Toomas Tammaru
toomas.tammaru@ut.ee
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Evolutionary and plastic responses of animal growth to different temperatures: adaptations and constraints

Final report of an ESF science meeting

1. Summary

Science meeting "*Evolutionary and plastic responses of animal growth to different temperatures: adaptations and constraints*",
http://www.ut.ee/~tiited/thermadapt/,
was held at the University of Tartu
http://www.ut.ee/,
Tartu, Estonia from April 28 to April 30, 2011. The meeting was organized by the European Science Foundation research networking programme "Thermal adaptation in ectotherms: Linking life history, physiology, behaviour and genetics"
http://www.esf.org/index.php?id=545,
and was additionally supported by the Estonian Doctoral School of Earth Sciences and Ecology
http://www.geoeco.ut.ee/.
There were 77 formal participants from 19 countries. Additionally, open access to plenary lectures was granted to students and faculty of the University of Tartu, and the Estonian University of Life Sciences.

The concept of the meeting was formulated as follows:

“The symposium aims to bring together evolutionary ecologists and physiologists working on temperature-driven a) plastic and b) evolutionary changes in 1) growth rates and 2) body sizes of various (invertebrate and vertebrate) ectothermic animals. Responses to temperature is a topic in which the interplay of different evolutionary forces (primarily, selection and constraints) is particularly obvious. Interdisciplinary efforts in this field are therefore likely to contribute substantially to an improved and more integrated understanding of evolutionary processes. Furthermore, clarifying conceptual and terminological problems in this field would serve the needs of both theoretical and applied research on thermal adaptation, and beyond.”

The meeting attracted numerous top specialists in the filed worldwide. The programme comprised 36 talks and there were about 25 poster presentations. All the oral presentations and most posters directly contributed to the central theme of the meeting. On the other hand, there was a great diversity in terms of approaches and study objects so there was a great opportunity to extend scientific horizons for all of the participants.

The meeting was successful also in practical terms. All the events happened exactly according the to the time schedule announced beforehand, there was only one last-minute cancellation.

2. Description of the scientific content

A central phenomenon in focus was the so-called **temperature-size rule (TSR)**, i.e. the quite universal pattern that ectothermic animals grow larger under lower temperatures despite of lower juvenile growth rates. The physiology and evolutionary ecology of this rule has received much research attention but the phenomenon as a whole is far from being understood. One of the primary aims of the meeting was to summarize and discuss recent advances in studying TSR.

In his keynote lecture, David Atkinson stated that TSR like other qualitative rules relating phenotypes to environments are probably multi-causal and should be analysed as complex quantitative phenomena. Nevertheless, despite the diverse mechanisms by which temperature can and does influence growth and development, common patterns may reveal mechanistic similarities that explain a high proportion of the variation. Atkinson discussed the progress in search for patterns in the relative responses of growth and development rates to temperature during ontogeny. It has been found the TSR is stronger in adults than in progeny, but that the strength of the response of growth and development to temperature shows no obvious common pattern among species as ontogeny progresses. An alternative approach focuses on how phenotypic limits or boundaries influence the range of possible evolutionary or phenotypic options. This approach places relatively greater emphasis on quantitative prediction of responses than on understanding the many details of individual ecological interactions with temperature. This framework may be useful for advancing a novel theory, and, in particular, clarifying the nature of constraints. This framework advances beyond current metabolic scaling theory by predicting variation in scaling relationships.

In another lecture, Jeffrey Arendt pointed out that reproductive allometry has not been considered in life-history theory in the past because it is usually assumed that organisms will always produce as many offspring as possible, for their body size, resulting in a single size-fecundity relationship. He presented evidence that reproductive allometry could actually be highly variable and provided an example where these differences may explain the temperature-size rule in a snail and an example where it doesn't in an insect. Arendt emphasized the need of good empirical studies to test the high number of hypotheses erected to explain the TSR.

Alexander Shingleton discussed the TSR from the perspective of a developmental biologist. He emphasized that while TSR is ubiquitous, the developmental mechanisms that regulate size with respect to temperature remain almost completely unknown. One explanation for the rule is that the thermal sensitivity of developmental rate is greater than that of growth rate, although the molecular and physiological mechanisms by which temperature affects the rate of growth and development are similarly unknown. He discussed the approaches to elucidate the proximate mechanisms that regulate thermal plasticity, using the fruit fly *Drosophila melanogaster* as the model system. It was shown that different tissues within *Drosophila* have different thermal plasticities and it was argued that such differences may hold the key to explaining the temperature-size rule at the developmental level.

