Biol Philos (2009) 24:155–159
DOI 10.1007/s10539-008-9150-x

Introduction: A Primer on Adaptationism

Patrick Forber

Received: 1 December 2008 / Accepted: 1 December 2008 / Published online: 23 December 2008

Thirty years ago Stephen Jay Gould and Richard Lewontin published a article called "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme." This article initiated the debate over the fate of *adaptationism*. While the prevalence and exact nature of adaptationism were not immediately clear in 1979, the target of Gould and Lewontin's critique was: the practice of accepting adaptation hypotheses too quickly based on little or no evidence. The critique generated a discussion of lasting influence, a discussion still relevant to both evolutionary biology and philosophy. Indeed, the reach of the *Spandrels* article is such that Rose and Lauder (1996, pp. 1–8) claim that one task of contemporary evolutionary biology is to articulate a viable "post-spandrels adaptationism." This special issue commemorates both the seminal article and the literature it inspired. The contributions here provide extensions and elaborations of many threads woven into this complex debate. There is little chance of successfully summarizing all complicated contours of the *Spandrels* literature in sufficient detail. Instead, I will briefly provide my take on why the article enjoys lasting relevance, and attempt to locate the contributions in the conceptual landscape.

The explanation for the *Spandrels* phenomenon rests on four features of the critique. First, the article attempts to identify and make explicit a coherent program of research in evolutionary biology with the goal of criticizing and reforming the practices of the program. Second, as the title makes clear, the *Spandrels* article uses rich cultural metaphors to inform our perspective on biological science. Third, the critique targets a specific and central sort of inference—inferring evolutionary origin from current utility—and the often lax evidential standards taken to warrant the inference. And fourth, the article argues for the evolutionary significance of development and constraint.

P. Forber (✉)
Philosophy Department, Tufts University, Miner Hall, Medford, MA 02155, USA
e-mail: Patrick.Forber@tufts.edu

The attempt to identify the “adaptationist programme” in evolutionary biology raised a deep conceptual question: what exactly *is* adaptationism? Philosophical analysis, due largely to Amundson (1988), Sober (1987, 1996) and Godfrey-Smith (2001), distinguishes three adaptationist theses. The first treats adaptationism as an *empirical* hypothesis about the frequency and power of natural selection—selection is ubiquitous, relatively free from constraints, and provides a sufficient explanation for the evolution of most traits. A second sees adaptationism as a *methodological* thesis—looking first for adaptation is a useful research strategy, even if adaptations tend to be rare. The third takes adaptationism to be an *explanatory* claim about the primacy of natural selection—explaining apparent design is the central problem for evolutionary biology and cumulative selection provides the only satisfactory answer. Lewens (this volume) continues this philosophical analysis, increasing the family of adaptationist theses to seven.

The philosophical analysis structures and clarifies much of the debate. Mayr defends a methodological version of adaptationism, arguing that biologists should explore selection hypotheses first because they are easier to test (Mayr 1983, p. 326). Dawkins (1986) and Dennett (1995) articulate versions of explanatory adaptationism (Godfrey-Smith 2001, pp. 339–340). For them, the importance of natural selection rests on its ability to explain adaptive complexity. Orzack and Sober’s proposed test of adaptationism engages the empirical thesis about the power and frequency of natural selection across the biological realm. Empirical adaptationism is true just in case natural selection provides a “sufficient explanation” of most phenotypic traits (Orzack and Sober 1994, p. 364).

Identifying the different theses of adaptationism raises two further lines of theoretical inquiry, the first on the relationship between adaptationism and optimality modeling, and the second on the possible coexistence and synthesis of adaptationist theses. The first line of inquiry has received significant attention (see, e.g., Dupré 1987; Orzack and Sober 2001). Orzack and Sober explicitly connect optimality models to their test of empirical adaptationism. Natural selection provides a sufficient explanation when a “censored” model fits the data in a precise quantitative way, and optimality models are the primary examples of censored models (Orzack and Sober 1994, p. 363). This coheres with the *Spandrels* article, which implicates optimization in the standard adaptationist method (Gould and Lewontin 1979, p. 585). But it could be possible, and even desirable, to disentangle the fate of optimality modeling from the fate of adaptationism, for optimality models play a central role in ecology and evolutionary biology (see, e.g., Roughgarden 1998). In response to the Orzack-Sober test, Brandon and Rausher (1996, p. 192) argue that the optimality of a trait and its history of selection are logically and biologically distinct ideas. Although Orzack and Sober (1996, p. 204) grant the logical point, they reply that optimality and selection are clearly related biologically. Potochnik (this volume) continues this investigation and defends the relative independence of optimality modeling.

