenues for future research:*

Are Bergmann clines adaptive or are they a physiological constraint (cf. temperature-size rule)?

Which organisms show them, and which don't?

How to disentangle season length and temperature effects on clines?

Which physiological and genetic mechanisms are involved, and is temperature the culprit after all?

How, in general, can we distinguish between adaptation and constraint, and which hypothesis-testing, experimental framework do we have to do so?

## **Evolution of plasticity in *Bicyclus* butterflies and seasonal temperatures**

Paul M. Brakefield

*Institute of Biology Leiden, The Netherlands*

[brakefield@rulsfb.leidenuniv.nl](mailto:brakefield@rulsfb.leidenuniv.nl)

We are using wing pattern and life history traits in *Bicyclus* butterflies to explore evolution in response to alternating environments. Many species of these butterflies live in highly seasonal environments in Africa. Both developmental plasticity and acclimation of a whole suite of traits are important in the survival of butterflies of the different generations in wet and dry seasons with high and low temperatures, respectively. We use a laboratory model species, *B. anynana*, to explore how the genetical and developmental architectures of different traits influence the tempo and direction of evolution. In addition, the processes of making an eyespot can be linked to the hormonal modulation of the developmental plasticity. Here, I will outline how the developmental plasticity and acclimation work, and show the results of some artificial selection experiments designed to explore the evolvability of the system, especially with respect to the responses to alternative rearing temperatures.

# **Apparent trade-off between standard metabolic rate and locomotor performance in resident populations of brown trout (*Salmo trutta*) across a thermal gradient**

J. M. Cano<sup>1</sup> and A. G. Nicieza<sup>2</sup>

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Adaptation to cold environments of ectotherm populations is expected to result in increased standard metabolic rates if resources are not limiting. However, it is still unclear how the maintenance of high standard metabolic rates would affect locomotor performance and its impact at the population level. We compared standard metabolic rate and swimming performance of Brown trout (*Salmo trutta*) populations inhabiting rivers with contrasting thermal conditions. To avoid environmental confounding effects, we tested offspring raised in controlled conditions. There were significant differences among populations and families for both traits, suggesting that the observed differentiation pattern has a genetic basis. We found a significant negative relationship between standard metabolic rate and swimming performance at the population level. On the other hand, standard metabolic rates tended to be negatively related to the temperature in the rivers of origin, whereas swimming performance was positively related to river temperature, but these trends were not significant. These results suggest that selection for traits positively linked with standard metabolic rates may result in lower relative prolonged swimming performance. The potential evolutionary consequences of the observed negative relationship are discussed.

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# The evolution of body size and shape: the evolutionary and developmental genetics approach

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Genetically based body size and shape differences among *Drosophila* populations from different climatic areas or after natural selection for temperature in the lab are well known. Usually, bigger individuals show larger structures with respect to the smaller ones, but the relationships between adult structures and total body size can significantly vary among populations and/or species. Development in multicellular animals is a process that involves both tight control and flexibility. Little is known about developmental mechanisms that generate allometry and about their relative evolutionary importance [1].

In *Drosophila*, the discovery that during development cell division within imaginal discs uses borders of clonal restriction as references [2, 3] offered the opportunity to develop models of how cells, through proliferation, generate morphological space of finite size and shape and to integrate quantitative studies in the development [4, 5, 6, 7]. Here we propose methods for combining developmental and quantitative studies to investigate the relative importance of integration versus modularity in the development and evolution.

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## **Evolutionary physiology of thermal responses: challenges in linking molecular mechanisms to population dynamics**

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The links from the thermal environment to large-scale patterns in species richness, which is derived from a concatenation of individual species distributions, used to be many and complex. Apparently, they are no longer. Little can be done by organisms to avoid the ‘tyranny of Boltzmann’. Is this the case and what are the implications of the assumptions made when saying so? The claims made by the metabolic theory of ecology mean that its implications for and assumptions regarding thermal responses in animals should be addressed. Doing so raises several issues that, given the diversity of the insects, remain surprisingly poorly explored. These include the relationship between microclimate and macroclimate, the field body temperatures of insects, and the scope for insect metabolic adaptation via changes in membrane properties, mitochondrial densities, and enzyme function. If Boltzmann’s tyranny turns out to be that of a petty clerk, the links from the thermal environment to population dynamics, which ultimately determines species ranges, resume their complexity with important roles reserved for phenotypic plasticity and evolutionary change. At the cellular and molecular levels much is known about insect thermal responses, but the role of membrane alterations and especially changes to polyunsaturated fatty acid composition are little explored. Likewise, the role of Hsps in mediating rapid and longer-term responses to the environment has not been comprehensively investigated. Moreover, the fitness consequences of adopting one thermal strategy over another in different environments are not well understood. In particular, models examining the evolution of thermal physiology, those examining the conditions under which phenotypic plasticity, adaptive population differentiation or some combination thereof arise, and those which determine how range limits are set in populations remain distinct despite their similarity. It might also be argued that stress responses are of little consequence in determining insect distributions because it is oxygen limitation of thermal tolerance that is most important. Such a statement begs the question of whether such limitation is significant in insects. More broadly it begs the question of the significance, for fitness, of short-lived extreme events, often lethal for a large component of a population, relative to longer-term sub-lethal stresses. This returns the question to the colour of environmental noise and how this varies spatially. These are among the significant questions that face insect thermal biologists who wish to link thermal adaptation to spatial variation in population dynamics, which in turn sets range limits.