Richard Walters suspected that the arguable ubiquity of the TSR may partly be an artefact caused by unnatural conditions in laboratory environments. In particular, alternative explanations that attempt to invoke developmental constraints must account for both taxonomic exceptions to the rule and the condition-dependence of thermal plasticity in respect to food quality and quantity. He presented further empirical evidence of the condition dependency of the TSR in two unrelated species of dung fly using a genetic experimental design and discuss the potential generality of these results in terms of mathematical and biophysical model predictions.

The adaptive nature of reaction norms of body size in response to temperature cannot be understood without knowing the **fitness profile of body size** itself. While the benefits of large size are typically easy to see, the counterbalancing costs of being large are much more elusive.

Karl Gotthard explained how ecological limitations in the form of realistic thermal conditions are likely to reduce the expected benefit of a larger insect size and thereby be an important factor for explaining why many temperate insects do not evolve to larger sizes. He also discussed how the presence of alternative developmental pathways leading to diapause or direct development in temperate insects may allow adaptive developmental plasticity in life history traits in relation to seasonal variation in thermal conditions. In a much studied organism, the butterfly *Pararge aegeria*, optimal body size is highly dependent on variation in thermal conditions during oviposition. Optimal size is also likely to vary over the flight season: i.e. developmental plasticity allowing the expression of different adult sizes over the season should be favoured by natural selection. This has been shown by exploring the fact that due to phenotypic plasticity, *P. aegeria* has two alternative diapause pathways. In support of the predictions, it was found that individuals destined for reproduction in warmer environment grew larger than individuals that were to reproduce under cooler conditions. The results demonstrate clear life history difference among developmental pathways but also latitudinal variation in the patterns of pathway specific expression of life history traits. This can be interpreted as footprints of differential selection on alternative developmental pathways.

Toomas Tammaru stressed that growth rates of insect larvae are often so high that it is hard to propose selective factors able to prevent the larvae from growing larger. He argued that one possibility to solve this puzzle is to assume constraints on larval growth. However, the concept of constraint used in quantitative genetics appears not to be appropriate here, and a different approach is needed. A way to reveal constraints on the long-term evolution of growth schedules is to find growth invariants, i.e. the features which are common to different species, as well as invariable within each species. It was proposed that, in insects, explicit attention to patterns at the level of particular larval instars is a productive way to achieve progress in this direction. Synthesising results of different case studies, he showed that there are, indeed, some surprisingly invariable patterns which point at constraints on within-instar growth increments. In contrast, reviewing entomological literature suggested that the number of larval instars is frequently variable both among and within insect species so that a fixed number of instars is at least not a universal constraint. Furthermore, an analysis of an empirically based life-history model of a particular insect species was presented. The model was based on empirical data on larval growth curves and mortality rates, the values used were supported by the results of meta-analytic reviews. The model showed that the number of instars could well be considered optimal within the conventional explanatory framework of life history theory. In contrast, explaining within-instar growth patterns of insect larvae appears indeed to require invoking the concept of constraint: there is no 'ecological' explanation for why not to grow little more within each instar.

Proximate mechanisms behind temperature-related body size plasticity in insects were addressed in talks by Joost van den Heuvel, Dmitry Kutcherov, Sergey Balashov, Tiit Teder and Vicencio Oostra. Similar questions had been studied on lizards by Lukas Kratochvil and Zuzana Starostova. Particular exciting aspects of temperature-related phenotypic plasticity were highlighted by Thomas Tully, Laura Härkönen, Franja Pajk, Santiago Salinas, Paula Lehtonen, Erica Leder, Santa Znotina and Andreas Nord.

Large size can only be attained by growing, and **high growth rates** per se may well incur fitness **costs.** The costs and benefits of rapid growth may well depend on temperature.

