Focal Symposium: *Limits of Adaptation*

29 April 2010
4:00-7:00 p.m.
Hörsaal 1, UZA 1
Biozentrum
Althanstrasse 9, Wien IX.

Nicholas Barton *IST Austria, Klosterneuburg*

Tim Lewens *University of Cambridge*

Russell Powell *University of Oxford*

Gregory Radick *Leeds University*

Program

Konrad Lorenz Institute for Evolution and Cognition Research
and
Department of Theoretical Biology, University of Vienna

Limits of adaptation

Can natural selection explain all aspects of biological evolution? Charles DARWIN himself famously didn't think so. For instance, he invoked "disuse" as the main explanation of the degradation of rudimentary organs, and (as Gregory RADICK will discuss in his contribution to this symposium) he thought of the expression of emotions as non-adaptive ancestral legacies rather than adaptations honed by natural selection.

In the early decades of the 20th century, natural selection and adaptation were often treated "almost apologetically" (Van Valen 2009: 267), to the point that speciation was often seen as a non-adaptive process. Not until the late 1930s and '40s, when convincing evidence for the importance of selection had accumulated, did adaptation become a central focus in evolutionary studies. (In the 1950s, Theodosius DOBZHANSKY had a framed dime on his office wall at Columbia University, the payoff from a bet with Sewall WRIGHT that the polymorphism of chromosomal inversions in *Drosophila pseudo-obscura* was maintained by natural selection.) Dismissing genetic drift as an important evolutionary force, the Modern Synthesis (synthetic theory of evolution) adhered to a strictly adaptationist account of evolution. Adaptation-ism "hardened" along with the Synthesis (Stephen Jay GOULD) in the 1950s, reaching its apex in the late 1970s in "pop" sociobiology and "pan-selectionist" molecular biology. Through the popular scientific writings of Richard DAWKINS, in particular, this "old" adaptationism (Rose and Lauder 1996) conquered the general media, where it lives on in daily announce-ments of the discovery of yet another gene "for" this or that trait.

Adaptationism came under serious attack toward the end of the 1960s, when George C. WILLIAMS in his *Adaptation and Natural Selection* (1966) criticized vague invocations of group or species selection (which charac-terized, for instance, the ethology of Vero Copner WYNNE-EDWARDS and Konrad LORENZ), proposals on optimization for which their seemed to be no viable mechanism, and other infirmities of adaptationist reasoning (Rose and Lauder 1996; Van Valen 2009). Simultaneously, Richard LEWONTIN's work on population genetics and electrophoresis (e.g., Lewontin and Hubby 1966) began to lay bare considerable amounts of evolutionary differentiation between species *and* great genetic variation within populations—two sorts of evidence that could not be plausibly explained in purely selectionist terms. Robust two-locus theory (e.g., Karlin and Feldman 1970) revealed that epi-stasis and linkage disequilibrium could undermine the "hill-climbing" effect of natural selection on mean fitness that had been assumed by both Ronald FISHER and Sewall WRIGHT. Rose and Lauder (1996), Pigliucci and Kaplan (2000), Lynch (2007), and Rose and Oakley (2007) discuss several more obstacles to the adaptationist stance.

Concern about the limits of adaptationist explanation was further fueled by GOULD's and LEWONTIN's 1979 influential paper, "The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist pro-gramme," which discredited "the glib style of reasoning about adaptation" (Rose and Lauder 1996: 1) that had become mainstream in post-World War II evolutionary biology (see also Selzer 1993; Pigliucci and Kaplan 2000). GOULD and LEWONTIN criticized adaptationism as an unscientific attitude that views all traits of organisms *a priori* as optimal "solutions" produced by natural selection, specifically for current function. They stressed instead the importance of the *contingencies of history*—structural or developmental constraints as studied in current evolutionary developmental biology ("Evo-Devo"), drift, gene flow, etc. (Ahouse 1998; Beatty and Desjardins 2009). They also questioned the validity of the tendency of many adaptationists to eagerly replace one failed "just-so story" by the next one, giving raise to a de-bate about the proper *methodological* framework to study adaptation (see, e.g., Orzack and Sober 2001; Stegmann 2005; Lewens 2007).