Along the other line of inquiry, Godfrey-Smith (2001) argues that empirical, methodological, and explanatory adaptationism are logically independent theses, and this increases the family of adaptationist (and anti-adaptationist) positions. However, there are complex connections of support between the three views; not all possible combinations are natural packages. For example, the truth of empirical adaptationism provides some support for both the explanatory and methodological theses. Part of the adaptationism debate concerns the conceptual connections between the different theses. Yet an even larger part of the debate concerns the truth of adaptationism, and in this respect perhaps it may be possible to reconcile adaptationist and anti-adaptationist views into a respectable synthetic view. Wilkins and Godfrey-Smith (this volume) follow up an idea in Godfrey-Smith and Wilkins (2008), and use "zoom" and "grain of resolution" on adaptive landscapes as part of a strategy to provide such a reconciliation.

The use of cultural metaphors to inform our perspective on biological science is the second feature of that contributes to the *Spandrels* lasting influence. Gould and Lewontin (1979, p. 584) chose examples from architecture and anthropology so that "the primacy of architectural constraint and the epiphenomenal nature of adaptation are not obscured by our biological prejudices." This exchange between culture and biology has a deep history and runs in both directions. To mention just one instance, in an analysis of punishment Nietzsche emphasizes the difference between current utility and origin, and uses biological examples to support his point (see esp. *GM* II 12), a connection Gould (2002, pp. 1214–1218) later endorsed enthusiastically. Perhaps some of the best evidence for the effectiveness of the exchange is that the architectural metaphor in the *Spandrels* article has influenced current biological terminology. A trait that is a byproduct of developmental, physical, or phyletic constraints is often called a "spandrel." Yet, as with any analogy between biology and culture or between organism and artifact, we can question the strength and usefulness of the connection. Houston (this volume) addresses this issue, arguing for a different perspective on the analogy between architecture and biology.

A third enduring feature of the critique is the focus on the nature of historical inference in evolutionary biology, and the evidence necessary to support such inferences. The *Spandrels* article specifically targets the evidential connection between the optimal utility of a trait for its current function and the historical hypothesis that the trait evolved by natural selection for that function: "One must not confuse the fact that a structure is used in some way (consider again the spandrels, ceiling spaces and Aztec bodies) with the primary evolutionary reason for its existence and conformation" (Gould and Lewontin 1979, p. 587). The existence of other biological factors in the evolutionary process confounds the historical inference from optimal current utility to origination due to direct selection. This focused criticism led to innovations in testing hypotheses of adaptation, including the incorporation of comparative methods and molecular data (Harvey and Pagel 1991; Rose and Lauder 1996; Orr, 2005). Two contributions continue the rich discussion on historical inference. Beatty and Desjardins (this volume), drawing upon additional work by both Gould and Lewontin, provide careful accounts of when and why history matters for each biologist. Forber (this volume) uses the problem of evidence found in the *Spandrels* article to construct a general strategy for evaluating the evidential support for any evolutionary inference.

The fourth, and perhaps the most important, feature contributing the to the *Spandrels* legacy is that it provides a forceful and attractive argument for the evolutionary significance of development and constraint. Gould and Lewontin

(1979, p. 594) resurrect the *Bauplan* concept and argue that "it does not deny that change, when it occurs, may be mediated by natural selection, but holds that constraints restrict possible paths and modes of change so strongly that the constraints themselves become much the most interesting aspect of evolution." Although the claim that constraints are generally the "most interesting aspect of evolution" is probably too strong, this proposal renewed the challenge from development for mainstream evolutionary biology (Amundson 1996, 2007), and led to focused discussion on the nature of constraint hypotheses (see, e.g., Maynard Smith et al. 1985; Amundson 1994; Pigliucci and Kaplan 2000). Van Valen (this volume) crafts a new response to the challenge from development.

The emphasis on development in the *Spandrels* article signified and perhaps even played a causal role in the rise of evolutionary developmental biology. As Lewens (this volume) argues, part of the article focuses on the criteria for individuating biological traits. Some recent evo-devo research follows this line of inquiry, investigating the nature of evolvability, modularity, and the concept of a biological character (see, e.g., Wagner and Altenberg 1996; Wagner 2001). Another primary line of inquiry in evo-devo, the nature and origin of evolutionary innovation, connects both to this issue of trait individuation and the nature and power of evolutionary constraints (see, e.g., Raff 1996; Müller and Wagner 2003; Love 2006). The success of evo-devo dispels any residual doubt over the evolutionary significance of development.

In short, these four features of the *Spandrels* article help explain both its immediate impact and its lasting influence. Moreover, these features form the foundation for an argument that the influence on both biology and philosophy is, on balance, beneficial. Scientific articles seldom have such an impact across disciplinary boundaries. When they do they demand our attention and are worth commemorating. The contributions herein continue exploration of the rich set of issues integrated into the multifaceted *Spandrels* article.