Focussing on costs of high growth rate, Neil Metcalfe explained that catch-up growth following earlier periods of food restriction may lead to deleterious effects later in life, but it is usually not clear whether these long-term effects are due to the growth acceleration or the earlier poor nutrition that triggered it. Manipulation of growth rates through temperature regimes allows one to separate effects of growth rate from those of nutritional state. Evidence was presented that fish show prolonged compensatory (accelerated) growth after periods of atypically cold temperatures, allowing them to return to a 'normal' size-at-age. Furthermore, results of a recent large-scale experiment were shown in which it was investigated how decelerating as well as accelerating growth trajectories affect subsequent swimming ability, breeding performance and lifespan of sticklebacks. Short periods of altered environmental temperatures (high, intermediate or low) triggered growth compensation in both directions once fish were returned to a common (intermediate) temperature regime. However, those compensating for low temperatures earlier in life (i.e. who then showed an accelerated growth trajectory) had reduced swimming endurance and reproductive investment, faster reproductive senescence and shorter life spans. Moreover, these effects were strongest when the perceived time available for growth compensation prior to breeding was shortest (shown by photoperiod manipulations). In contrast, those fish with a decelerating growth trajectory as a result of exposure to high temperatures early in life showed an improved locomotor and breeding performance and increased lifespan compared to steadily-growing controls. These results clearly demonstrated that temperature, in influencing the shape of the growth trajectory, has diverse and prolonged effects on performance independent from any effect on final adult size.

Robby Stoks addressed analogous questions on the basis of his studies on insect growth. He told that physiological costs of rapid growth may contribute to the observation that organisms typically grow at submaximal rates. Although, it has been hypothesized that faster growing individuals would do worse in dealing with suboptimal temperatures, this type of cost has never been explored empirically. Furthermore, the mechanistic basis of the physiological costs of rapid growth is largely unexplored. He reported results of an experiment in which the larvae of a damselfly from two univoltine northern and two multivoltine southern populations were reared at three temperatures and after emergence given a cold shock. Cold resistance, measured by chill coma recovery times in the adult stage, was lower in the southern populations and this could be explained by their faster larval growth rates. In accordance with their assumed role in cold resistance, Hsp70 levels were lower in the southern populations, and faster growing larvae had lower Hsp70 levels. Yet, individual variation in Hsp70 levels did not explain variation in cold resistance. Evidence was provided for a novel cost of rapid growth: reduced cold resistance. Empirical results indicate that the reduced cold resistance in southern populations of animals that change voltinism along the latitudinal gradient may not entirely be explained by thermal selection per se but also by the costs of time constraint-induced higher growth rates. This also illustrates that stressors imposed in the larval stage may carry over and shape fitness in the adult stage and highlights the importance of physiological costs in the evolution of life-histories at macro-scales.

Fredrik Sundström reported the results of a study in which evolutionary ecology of growth rate could be studied using different selection lines of a fish. In particular, it was shown that genetic variants of coho salmon (wild-type and transgenic for over-production of growth hormone with a daily growth potential about twice that of wild-type) show genotype-by-temperature interactions in their relative development and growth at temperatures ranging from 8 to 18°C. During development (from eyed eggs to hatch), differences in timing increased with decreasing temperature with transgenic fish generally developing faster than wild-type. Transgenic fish generally also grew faster (from first-feeding) than wild-type, but here the difference increased with increased temperature; hence a genotype-temperature interaction across ontogenetic stages. In addition, while wild-type fish appeared to reach a maximum growth rate at around 12°C, transgenic fish continued to growth more rapidly up to at least 16°C. The data showed that a small genetic change can have dramatic effects on temperature responses of animals, and how this can be mediated by changes in hormonal regulation. It was suggested that the slow winter growth of salmon is, at least partly, an adaptation to low availability of food during this season, and that if conditions change (i.e. more food becoming available) these fish would evolve more rapid growth. Ecological relevance of the findings was discussed also taking into account costs of rapid growth, mainly from predation risk.

It is frequently assumed that growth rate is involved in biochemically based trade-offs, including those affecting organism’s immune function. This was discussed in contributed talks by Jenni Prokkola and Inese Kivleniece.

Latitudinal (and other geographic) **variation in body size** and respective thermal reaction norms may be seen as a footprint of temperature-specific natural selection of these traits.