## Phenotypic thermal plasticity: Various adaptive aspects in *Drosophila*

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Temperature is a most important factor of the environment and, according to weather and season, development will occur under very variable conditions. These variations induce a phenotypic plasticity of almost all morphological and physiological characteristics of ectotherms. We have investigated the shapes of the response curves (the reaction norms, RN) of a diversity of traits in response to an environmental temperature gradient. According to the trait investigated, the shapes are very variable so that, for a long time, the reaction norms were assumed to be independent of natural selection and adaptation. In other words, each norm could be the consequence of complex and unknown interactions between developmental genes and temperature, that is a kind of random evolutionary walk.

We have worked out specific techniques (isofemale lines, polynomial adjustments) for describing R N shape. For each trait, we have compared the shapes either among geographic populations of the same species adapted to different climates, or among species with very different thermal ranges. In all cases, it has been found that the R N shape of a trait ( its plasticity) was evolving in agreement with ecological adaptation of populations or species. Natural selection modifies not only the mean value of a trait (eg producing a latitudinal cline), but also its reactivity to a thermal gradient, that is its plasticity. It is argued that an **eco-devo** approach should always be implemented when investigating ecological adaptations of populations or species

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## Deconstructing the physiology of thermal reaction norms

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We describe an endocrine-based physiological mechanism that explains how insects translate variation in diet and temperature into reaction norms of body size and development time using the holometabolous insect *Manduca sexta* (Sphingidae). Body size and development time are controlled by three factors: (i) growth rate, (ii) the timing of the cessation of juvenile hormone secretion (measured by the critical weight) and (iii) the timing of ecdysteroid secretion leading to pupation (the interval to cessation of growth [ICG] after reaching the critical weight). Thermal reaction norms of body size and development time are a function of how these three factors interact with temperature. Body size is smaller at higher temperatures, because the higher growth rate decreases the ICG, thereby reducing the amount of mass that can accumulate. Development time is shorter at higher temperatures because the higher growth rate decreases the time required to attain the critical weight and, independently, controls the duration of the ICG. Recent results from a simultaneous selection experiment on body size and development time indicate that the responses to selection of these life history traits are determined by differences in synergistic and antagonistic selection among the three underlying physiological traits. Life history evolution along altitudinal, latitudinal and seasonal gradients may occur through differential selection on growth rate and the duration of the two independently controlled endocrine determinants of the growth period.



# Temperature Dependence of Body Size: from Biophysics to Adaptation

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Many models have been proposed to describe the temperature dependence of development rate, from the degree-day summation to the biophysical Sharpe-Schoolfield model. The Sharpe-Schoolfield model can be used to describe phenotypic plasticity in development rate [1,2], growth rate and insect size [3,4]. Parameter change in the model immediately explains genetic variation for phenotypic. The optimal temperature for organismal functioning is implicit in the biophysical mechanism rather than equalling the temperature of highest development rate or highest growth rate.

By way of the Sharpe-Schoolfield model biophysics can be used to explain size differences over temperatures. Selection on development rate or growth rate would translate into selection on the parameters of the model. So would selection for enzyme efficiency or enzyme stability. The Sharpe-Schoolfield model can therefore be used to link adaptation at the physiological level to phenotypic plasticity in body size. We can see why phenotypic plasticity is adaptive, or not, what traits are the prime movers of adaptation and what traits might be easily observed but not be adaptive themselves. Body size becomes a trait that might be directly selected or be totally the result of selection on enzyme performance.

The Sharpe-Schoolfield model can be used to model the existence of clines in body size between populations or related species living in different geographical areas. Clines in body size emerge from the model as the consequence of differences in the range of temperature adaptation, specifically in the lowest viable temperature [5].

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# Genetic and environmental effects on thermal adaptation in butterflies

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Geographical variation in traits related to fitness is often the result of adaptive evolution. Particularly strong support for this notion comes from clinal variation, suggesting a contribution of directional selection to the differentiation among populations [1-4]. Geographic gradients are of special interest for the study of climatic adaptation because the climate strongly varies with geographical variables. Although several environmental factors may impact on the physiology of individuals, temperature is thought to be one of the most important selective agents, influencing virtually all aspects of the ecology and evolution of ectotherms [5, 6].