What does "post-spandrel" adaptationism look like? Michael ROSE and George LAUDER (1996) discern three trends:

(1) A variety of technical improvements on the "old" adaptationism, such as the more formal use of phylogenies and the sustained inference of the ac-tion of selection from DNA sequences "have not so much changed its direction as strengthened its force" (p. 4). Moreover, while evolutionary biologists distanced themselves from adaptation(ism) during the 1980s, scientists from other fields as well as engineers, working, for instance, in artificial intelligence or automated design, have begun to embrace it ("gen-etic algorithms").

(2) Recent studies of natural selection in the wild represent a striking advance over previous work.

(3) Disciplines such as comparative morphology and biomechanics, which in the past relied frequently but often gratuitously on the concept of adap-tation, have greatly restricted their inferences of adaptation, focusing instead on what they do best.

A serious new challenge for adaptationism comes from EvoDevo; it relates to the remarkable conservatism that is increasingly found in the "developmental-genetic toolkit" (Carroll et al. 2001) across all animal phylo-geny. Such conservation is profoundly paradoxical from the Synthesis perspective (Newman 2006). Other challenges come from comparative genomics and systems biology. Thus, according to Koonin (2009: 1011), "evolutionary-genomic studies show that natural selection is only one of the forces that shape genome evolution and is not quantitatively dominant, whereas non-adaptive processes are much more prominent than previously suspected." Debate over empirical, conceptual, methodological, and other aspects of adaptation will continue, but at a "higher level"—or so one may hope.

The main aim of the symposium is to assess the ongoing debate over the limitations of adaptationist thinking, broadly speaking—including the varieties of adaptationism, its relation to optimization approaches, and its testability—from scientific, historical, and philosophical perspectives.

References

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Lynch M (2007) The frailty of adaptive hypotheses for the origins of organismal com-plexity. PNAS 104, Suppl. 1: 8597-8604.

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Werner Callebaut
Scientific Manager

Gerd B. Müller
Chairman

Limits of Adaptation

Schedule

4:00 p.m.	*Opening* **Gerd B. Müller**, Chairman, KLI
4:05 p.m.	*Lorenz, Darwin, and the Limits of Adaptation* **Gregory Radick**
4:30 p.m.	*Justifying Adaptationism: The Case of EvoDevo* **Tim Lewens**
4:55 p.m.	*Convergent Evolution and the Limits of Natural Selection* **Russell Powell**
5:20 p.m.	*Genetic Limits to Adaptation* **Nicholas Barton**
5:45 p.m.	Coffee break
6:00 p.m.	*Round table discussion among the speakers* **Werner Callebaut**, Moderator
6:20 p.m.	*Open discussion*
7:00 p.m.	*End*

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Lorenz, Darwin and the Limits of Adaptation

It is famously hard to prove a negative. But that hasn't stopped evolutionists, from Charles DARWIN's day forward, from arguing that certain traits are "non-adaptive." In his book, *The Expression of the Emotions in Man and Animals* (1872), DARWIN set out a thorough case for emotional expressions as non-adaptive ancestral legacies, rather than adapations honed by natural selection. A well-known modern edition of the book carried a preface by Konrad LORENZ, who is credited with the revival of interest in the 20th century in the biological study of instinctive behaviour. And LORENZ too, in his classic papers of the 1930s, sought to analyse the form of animal signals as clues to ancestral relationships rather than adapative-environmental ones. For both men, but for quite different reasons, behavioural traits came to be prized precisely to the extent that they resisted characterization as adaptive. And for both, later science has returned rather different verdicts—verdicts, moreover, which help us appreciate anew the power as well as the limits of adaptationist thinking.

Biographical note

Gregory RADICK is Senior Lecturer in History and Philosophy of Science (HPS) at the University of Leeds. His main area of research is the history of biology and the human sciences since the 18th century, although he has also published on the philosophy of science (especially biology), the philos-ophy of history, and social and ethical issues surrounding the new genetic/ genomic technologies.

His particular interests include: animal mind, language and behaviour; Darwinism and its contexts; Mendelism and its rivals; the epistemology of scientific instruments; intellectual property in the sciences; the relations between genetics and eugenics; and the theory and practice of counterfactual history.

