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Evolution of Thermal Reaction Norms for Growth Rate and Body Size in Ectotherms: An Introduction to the Symposium[1]

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Although the size of an organism is influenced by many features of its environment, the relationship between temperature and body size has captivated generations of biologists. From the renowned observations by Bergmann (1847) to the phylogenetic comparative studies by our contemporaries (*e.g.*, Ashton *et al.*, 2000), evidence of a widespread relationship between temperature and adult body size has been offered repeatedly for various groups of animals. This relationship, which has come to be known as Bergmann's rule, is an increase in the body size of a species with a decrease in environmental temperature. Bergmann's rule was inspired initially by endotherms, but numerous species of ectotherms also exhibit Bergmann's clines in body size (de Queiroz and Ashton, 2004). Furthermore, lab studies have shown that a higher temperature during ontogeny generally results in a smaller size at maturity (Atkinson, 1994, 1995). This thermal plasticity of size could be one of the most taxonomically widespread patterns of phenotypic variation, having been observed in bacteria, protists, plants and animals. Moreover, the correspondence between trends in artificial and natural environments suggests that thermal plasticity causes some of the geographic variation in body size within ectothermic species.

Both proximate and ultimate explanations for temperature-size relationships have been proposed, debated, rejected and revised (Berrigan and Charnov, 1994; Sibly and Atkinson, 1994; Perrin, 1995; Sevenster, 1995; Atkinson, 1996; Atkinson and Sibly, 1996; van der Have and de Jong, 1996: Van Voorhies, 1996; Partridge and Coyne, 1997; Angilletta and Dunham, 2003; reviewed by Atkinson and Sibly, 1997). Still, there is little consensus on the key mechanisms that are responsible these relationships. For example, Van Voorhies (1996) proposed that Bergmann's clines were caused by increasing cell size with decreasing developmental temperature, but Partridge and Coyne (1997) pointed out that larger bodies are not necessarily achieved by having larger cells. Attempts to secure an ultimate explanation for temperature-size relationships have met with similar difficulties; indeed, few models of life-history evolution predict relatively large sizes at maturity in environments that retard growth, such as cold environments (Berrigan and Charnov, 1994).

One of the major limitations of current models is the manner in which they treat the thermal plasticity of growth rate. Optimization models that predict larger body sizes in colder environments do so because they impose unrealistic constraints on growth (Angilletta and Dunham, 2003). Yet, recent studies of diverse animals have shown that reactions norms for growth rate can evolve rapidly along thermal clines. When reared under common environmental conditions, individuals from colder environments often grow faster than their conspecifics from warmer environments (reviewed by Arendt, 1997; Angilletta *et al.*, 2002). Such studies have led to a synthesis of ideas concerning the evolution of co-gradient and counter-gradient variations in growth rate (see Conover and Schultz, 1995). Because growth rate has major ramifications for adult body size, efforts to understand temperature-size relationships would benefit greatly from an explicit consideration of the evolution of growth rate.

Given the complex of behavioral and physiological processes that determines growth rate and body size, no single mechanism is likely to prevail as a general explanation for temperature-size relationships. Rather, we believe the mechanisms that underlie the evolution of thermal plasticity will be complex, and more progress will be made through the collective study of numerous model systems. To this end, we brought together researchers who have studied different taxonomic groups, sought different levels of explanation (proximate *vs.* ultimate), and adopted different approaches to achieve these explanations. Our goals were to discuss the validity of temperature-size relationships, the proximate and ultimate mechanisms underlying these relationships, and the theoretical and empirical problems that remain to be solved. Among the questions that were addressed, three stand out as particularly important:

1. How diverse are temperature-size relationships in ectothermic animals, and what general patterns (if any) are evident within major taxonomic groups?
2. Why does the thermal sensitivity of growth rate evolve differently among closely related species (*i.e.*, co-gradient *vs.* counter-gradient variation in growth rate)?
3. To what extent can the mechanisms that produce relationships among temperature, growth rate, and body size in well-studied species be generalized to other species?

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Although other symposia have addressed issues concerning thermal adaptation, our symposium is the first to focus on the evolution of thermal reaction norms for life-history phenotypes. In 1995, Ian Johnston and Albert Bennett organized a symposium titled *Phenotypic and Evolutionary Adaptation to Temperature*, which was sponsored by the Society for Experimental Biology. Their symposium brought together a group of illustrious researchers whose interests ranged from the biochemical level to the organismal level (see Johnston and Bennett, 1996). Several participants in this symposium, including David Atkinson and Linda Partridge, addressed the thermal adaptation of life-history; their contributions further defined the proximate mechanisms for temperature-size relationships and consolidated the potential explanations for their evolution. Building on the success of this symposium, the Society for Experimental Biology sponsored a second one titled *Temperature and Development*, which resulted in further discussion of thermal plasticity of life-history phenotypes (see Atkinson and Thorndyke, 2001). Both of these symposia contributed to the growing interest in thermal reaction norms for growth rate and body size, but neither was focused directly on these phenomena. Thus, our symposium was the first to unite researchers using diverse approaches to understand the evolution of thermal plasticity of life-history phenotypes. The result was an intense and rewarding exchange of ideas that is evident from the papers in this volume.