By comparing Copper butterfly populations from low and high altitudes, we will demonstrate differences in life-history variables, which are presumably attributable to temperature adaptation. Special attention will be paid to variation in pupal melanization (which increases with increasing altitude) and its functional ecology, and to the butterflies' temperature stress resistance. The latter, using chill-coma recovery and heat-knock down assays [2-4, 7], was found to predictably vary across populations and in relation to ambient temperature conditions. High altitude populations show reduced heat but increased cold stress resistance, paralleling the patterns based on differences in acclimation temperatures.

Environmental effects (developmental environment, acclimation, hardening, age, food stress; [2-4, 7-8]) on temperature stress resistance were further investigated in the butterfly model *Bicyclus anynana*. While effects of acclimation (and developmental) temperature were as expected and highly repeatable, effects of hardening, age and food stress remained largely inconclusive.

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# Behavioural regulation of body temperature: current views and future perspectives

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Body temperature in ectotherms influences all aspects of their physiological and behavioural performance. The fact that terrestrial ectothermic vertebrates have the ability to maintain relatively high and constant body temperature by behavioural means was recognised early [1]. It has been shown recently that the effective thermoregulatory behaviour can result in relatively stable and similar activity body temperatures across thermally different habitats, and hence, has the potential to constrain physiological evolution [2]. The general predictions derived from the cost-benefit model of thermoregulation [3] and the widely used research protocol [4] to quantify thermoregulatory strategy opened the possibility for having a large number of directly comparable studies testing the model's predictions. However, both field and especially experimental studies rigorously testing the models' predictions are rare. In this presentation, we will summarize the results up to date about ectotherm thermoregulatory strategies (e.g. active thermoregulation or thermoconformity) in the light of the model's predictions. As reptiles, mainly lizards, serve as models in studies of behavioural thermoregulation in ectotherms, we will focus on studies dealing with this taxon. We will also discuss about some problems and possible solutions for problems with current approaches to understand thermal quality of environment and 'thermal challenge'. Finally, we will present some perspectives and suggestions which might prove helpful in achieving a better understanding of the mechanism, the role and the evolution of ectotherm thermoregulatory behaviour.

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## **Linking field fitness with genetic polymorphisms under thermal selection in *Drosophila***

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Lists of candidate genes for thermal adaptation are emerging from studies of comparative genomics, microarray comparisons, and quantitative genetic analyses. However so far there have been few cases that successfully link genetic polymorphisms in these genes to adaptive shifts in natural populations. We are testing the feasibility of using a combination of clinal studies, field releases, field cage experiments and laboratory tests to develop such links in *Drosophila melanogaster* from the tropical-temperate cline in eastern Australia. We illustrate the approach with recent data collected on the *frost*, *Dca*, *Adh* and *hsp68* polymorphisms.

## Latitudinal impacts of climate warming on terrestrial ectotherms

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The biological impacts of climate warming over the next century are predicted to increase with latitude [1], paralleling a latitudinal increase in the magnitude of warming [2]. However, the biological impact depends not only on the degree of warming, but also on the physiological sensitivity of organisms to that warming [3]. We show that tropical lizards are relatively sensitive to warming temperatures and also have limited capacity to compensate via acclimation [4]. Moreover, many tropical forest lizards are already experiencing near-stressful environmental temperatures, whereas temperate-zone lizards and open-habitat tropical lizards generally have ready access to thermal refugia. By integrating these physiological data with global climate projections, we develop climate safety maps, which predict that tropical forest lizards will suffer from climate warming far sooner than will temperate zone ectotherms, which may in fact benefit in the short term. Because lizard diversity is high in tropical forests and because tropical animals are especially vulnerable to temperature shifts, the biological impact of climate warming will be greatest on tropical forest lizards.

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# A trait-based approach to predicting species distributions: integrating mechanistic thermal niche modelling with GIS data

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Climate change is likely to cause major changes in the distribution and abundance of ectothermic pests, disease vectors, and threatened species. While mitigation strategies rely critically on our ability to predict these changes, current approaches mainly rely on correlations between distribution points and climatic data (e.g. regression models, BIOCLIM, GARP). These approaches may have serious limitations when extrapolating to novel conditions [1-3] and cannot easily incorporate evolutionary potential. We show how it is now possible to infer constraints on distribution and abundance based on how organismal traits interact with environmental conditions to affect fitness, using biophysical models in conjunction with GIS data on climate and topography. We illustrate the approach with two Australian examples; the gecko *Heteronotia binoei* and the mosquito *Aedes aegypti*. We also discuss how a trait-based approach allows explicit incorporation of evolutionary potential into predictions of distribution and abundance under climate change.