He is Reviews Editor of the *British Journal for the History of Science* (BJHS) and a Council member of the International Society for the History, Philosophy, and Social Studies of Biology. Awards and honors include the Singer Prize of the BSHS; the Charles and Katharine Darwin Research Fellowship at

Darwin College, Cambridge University; a Leverhulme Trust Research Fellowship; and grants from the British Academy, the Royal Society, the Templeton Foundation and the Arts and Humanities Research Council.

Selected Publications

Dixon M, Radick G (2009) Darwin in Ilkley. Stroud: History Press.

Hodge J, Radick G, eds (2009) The Cambridge Companion to Darwin. 2nd ed. Cam-bridge UP.

Radick G (2008) "Race and language in the Darwinian tradition (and what Darwin's language-species parallels have to do with it)." Studies in History and Philosophy of Biological and Biomedical Sciences 39: 359-370.

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Tim Lewens

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Justifying Adaptationism: The Case of EvoDevo

It is hard to justify adaptationism if we view it as a hypothesis. It is easier to justify it if we view it as a heuristic. This much is familiar. But which heu-ristic? Adaptationism invites us to ask not just how canonical phenotypic traits may have been favoured by natural selection, but how systems of inheritance and development may have been so favoured. In this way, adaptationism opens up for question many features of the biological world that other programmes may take for granted. But even this way of justifying adaptationism has significant limitations.

Biographical note

Tim LEWENS is Lecturer in the Department of History and Philosophy of Science at the University of Cambridge. His book, *Organisms and Artefacts* (2004), examines the language and arguments for design in biology and philosophy. In an interview with Paul WHITE of the Darwin Correspondence Project (available at http://www.darwinproject.ac.uk/interview-with-tim-lewens), Dr. LEWENS discusses the role of DARWIN in modern science, the arguments for intelligent design in nature, the implications of evolution for religious belief, and the importance of a historical understanding of DARWIN's work.

Selected publications

Lewens T (2009) Innovation and population. In: Functions in Biological and Artificial Worlds: Comparative Philosophical Perspectives (Krohs U, Kroes P, eds), 243-257. MIT Press.

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Convergent Evolution and the Limits of Natural Selection

DARWIN tended to downplay the importance of convergent evolution, or the independent origination of similar biological forms, in part because it raised complications for the inference of common descent. In recent years, however, convergent evolution ('homoplasy') has been making a comeback of sorts, figuring prominently into some philosophical and biological argu-ments for strong versions of the adaptationism thesis. Pervasive homoplasy is thought to support the claim that the evolution of organismic form is highly constrained externally and only weakly constrained developmentally. As a consequence, homoplasy is often interpreted as demonstrating the power of natural selection to overcome internal constraints, and in turn as contra-dicting Stephen Jay GOULD's argument for the radical contingency of complex life. However, recent work in evolutionary development is calling this interpretation into question, and underscoring the need for a more re-fined definition of homoplasy.

Biographical note

Russell POWELL is an Arts & Humanities Research Council fellow at the Oxford Uehiro Centre for Practical Ethics, a research associate in the Program on Ethics of the New Biosciences and the Centre for Neuroethics, and a research member at Wolfson College, all at Oxford University. He studied philosophy at SUNY Binghamton (BA, 1999) and Duke University (PhD, 2008), law at New York University Law School (JD, 2002), and biology at Duke University (MS, 2005). In his dissertation, *Reading the Book of Life: Contingency and Convergence in Macroevolution* (supervisor: Alexander ROSENBERG), he explored the nature of macroevolutionary contingency in the context of the question, "Is the shape of life the result of predictable optimizing processes, or does it represent the fluky culmination of an eminently unrepeatable series of contingencies that took place early in the history of life?" He examined and related the concepts of contingency, convergence, and homology in macroevolution, with a focus on the GOULD-CONWAY MORRIS debate about the replicable nature of metazoan (animal) evolution. Before moving to Oxford, he worked at Georgetown University and Johns Hopkins University.

Selected publications

Powell R, Clarke S (under preparation) Is religion an adaptation or a by-product?

Powell R (under review) The future of human evolution.

Powell R, Buchanan A (forthcoming) Breaking evolution's chains: The prospect of deliberate genetic modification in humans. Journal of Medicine and Philosophy.

Powell R (forthcoming) What's the harm? An Evolutionary theoretical critique of the precautionary principle. Kennedy Institute of Ethics Journal 20(1).