These aspects were critically discussed by Shai Meiri who had studied the effects of body (680 species) and environmental temperatures (mean annual temperature within the range, >4400 species) on a large dataset of lizard species traits, distribution and phylogeny. Surprisingly, the two temperature measures are not correlated - even when activity times are accounted for. A weak, positive, association emerges only when phylogeny is accounted for. Therefore the effects of temperature on body size (Bergmann's Rule) and reproduction using both body and environmental temperatures were tested for. There was no relationship between environmental temperatures and lizard body size, despite a weak positive association of body size with body temperatures. Thus Bergmann's Rule does not hold in. Clutch size decreases with environmental temperatures, as is known in birds (Ashomle's Hypothesis), but this relationship is weak. Age at first breeding decreases and the number of clutches laid annually increases with environmental temperatures, and thus the overall mass of hatchlings produced yearly increases with temperature, even though hatchling size does not. Body temperature is unrelated to any of these traits, except, weakly, to hatchling size.

Latitudinal trends in various traits, and well as genetic basis for the among-population differences were discussed by Miguel Olalla Tarraga, Terezia Horvathova, Dmitry Musolin, Maria Tuomaala, April Hayward, David Berger, Sami Kivelä, Konstantinos Sagonas, Marco Katzenberger and Anu Valtonen.

3. Assessment of the results

The meeting was held as planned, and was successful in all respects. This event brought together scientists who apply very different methods and model systems to approach research questions which have much in common. No doubt, the meeting had a stimulating impact on integrative thinking and establishing new collaborative contacts, i.e. it had a positive impact which can only be evaluated retrospectively.

It is a subjective impression of the organisers that the meeting indicated that there is a great unused potential in the systematic use of the concept of constraint for clarifying and unifying (in a positive sense) creative thinking in evolutionary biology.

4. Final programme

“Thermadapt” science meeting

Evolutionary and plastic responses of animal growth to different temperatures: adaptations and constraints

PROGRAMME

Wednesday, April 27

16.00 – 22.00 Registration desk at hotel London

Thursday, April 28

8.45 – 11.00	Plenary talks (Athena)		
	Welcome		
	David Atkinson (45 min)	A fresh look at relationships between temperature, body size and biological rates	
	Jeff Arendt (45)	Reproductive allometry and the temperature-size rule; being bigger in the cold is adaptive for some, but not all	
11.00 – 11.20	Coffee break		
11.20 – 13.00	**Karl Gotthard** (45)	The evolution of body size and alternative developmental pathways in temperate butterflies	
	Toomas Tammaru (30)	Determination of body size in Lepidoptera: looking for constraints	

13.00 – 14.30	Lunch	
14.30 – 16.30	Session „Insect Plasticity“ (London)	
	Richard Walters	Condition dependency of the temperature-size rule
	David Berger	Does temperature-specific genetic variance for body size and development rate predict population divergence in *Sepsis punctum*?
	Sami Kivelä	Genetic and phenotypic variation in juvenile development in relation to temperature and developmental pathway in a geometrid moth
	Thomas Tully	The shape and genetic variation of thermal reaction norms for growth and maturation in the collembola *Folsomia candida*
	Vincent Foray	Impact of fluctuating thermal conditions on reaction norms in a parasitoid wasp
	Tiit Teder	Sex differences in developmental plasticity
16.30 – 17.00	Coffee break	
17.00 – 19.00	Session „Geography“	
	Miguel Olalla Tárraga	The biogeography of body size in terrestrial vertebrates: linking ecological and evolutionary approaches
	Terezia Horvathova	Geographic and climatic patterns of life history variation in the world's most widespread reptile
	Dmitry Musolin	Some like it hot or Too hot to handle? Range expansion and life-history responses to climate warming of the southern green stink bug *Nezara viridula* (Insecta: Heteroptera: Pentatomidae)
	Maria Tuomaala	Latitudinal variation in wing melanisation in the green veined white butterfly (*Pieris napi*): role for adaptation to cold?
	April Hayward	Latitudinal variation in the temperature-dependence of ecosystem respiration rate
	Anu Valtonen	Are northern populations more sensitive to temperatures than southern populations?
19.00	Unguided foraging in the town	

Friday, April 29

9.00 – 10.20	Session “Plasticity II” (London)	
	Lukáš Kratochvíl	Development, proximate control and phenotypic plasticity of sexual size dimorphism in the tropical lizard *Paroedura picta* (Squamata: Gekkonidae)