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## **Evolutionary responses of insects to rapid climate change: development time, size and thermal sensitivity**

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Human-induced climate change will involve specific changes in diurnal, seasonal, and latitudinal patterns of climate, not simply increases in average temperatures. I will discuss how different aspects of temperature variation may affect different components of fitness in insects, and the consequences for the opportunity for selection and evolutionary response in growth and development, body size, and thermal sensitivity. There is abundant evidence for selection (and evolution) on size in natural populations acting through multiple fitness components, and more limited evidence (mostly from plants) for selection of growth or development time. By contrast, we have much less information about selection or rapid evolution of thermal sensitivity in natural field environments. I will describe a simple theoretical model that relates patterns of temperature variation to selection on thermal sensitivity of growth rate, and discuss an experimental laboratory test of the model. The results suggest that the temporal dynamics of temperature variation influence how climate change causes selection on thermal sensitivity.

## **Using shape analysis to gauge the effects of temperature and thermal adaptation**

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Temperature has fundamental effects on the physiological and developmental processes of ectothermic organisms. It is perhaps not surprising, therefore, that morphological traits are affected by it. I summarise results from the literature and ongoing studies in my lab that use the methods of geometric morphometrics to show that temperature has significant effects on shape in various organisms.

A simple theoretical model of a developmental process and its genetic control shows that temperature can interact with the effects of many genes on a morphological phenotype. Even though none of the loci in the model is specified as a “reaction norm gene”, the nonlinearity of the model interacts with the temperature dependence of physical processes in the model so that many genes can influence the reaction norm. This suggests a considerable evolutionary plasticity of developmental reaction norms.

Empirical data from morphometric studies are consistent with this expectation in that the reaction norms of shape tend to be nonlinear. Studies also show differences in covariance structure associated with geographic origin of populations (north-south as well as climatic differences from oceanic to Mediterranean). Empirical studies of temperature adaptation of shape are just beginning, and much more work is required.



## Cell size, temperature, and body size optimization in ectotherms

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Temperature-size rule states that ectotherms usually grow slower in cold, but attain larger final size due to postponed maturation and prolonged growth period. Such response to temperature is observed in laboratory-reared animals and lays behind geographical clines in body size. One possible proximate mechanism involved in dwarfing at higher temperatures is an inverse relation between temperature and cell size. However, if this relation was purely mechanistic, we could expect evolution of mechanisms compensating for fitness losses associated with the reduction of body size through dropping cell size (e.g., an increase of cell number). Existence of many parallel geographic clines in body size suggests their adaptive character, and implies adaptiveness of changes in cell size along the clines. Models of optimal resource allocation show that prolonged growth period overcompensating slower growth can be optimal in determinately and indeterminately growing ectotherms, if body size-scaling of resource acquisition and metabolism depend on temperature [1]. Cell size and membrane permeability are known determinants of metabolic rates of organisms; changes in cell size through ontogeny and cellular differences between organisms are postulated to shape size-scaling of metabolism on within- and between-species levels. We argue that integration of cellular effects of temperature on size-scaling of metabolism with optimization theory promises finding an ultimate explanation for temperature-size rule in ectotherms.

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## Thermal adaptation and environmental stress: from selection experiments to gene expression studies and field releases

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We are studying adaptation to genetic and environmental stresses relevant and its evolutionary implications with particular emphasis on thermal adaptation and the heat shock response [1]. To achieve our research goals, we study correlated responses in lines selected for resistance to various environmental stresses as heat, cold, starvation and desiccation as well as lines selected for increased lifespan [2], which often has been shown to be related to stress resistance traits. Results on the phenotypic level are related to results on the DNA level, studying gene regulation in the same stress selected lines using Affymetrix gene chips at different time points after being exposed to a heat or cold hardening treatment [3]. To complement these expression studies and to assess the role of putative candidate genes we use knockout or mutant lines and do quantitative PCR [4]. Further, we map quantitative trait loci (QTL) responsible for thermal stress resistance [5], study DNA sequence variation in candidate genes and the relation of candidate gene variation to variation in resistance traits in natural populations and selection lines. Finally, we use some of the same selection lines to study fitness in the wild using release-recapture experiments or bridge the gap between laboratory experiments and studies of thermal adaptation in the wild [6].

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## Thermal adaptation along a latitudinal gradient

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Common frogs (*Rana temporaria*) display extensive variation in the degree of melanistic pigmentation in their integument, some individuals being almost black, others being entirely devoid of this pigmentation. This variability is known to be associated with differences in heating rates in this actively thermoregulating species. We investigated the possible adaptive nature of this variability by quantifying the variation in the degree of melanistic pigmentation in 11 common frog populations spanning a 1600 km long latitudinal gradient across Scandinavian peninsula. We also conducted a common garden experiment to investigate the genetic basis of the variability in pigmentation which also allowed us to test – with the aid of  $Q_{ST} - F_{ST}$  comparisons - whether the degree of differentiation in the melanistic coloration among populations is consistent with selective explanations. Isolation and characterization of nucleotide variation in melanocortin 1 (MC1R) receptor was conducted to explore possible associations between phenotypes and MC1R alleles.