Acknowledgements I owe a significant debt to Kim Sterelny for the opportunity to prepare this special issue, and for invaluable help with both the content and the editorial process. I would also like to thank everyone who expressed positive interest in the production of an issue commemorating the *Spandrels* article, especially (but certainly not limited to) the contributors herein.

References

Amundson R (1988) Logical adaptationism. Behav Brain Sci 11:505–506

Amundson R (1994) Two concepts of constraint: adaptationism and the challenge from developmental biology. Philos Sci 61:556–578

Amundson R (1996) Historical development of the concept of adaptation. In Rose MR, Lauder GV (eds) Adaptation. San Diego, Academic Press, pp 11–53

Amundson R (2007) The changing role of the embryo in evolutionary thought: roots of Evo Devo. Cambridge, Cambridge University Press

Beatty J, Desjardins EC (2009) Natural selection and history. Biol Philos

Brandon R, Rausher MD (1996) Testing adapationism: a comment on Orzack and Sober. Am Nat 148:189–201

Dawkins R (1986) The blind watchmaker. New York, WW Norton

Dennett DC (1995) Darwin's dangerous idea. New York, Simon and Schuster

Dupré J (1987) The latest on the best: essays on evolution and optimality. Cambridge, MIT Press
Forber P (2009) *Spandrels* and a pervasive problem of evidence. Biol Philos
Godfrey-Smith P (2001) Three kinds of adaptationism. In Orzack SH, Sober E (eds) Adaptationism and optimality. Cambridge, Cambridge University Press, pp 335–357
Godfrey-Smith P, Wilkins JF (2008) Adaptationism. In Sarkar S, Plutynski A (eds) A companion to the philosophy of biology. Oxford, Wiley-Blackwell
Gould SJ (2002) The structure of evolutionary theory. Cambridge, Belknap, Harvard University Press
Gould SJ, Lewontin RC (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc R Soc Lond B Biol Sci 205:581–598
Harvey PH, Pagel MD (1991) The comparative method in evolutionary biology. Oxford, Oxford University Press
Houston AI (2009) San Marco and evolutionary biology. Biol Philos
Lewens T (2009) Seven types of adaptationism. Biol Philos
Love A (2006) Evolutionary morphology and evo-devo: Hierarchy and novelty. Theor Biosci 124:317–333
Maynard Smith J, Burian RM, Kauffman S, Alberch P, Campbell J, Goodwin B, Lande R, Raup D, Wolpert L (1985) Developmental constraints and evolution: a perspective from the mountain lake conference on development and evolution. Q Rev Biol 60(3):265–287
Mayr E (1983) How to carry out the adaptationist program? Am Nat 121(3):324–334
Müller GB, Wagner GP (2003) Innovation. In Hall BK, Olson WM (eds) Keywords and concepts in evolutionary developmental biology. Cambridge, Harvard University Press, pp 218–227
Orr HA (2005) The genetic theory of adaptation: a brief history. Nat Rev Genet 6:119–127
Orzack SH, Sober E (1994) Optimality models and the test of adaptationism. Am Nat 143:361–380
Orzack SH, Sober E (1996) How to formulate and test adaptationism. Am Nat 148(1):202–210
Orzack SH, Sober E (2001) Adaptationism and optimality. Cambridge, Cambridge University Press
Pigliucci M, Kaplan J (2000) The fall and rise of Dr Pangloss: adaptationism and the *Spandrels* paper 20 years later. Trends Ecol Evol 15(2):66–70
Potochnik A (2009). Optimality modeling in a suboptimal world. Biol Philos
Raff RA (1996) The shape of life: genes, development, and the evolution of animal form. Chicago, University of Chicago Press
Rose MR, Lauder GV (1996) Adaptation. San Diego, Academic Press
Roughgarden J (1998) Primer of ecological theory. Upper Saddle River, Prentice Hall
Sober E (1987) What is adaptationism? In Dupré J (eds) The latest on the best. Cambridge, MIT Press, pp 105–118
Sober E (1996) Evolution and optimality: feathers, bowling balls, and the thesis of adaptationism. Philos Exch 26:41–55
Van Valen L (2009) How ubiquitous is adaptation? A critique of the epiphenomenist program. Biol Philos
Wagner G (2001) The character concept in evolutionary biology. San Diego, Academic Press
Wagner GP, Altenberg L (1996) Complex adaptations and the evolution of evolvability. Evolution 50:967–976
Wilkins JF, Godfrey-Smith P (2009) Adaptationism and the adaptive landscape. Biol Philos