The eleven papers that follow provide complementary perspectives on the major themes of the symposium: (1) Ashton (p. 403), and Blanckenhorn and Demont (p. 413) outline the diversity and generality of temperature-size relationships in tetrapods and arthropods, respectively; (2) Bayne (p. 425), Davidowitz and Nijhout (p. 443), and Sears and Angilletta (p. 433) discuss the proximate mechanisms by which temperature affects growth rate and body size in various ectotherms; (3) Kingsolver *et al.* (p. 450) provide a broad overview of natural selection of growth rate and body size, whereas Gilchrist and Huey (p. 461), and Gotthard (p. 471) examine evolutionary explanations in certain insects. Finally, Charnov and Gillooly (p. 494), Kozłowski *et al.* (p. 480), and Angilletta *et al.* (p. 498) offer theoretical perspectives on the evolution of temperature-size relationships. We hope these papers will fuel continued interest in the puzzling patterns of thermal plasticity and guide future efforts to reveal their causes.

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REFERENCES

Angilletta, M. J. and A. E. Dunham. 2003. The temperature-size rule in ectotherms: Simple evolutionary explanations may not be general. Am. Natur. 162:332–342.
Angilletta, M. J., P. H. Niewiarowski, and C. A. Navas. 2002. The evolution of thermal physiology in ectotherms. J. Therm. Biol. 27:249–268.
Arendt, J. D. 1997. Adaptive growth rates: An integration across taxa. Quart. Rev. Biol. 72:149–177.
Ashton, K. G., M. C. Tracy, and A. de Queiroz. 2000. Is Bergmann's rule valid for mammals? Am. Natur. 156:390–415.
Atkinson, D. 1994. Temperature and organism size—a biological law for ectotherms? Advances in Ecol. Res. 25:1–58.
Atkinson, D. 1995. Effects of temperature on the size of aquatic ectotherms: Exceptions to the general rule. J. Therm. Biol. 20: 61–74.
Atkinson, D. 1996. Ectotherm life history responses to developmental temperature. *In* I. A. Johnston and A. F. Bennett, (eds.), *Animals and temperature: Phenotypic and evolutionary adaptation*, Pp. 183–204. Cambridge University Press, Cambridge.
Atkinson, D. and R. M. Sibly. 1996. On the solution to a major life-history puzzle. Oikos 77:359–364.
Atkinson, D. and R. M. Sibly. 1997. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. Trends Ecol. Evol. 12:235–239.
Atkinson, D. and M. Thorndyke. 2001. *Environment and animal development: Genes, life histories and plasticity.* BIOS Scientific Publishers, Oxford.
Bergmann, C. 1847. Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Gottinger Studien 3:595–708.
Berrigan, D. and E. L. Charnov. 1994. Reaction norms for age and size at maturity in response to temperature: A puzzle for life historians. Oikos 70:474–478.
Conover, D. O. and E. T. Schultz. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. Trends Ecol. Evol. 10:248–252.
de Queiroz, A. and K. G. Ashton. 2004. The phylogeny of a species-level tendency: Species heritability and possible deep origins of Bergmann's rule in tetrapods. Evolution 58:1674–1684.
Johnston, I. A. and A. F. Bennett. 1996. *Animals and temperature: Phenotypic and evolutionary adaptation.* Cambridge University Press, Cambridge.
Partridge, L. and J. A. Coyne. 1997. Bergmann's rule in ectotherms: Is it adaptive? Evolution 51:632–635.
Perrin, N. 1995. About Berrigan and Charnov's life history puzzle. Oikos 73:137–139.
Sibly, R. M. and D. Atkinson. 1994. How rearing temperature affects optimal adult size in ectotherms. Funct. Ecol. 8:486–493.
Sevenster, J. G. 1995. Equations or organisms? A comment on Berrigan and Charnov. Oikos 73:405–407.
van der Have, T. M. and G. de Jong. 1996. Adult size in ectotherms: Temperature effects on growth and differentiation. J. Theor. Biol. 183:329–340.
Van Voorhies, W. A. 1996. Bergmann size clines: A simple explanation for their occurrence in ectotherms. Evolution 50:1259–1264.