## Latitudinal variation in body size of the fruit fly *Drosophila*

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Several ectothermic animals show latitudinal-genetic clines of increasing body size at higher latitudes. These clines are particularly well documented in *Drosophila* species, and a substantial body of work has appeared on their functional significance and genetic basis. Temperature is implicated as a selective agent, because body size in *Drosophila* also shows an evolutionary increase with lower temperature laboratory culture. However, it is not at all clear why temperature should act as a selective agent for body size in a small, ectothermic animal. Interestingly, many ectotherms also attain larger body size with growth at lower temperatures, implying that energy budgets for growth may be changed by temperature. This body of work will be discussed and some possible future approaches outlined.

# **Mechanistically modeling the impact of past and future air temperature changes on ectotherms across a continent: the effect of body size, activity thresholds and diurnal vs. nocturnal activity patterns**

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We use an extensively lab and field tested state-of-the-art microclimate and ectotherm model [1,2,3,4] that incorporates coupled animal heat and mass transfer with local environments. The models calculate behavioral responses based on morphological and physiological properties. We explore the consequences of body size, activity thresholds and diurnal vs. nocturnal activity patterns for ectotherms ranging in size from *Drosophila* to large Varanids across the continent of Australia. These models are spatially explicit at a resolution of 0.5 km for topography, vegetation, and climate. Transient and steady-state calculations are done on an hourly basis for the average day for each month of the year for present, future and last glacial maximum climates. We illustrate significant effects of behavioral temperature preferences, diurnal vs. nocturnal habit and how the transients associated with differences in body size impact activity time available for foraging, metabolic and water requirements, and requisite feeding rates. These calculations can be used to identify key variables affecting distribution limits.

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## Physiological mechanisms linking climate to ecosystem change

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Through functional analyses, integrative physiology should link molecular biology with ecology and, thereby, provide access to the mechanistic bases of organismic responses to environmental alterations, including climate change [1]. Such an approach also contributes to an integrative understanding of evolutionary history [2,3]. Our physiological studies in marine animals, at molecular, cellular and organismic levels currently aim to clarify the mechanistic basis of bio-geographical patterns on large scales, i.e. in a latitudinal cline, as they are determined by various climate regimes and associated abiotic factors like temperature, oxygen or CO<sub>2</sub> [4]. By identifying the tradeoffs and constraints involved in environmental adaptation the principle reasons should become accessible that limit each species to specific habitats [4]. Current hypotheses address the bio-energetic consequences of thermal adaptation with important implications for growth, reproductive output, capacity for motor performance, lifestyle strategies including aging and possibly, even biodiversity.

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## Net fitness evolution in a warming world: the case of *Drosophila subobscura*

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Responses to environmental change can be caused either by large-scale population-level migration of individuals better adapted to the altered climate conditions or by evolutionary adjustments within populations. How will temperate (i.e., cold-tolerant) species cope with contemporary rapid global warming? Using replicated lines of *Drosophila subobscura* that had been allowed to evolve for 4 yr at a range of temperatures covering much of the physiologically tolerable range of the species (cold: 13 °C ; optimum: 18 °C ; warm: 22 °C ) I show here that this native Palearctic species, which spread explosively on North and South America in the late 1970s and early 1980s and has also recently expanded some 500 Km to the north in Scandinavia [1-2], does not suffer a loss in net fitness after extended thermal evolution in a temporally stable warm environment. On the contrary, whereas warm-adapted populations perform well at a wide range of temperatures net fitness is severely reduced in cold-adapted populations when transferred to warmer conditions. These findings support the idea that the exceptionally fast world-wide genetic shifts in response to increasing temperature may not reflect local adaptation as previously suggested [3-6], but a displacement of genotypes from higher latitudes by progressive invasion from ‘warm-climate’ populations.

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## Chromosomal variability and thermal adaptation in *Drosophila subobscura*

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The magnitude and direction of shifts over time in chromosome inversion frequencies and in ambient temperature for populations of *Drosophila subobscura* on three continents have shown that climate has warmed over the time intervals considered, and the chromosomal inversions characteristic of warm latitudes have increased in frequency in a corresponding manner. Here we present the results obtained from the analysis of two marginal Scandinavian populations (Sunne in Sweden and Droback in Norway), which reinforce the previous observations, and discuss the issue of whether the pattern of chromosomal variability observed is the result of local adaptation or migration from the south. The chromosomal variability, quantified by Shannon's entropy as a measure of heterogeneity, has increased in most new samples as compared to the historical ones. This effect cannot be attributed to different sample sizes. Using a multidimensional analysis, we obtain, in the genetic space, a direction which maximally correlates with the first principal component of temperature data and thus can be interpreted as thermal adaptation. Other direction in the genetic space is computed, orthogonal to the previous one, in order to obtain an optimal bidimensional graphical output. Also, we analyze the biological meaning of other genetic directions, as the one that maximally correlates with the second principal component of temperature (this later reflecting thermal amplitude along the year), or the one maximally correlated with the entropy.