	Joost Van den Heuvel	The predictive adaptive response: modeling the life history of *Bicyclus anynana*
	Sergey Balashov	Growth rate as a determinant factor for development time in insects
	Laura Härkönen	Seasonal variation in offspring size and cold tolerance of a viviparous ectoparasite – A battle between the host and the parasite
10.20 – 10.40	Coffee break	
10.40 – 12.00	**Franja Pajk**	Intergenerational temperature change and its effect on growth and fitness of a key freshwater herbivore *Daphnia* – interaction with food quality
	Santiago Salinas	Thermal transgenerational plasticity in sheepshead minnows
	Paula Lehtonen	Identifying transcriptional networks involved in thermal stress in the threespine stickleback
	Erica Leder	Inheritance of expression in response to thermal stress in threespine stickleback
12.00 - 13.15	**Poster session**	
13.15 – 14.30	Lunch	
14.30 – 18.30	Excursion to see an open air experiment on global warming, informal open-air discussions	
19.00	Unguided foraging in the town	

Saturday, April 30

9.00 – 11.00	Plenary talks (Athena)	
	Alexander Shingleton (45)	The thermal regulation of body and organ size: a developmental perspective
	Neil Metcalfe (45)	Long–term fitness consequences of temperature-induced changes in growth trajectory in fish
11.00 – 11.20	Coffee break	
11.20 – 13.00	**Shai Meiri** (45)	What kind of thermal regime does lizard evolve to meet?
	Robby Stoks (30)	A role for physiological constraints in the latitudinal differentiation of thermal growth reaction norms?
13.00 – 14.30	Lunch	

14.30 – 16.30	Session „Physiology“		
	(London)		
	Dmitry Kutcherov	Photoperiodic control of thermal plasticity for development rate in insects	
	Vicencio Oostra	Developmental and hormonal mechanisms underlying temperature-induced seasonal plasticity in life history strategies	
	Jenni Prokkola	Gene-by-environment interactions and phenotypic effects of temperature on immune defense and life-history traits in *Tenebrio molitor*	
	Santa Znotina	Consistent individual differences and their thermal regulation in anti-predator behaviour in mealworm beetles *Tenebrio molitor*	
	Inese Kivleniece	Temperature mediated trade-off between encapsulation response and attractiveness in male mealworm beetles *Tenebrio molitor*	
	Andreas Nord	Patterns, processes and functional explanations in avian thermoregulation during winter	
16.30 – 18.00	Coffee and looking around		
18.00 – 19.20	Session „Vertebrate“		
	Zuzana Starostová	Temperature-induced phenotypic plasticity in growth and body size in the gecko *Paroedura picta*	
	Konstantinos Sagonas	Does body size affect thermal biology? The case of an endemic lizard in Skyros Archipelago (East Mediterranean, Greece).	
	Marco Katzenberger	So, which is the optimum temperature for an amphibian? Comparing optimum temperatures across life-traits and life-stages	
	Fredrik Sundström	Different reaction norms in development and growth at different temperatures in two genetic variants of coho salmon	

20.00	Dinner at London	
night	student celebrations (Walpurgis night)	observe, join or ignore (if possible) http://en.wikipedia.org/wiki/Walpurgis_Night
22.30	light performance	

Sunday, May 01

Dispersal

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5. Clarifications to the financial report

Accommodation includes, in addition to direct accommodation costs, also the rent paid for lecture halls and poster boards, and some related minor costs, i.e. all costs directly related to creating the appropriate infrastructure.

Meals include taxes (a minor amount) which are, according to Estonian law, applicable to covering catering costs of employees of the University of Tartu, i.e. the organisation formally covering the costs.

Travel includes**,** in addition to long-distance travel of the participants, also transportation during an excursion to a fieldwork site (open-air climate warming experiment, of direct relevance to the topic of the meeting).

Local administrative costs consist of printing the abstract book (EUR 492), and salary paid to people involved in organising the meeting (EUR 2126.35). The total, EUR 2618.35 slightly exceeds the permitted 10% of the budget. The problem arose because the organisers were unaware that costs of printing the abstract book should be indicated as “local administrative costs”.