Powell R (2010) The evolutionary biological implications of human genetic en-gineering. Journal of Medicine and Philosophy.

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Genetic Limits to Adaptation

Abstract

Natural selection is the only process that causes the systematic evolution of adaptations—devices that aid survival and reproduction. It has been difficult to set limits to the rate of adaptation. KIMURA showed that HALDANE's "cost of selection" corresponds to a limit on the rate at which selection can accumulate information. However, that limit is relaxed by certain kinds of gene interaction. A more robust limit is set by the rate of recombination, which brings together favourable mutations. High rates of recombination may be maintained as an adaptation to facilitate faster adaptation.

Biographical note

Nicholas Hamilton BARTON was the first professor to join the newly founded Institute of Science and Technology (IST) Austria in Klosterneuburg in 2008. He graduated from the University of Cambridge with a first-class degree in Natural Sciences in 1976 and gained his PhD at the University of East Anglia (supervisor: Godfrey HEWITT) in 1979. He became a Lecturer in the Department of Genetics and Biometry at University College London in 1982. Prof. BARTON is mostly known for his work on hybrid zones, often using the toad *Bombina bombina* as a model organism, and for extending the mathematical machinery needed to investigate multilocus genetics. Specifically, he has investigated epistasis, the evolution of sex, speciation, and the limits on the rate of adaptation, which he will address in his contribution to the symposium.

BARTON moved to the University of Edinburgh in 1990, where he contributed to implementing the university's strong tradition in quantitative and popu-lation genetics, making Edinburgh one of the foremost research institutions of genetics in the world. He became a professor in 1994. He is a Fellow of the Royal Society in London and of the Royal Society of Edinburgh. He re-ceived a Wolfson Merit Award in 2005. In the Darwin Year 2009, Barton received the Darwin-Wallace Medal by the Linnean Society. The medal is considered to be the most prestigious award in the field of evolutionary biol-ogy. Until now, it has been awarded only every 50 years, beginning in 1908, to commemorate the joint presentation by Charles DARWIN and Alfred Russel WALLACE of their

two famous papers on the evolution of species in 1858. In 2007, BARTON, along with Derek BRIGGS, Jonathan EISEN, David GOLDSTEIN, and Nipam PATEL, produced *Evolution,* an undergraduate text-book that integrates molecular biology, genomics, and human genetics with traditional evolutionary studies.

At the IST, the BARTON group studies diverse topics in evolutionary genetics, focusing on the evolution of populations that are distributed through space and experience natural selection on many genes. The recent development of techniques for assaying large numbers of genetic markers, and indeed complete sequences, make analysis of the interactions amongst large numbers of genes essential.

Selected publications of the Barton Group

Bridle J, Polechová J, Kawata M, Butlin R (in press) Why is adaptation prevented at ecological margins? New insights from individual-based simulations. Ecology Letters.

Polechova J., Barton NH, Marion G (2009) Species range: Adaptation in space and time. American Naturalist 174: E186-204.

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Free A, Barton NH (2007) Do evolution and ecology need the Gaia hypothesis? TREE 22: 611-619.

Kirkpatrick M, Barton N (2006) Chromosome inversions, local adaptation, and speciation. Genetics 173: 419-434.

Roze D, Barton NH (2006) The Hill-Robertson effect and the evolution of recombination. Genetics 173: 1793-1811.

Location and time

The focal symposium is held in **Hörsaal 1, UZA 1**, Biozentrum, Althanstrasse 9, Wien IX., on **Thursday 29 April, 4:00-7:00 p.m.**

A follow-up discussion with the speakers takes place at the Konrad Lorenz Institute for Evolution and Cognition Research (**KLI**), Adolf-Lorenz-Gasse 2, 3422 Altenberg, **the next day, 4:15-6:00 p.m.**

The KLI can easily be reached by train: The S40 (in the direction of Tulln) leaves Wien Franz-Josefs-Bahnhof at **2.56** and **3.32** p.m. The ride to Greifenstein/Altenberg takes 28 minutes. Upon leaving the station, take a right turn and walk for about 8 minutes until you reach a wooden chapel. At that crossing, the KLI, which is located in the Lorenz mansion, can be seen across the street.

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