## Genetic adaptation to temperature increase: first results on a mesocosm experiment

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While several long-term studies demonstrated the occurrence of micro-evolutionary responses that may allow local persistence of populations under global warming, rigorous experimental proof for present evolutionary potential to cope with increasing temperatures under semi-natural conditions is scarce. We set up a series of experiments where we combine the realism and rigid, replicated experimental design of large-scale mesocosm studies where populations of several zooplankters (*Simocephalus vetulus*, *Daphnia magna* and *Daphnia pulex*) are exposed for several years to different global warming scenarios with life table experiments in laboratory conditions at different temperatures that eliminate confounding, non-genetic factors. So far, our results provided evidence for a rapid micro-evolutionary response to global warming in both survival and the subcomponents of individual performance (age at reproduction and number of offspring) in *S. vetulus* [1], which may allow populations of this species to persist locally under predicted scenarios of global warming. We are currently exploring whether the evolutionary potential to cope with increasing temperatures is differentially expressed in the absence and presence of biotic interactions and to what extent thermal adaptation affects intra- and interspecific biotic interactions and may buffer against immigration by southern genotypes/species. Such micro-evolutionary responses may help explain the outcome of previous mesocosm studies finding only marginal effects of global warming at the community level in zooplankton.

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## **Growth allometry of lepidopteran larvae: a life-history perspective**

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Limited amount of information is available on growth allometry of insect larvae. In life history studies, it is often assumed that insect larvae grow exponentially. This allows one to expect that potential rewards of extending growth periods are high in terms of increased adult body weights, and fecundities. It is therefore a challenge to find costs of large size which were able to counterbalance the fecundity advantage of attaining larger sizes. We report results of a study that examined growth allometry in various species of lepidopteran larvae. An original methodology is proposed to deal with problems arising from the complexity of insect growth curves, and the high sensitivity of growth rates to environmental conditions. We found that instantaneous absolute growth rates of larvae are related to body size by an allometric exponent which typically, though not invariably, lies in the range of 0.67...0.75, expected on physiological basis. There were significant differences between the species but values of the exponent as high as 1 (exponential growth), and as low as 0 (linear growth) could safely be excluded. In terms of relative growth rates, larvae typically grew 35% slower in the beginning of their last larval instar, as compared to the penultimate one. The growth of lepidopteran larvae thus clearly deviates from the exponential model, and more realistic power functions have to be used when analysing insect growth and size in the context of evolutionary ecology, including studies on thermal adaptation.

## **Flying heliotherms in changing landscapes: behaviour, life history and thermal environment in speckled wood butterflies**

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As patterns of resource use change with the process of habitat fragmentation, selection regimes may consequently alter phenotypic traits including behaviour, morphology and life history. Field studies on habitat fragmentation have particularly focused on changes for dispersal, but altered environmental conditions in fragments may have wider significance for ectotherms like flying heliotherms (butterflies). The speckled wood (*Pararge aegeria* L.) is mainly confined to woodland, but the butterfly increasingly occurs in landscapes with only a minor woodland aspect (like agricultural landscape). From a series of comparative studies among continuous woodland and fragmented agricultural landscape populations, I explore several aspects of the adaptation process that is most likely to accompany such a habitat expansion. Laboratory experiments showed that females of woodland landscape origin reached higher fecundity than did agricultural landscape females at low temperature, but this reversed at high ambient temperature. Males, and not females, were furrer in agricultural landscapes which improves their thermal isolation capacity. We also studied how variation in temperature affects different aspects of flight ability (take-off flight performance, flight endurance). I will integrate the results of our studies on this model system to explore the further perspectives on thermal adaptation within an explicit behavioural, morphological and life history framework and discuss the need to integrate physiological approaches.

## Questions or avenues to be pursued in the near future

Unordered and non-comprehensive list of quintessential questions or avenues to be pursued in the field of thermal adaptation in the near future, complementing the speakers' abstracts:

1. How can the thermal ecology/evolutionary biology perspective help in predicting the impact of climate change on species from a mechanistic point of view?
2. Principles of biophysical ecology and GIS data can bridge the gap between species distributions, the direct interactions between organisms and their thermal environment.
3. (How) do the adaptations to temperature we see today reflect the necessity for all of the present biota to have survived though the Pleistocene?
4. What are the evolutionary, genetic and developmental mechanisms underlying size changes of ectotherms with temperature?
5. We need to understand better how temperature effects are integrated via hormones in organisms. It might turn out that a plethora of phenomena (life history, diapause, colour) are caused by the same hormonal change.
6. How is the diapause decision influenced by a combination of photoperiod (giving the date), the internal state (mass achieved, hormonal state, sex...) and cues of future growth conditions, including temperature and diet?
7. What is the degree of evolutionary conservatism of temperature niches that should ultimately determine what will happen to species when climate changes?
8. One focus should be the interaction between behaviour and the capacity for physiological evolution.
9. We should promote the study of thermal adaptation from several directions via (i) phylogenetic comparative studies, (ii) studies demonstrating links between thermal traits, organismal performance, and fitness under natural conditions, and (iii) development of more realistic models about the evolution of thermal traits enabling formulation of testable predictions.
10. Does the metabolic theory of ecology provide an adequate basis for understanding thermal responses? If not, what is missing from (or wrong with) the theory?
11. Will climate change have strong negative impact on tropical ectotherms?
12. How do we usefully integrate physiological knowledge into models of thermal niche, geographic range and population demography?

13. How do changes in the thermal environment (e.g. climate change) generate selection on physiology, morphology and reaction norms in nature?
14. What is the impact of climate change on the physiology, life history, and ecology of species? Do impacts differ for aquatic vs. terrestrial species, or for ectothermic versus endothermic species?
15. How will climate change impact biological interactions and ecosystem services?
16. What is the geographic impact of climate change? Will the impact be greatest at high latitudes, or in the tropics? For this we need to know about geographic patterns of sensitivity to climate change.
17. What was the impact of past-climate change on organisms? Thus what can we learn from paleontology, perhaps drawing lessons from patterns observed in the glacial-interglacial cycles?
18. Is evolution fast enough to modify ecological outcomes of climate change?
19. Anthropogenic change involves more than climate change: populations will be isolated and fragmented, leading to small effective population sizes, possibly increased inbreeding, and reduced gene flow and recolonization. How can we integrate climate change with these "demographic" influences?
20. What are the effects of a species' thermal adaptation for its (temperature/latitude-dependent) biotic interactions (competition, predation, parasites)? / In other words, what are and how strong are the feedback loops of micro-evolution to community and ecosystem ecology.
21. Is the evolutionary potential to temperature realized to the same extent in the absence and presence of biotic interactions?
22. What is the role of community context, species sorting versus gene sorting?
23. What is the role of dispersal for local population persistence under global warming? (negative competitive effects, input adaptive genes)
24. How do meta-population and meta-community structure affect the responses of organisms to global climate change.
25. What are fitness effects associated with size changes along thermal gradients?
26. Temperature-size rule: Underlying mechanisms / causes (including testing theoretical models), adaptive significance.
27. Global patterns concerning temperature ranges / thermal limits, acclimation responses, thermal stress tolerance.
28. Impact of global warming on specific species / case studies.

- 29.** How does adaptation to temperature affect how predator and prey interact and thus ultimately how do predators and prey become selective forces for each other?
- 30.** How does temperature affect mate searching abilities and thus sexual selection by scramble competition?
- 31.** It is very important to quantify how fast can evolution occur in nature and to ascertain whether evolutionary trajectories are predictable or idiosyncratic. Recently introduced species that quickly colonize large areas offer special opportunities to address both the speed and predictability of evolution on a geographic scale.
- 32.** Climate change and particularly global warming is altering the geographic ranges, abundances, phenologies and biotic interactions of organisms. Climate change may also alter the genetic composition of species. In this regard it is fundamental to assess the shifts in the genetic composition of populations due to global warming, to obtain time series of genetic data on continental or global scales.
- 33.** The coexistence of plastic responses of body size to temperature and geographical clines is one of the most interesting problems.
- 34.** We should produce spatially explicit models predicting evolutionarily response to global warming, i.e. a model of range shifts that also incorporates evolutionary changes.
- 35.** Close the gap between the approaches of population genetics and optimality models. Population genetics is explicit about the rate of evolutionary change whereas the optimality approach is not.
- 36.** It is important to collecting and preserve random samples in museums. We are in real hurry in documenting the state of the world as it was before global warming. Systematic documenting of the current state of populations should be announced worldwide.
- 37.** Thermal adaptation research will be particularly useful if it can help predict and mitigate ecological impacts of thermal change.
- 38.** We should try to improve our understanding of evolutionary and plastic body size responses to temperature. Promising ways forward include investigating patterns of thermal covariation between size and other traits (biological rates and efficiencies) that might help explain mechanisms, taking a more quantitative approach to size-temperature relations, and attempting to test hypotheses for temperature-size plasticity using experimental evolution.

**39.** We should try to use what we know about ecology, genetics and development to predict when and where in terms of climate change we can expect plasticity and habitat tracking as opposed to (or in combination with) adaptation via genetic change.

# Participation List

## Speakers

Dr. David Atkinson Liverpool, (UK)  
Professor Kuke Bijlsma Haren, (NL)  
Professor Wolf Blanckenhorn Zürich, (CH)  
Professor Paul M. Brakefield Leiden, (NL)  
Dr. José M. Cano Helsinki, (FI)  
Professor Sandro Cavicchi Bologna, (IT)  
Professor Steven L. Chown Matieland, (ZA)  
Professor Goggy Davidowitz Tucson, (US)  
Dr. Gerdien De Jong Utrecht, (NL)  
Professor Luc De Meester Leuven, (BE)  
Dr. Klaus Fischer Bayreuth, (DE)  
Dr. Patricia Gibert Villeurbanne Cedex, (FR)  
Dr. Gábor Herczeg Budapest, (HU)  
Professor Ary A. Hoffmann Parkville, (AU)  
Professor Raymond B. Huey Washington, (US)  
Dr. Michael Kearney Melbourne, (AU)  
Professor Joel G. Kingsolver Chapel Hill, North Carolina, (US)  
Dr. Christian P. Klingenberg Manchester, (UK)  
Professor Jan Kozłowski Kraków, (PL)  
Professor Volker Loeschke Aarhus C, (DK)  
Professor Juha Merilä Helsinki, (FI)  
Professor Linda Partridge London, (UK)  
Professor Warren P. Porter Madison, (US)  
Professor Hans O. Pörtner Bremerhaven, (DE)  
Professor Mauro Santos Bellaterra (Barcelona), (ES)  
Professor Luis Serra Barcelona, (ES)  
Professor Toomas Tammaru Tartu, (EE)  
Professor Hans van Dyck Louvain-la-Neuve, (BE)

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Dr. Antón Brancelj Ljubljana, (SI)  
Dr. Jordi Catalán Blanes, (ES)  
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Professor Antonio Fontdevila Bellaterra (Barcelona), (ES)  
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Dr. Sara Guirao Rico Barcelona, (ES)  
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Dr. Torsten N. Kristensen Aarhus C, (DK)  
Dr. Anssi Laurila Uppsala, (SE)  
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Dr. Margarida Matos Lisboa, (PT)  
Dr. Francesc Mestres Barcelona, (ES)  
Dr. Jordi Moya Almeria, (ES)  
Ms. Laia Navarro i Martin Barcelona, (ES)  
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Dr. Alex Ritcher Barcelona, (ES)  
Mr. Xavier Santos Barcelona, (ES)  
Professor Christian Schlötterer Wien, (AT)  
Dr. Carmen Segarra Barcelona, (ES)  
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Dr. Francesc Uribe Porta Barcelona, (ES)  
Ms. Wendy Van Doorslaer Leuven, (BE)  
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## 2<sup>nd</sup> Steering Committee meeting

On Sunday 18 March, following the expert meeting, we held the 2<sup>nd</sup> Steering Committee meeting. We arrived at the following decisions regarding the meeting. A few additional decisions regarding other programme matter were also reached.

### (1) *Expert meeting conclusions:*

- A list of questions brought up during the meeting should be requested from all participants via email to complement the speakers' abstracts. A listing of questions we received in response are included here.
- For the moment it was decided that focusing on only some of the many interesting areas, questions and (sub)topics for further study is premature at this point. The programme should remain open to all topics for the moment to better integrate the field, and a narrowing-down of topics should, if at all, happen only during the later stages of the programme.
- Anyone can propose to organize a workshop on particular, more specific topics, for which the programme will be happy to provide money.
- The present final report of the expert meeting should be publicized on the ESF webpage. This might include 4 to 5 DVDs, as all of the speakers were filmed.
- It was suggested to perhaps write a 'perspective' kind of paper, e.g. for a reviews journal like TREE. This would also advertise the network. However, several steering committee members found it difficult to put everything in two pages, as the field is too diverse to integrate easily in such a short format.

### (2) *ThermAdapt brochure:*

- It was decided to finalize the ThermAdapt brochure and thereafter produce a similar poster for advertisement. Pictures were subsequently gathered for the brochure by e-mail and the brochure is now in press at ESF. Gerdien de Jong will take care of the poster once the brochure is finished.

### (3) *ThermAdapt web site:*

- All steering committee members, plus anyone else interested, should prepare research descriptions of their groups to be advertised on the web. This web page has by now been added to the ESF ThermAdapt web site. Additional descriptions can be added any time.

### (4) *ESF ThermAdapt grant applications:*

- The first 'round of travel and workshop grants' were reviewed. This was finalized after returning home via e-mail. The successful applicants were notified in the meantime by ESF. As only one short-visit grant was of satisfactory quality, it was decided that the next call will be launched in summer, which has been done in the meantime.

### (5) *Future plans:*

- The next Steering Committee meeting should preferably be attached to an already existing conference, in winter or next spring (to be decided)
- Mauro Santos offered to organize another scientific meeting in Barcelona when closing the programme, 4 years from now.