

## Seven types of adaptationism

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**Abstract** Godfrey-Smith (2001) has distinguished three types of adaptationism. This article builds on his analysis, and revises it in places, by distinguishing seven varieties of adaptationism. This taxonomy allows us to clarify what is at stake in debates over adaptationism, and it also helps to cement the importance of Gould and Lewontin's 'Spandrels' essay. Some adaptationists have suggested that their essay does not offer any coherent alternative to the adaptationist programme: it consists only in an exhortation to test adaptationist hypotheses more thoroughly than was usual in the 1970s. Here it is argued that the 'Spandrels' paper points towards a genuinely non-adaptationist methodology implicit in much evolutionary developmental biology. This conclusion helps to expose the links between older debates over adaptationism and more recent questions about the property of evolvability.

**Keywords** Adaptation · Adaptationism · Evolutionary developmental biology · Evolvability · Godfrey-Smith · S. J. Gould · R. C. Lewontin · Spandrels

'...we must omit an extended discussion of the vital issue "What is a trait?" Some evolutionists may regard this as a trivial, or merely a semantic problem. It is not. Organisms are integrated entities, not collections of discrete objects.'  
The Spandrels of San Marco, p. 585.

### Seven adaptationisms

We can usefully distinguish seven types of adaptationism. In some ways this number is arbitrary. We could cut our seven up more finely still, and we can

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certainly make useful observations through the lens of a taxonomy that recognises fewer [e.g. Godfrey-Smith (2001)]. Picking these seven enables more than just an Empsonian pun in my title. It gives us a sharp enough resolution of the terrain to expose the details of what is at stake in the debates over adaptationism, and it also illuminates the significance of Gould and Lewontin's (1979) *Spandrels* paper in two main ways. First, my discussion will demonstrate the need to answer their question of 'what is a trait?' Second, I try to counter the commonly held view among many adaptationists that the importance of *Spandrels* is largely negative, that it contains some reasonable methodological cautions to a successful research programme while failing to offer any positive alternative for how to do biology. In brief, by forcing us to think about how traits are generated in development, Gould and Lewontin point to a genuine alternative methodology that has already given promising answers to some of the same questions that interest mainstream adaptationists. Both of these main conclusions show how themes underlying older debates over adaptationism are closely related to the concerns of more recent debates surrounding evolvability (see Pigliucci 2008 for a useful and brief survey of notions of evolvability).

Godfrey-Smith recognises three kinds of adaptationism. Here I add another kind, and I divide two of the kinds into sub-types. The three forms of *empirical* adaptationism express some hypothesis about the evolutionary process. The two forms of *methodological* adaptationism instead support some heuristic—a view not about the nature of evolution, but about how best to investigate it. *Disciplinary* adaptationism (which corresponds fairly closely to Godfrey-Smith's 'explanatory adaptationism') is a view about what is worthy of investigation, and *epistemological* adaptationism is a view about our chances of finding the answers to the questions we pose.

I will begin by laying out my seven types of adaptationism all together, and then I will explain why I choose to carve in such a way, and how I draw contrasts where there may seem to be none.

#### A Empirical adaptationisms

1. *Pan-selectionism*—natural selection is the most significant of the evolutionary forces that act on populations.
2. *Good-designism*—evolutionary processes tend to result in organisms with suites of well-designed traits. Most lineages are highly evolvable.
3. *Gradualism*—adaptation is always the result of selection acting on gradual variation.

#### B Methodological Adaptationisms

4. *Weak heuristic adaptationism*—those traits that are adaptations are likely to be correctly recognised as such only if we begin by assuming that all traits are adaptations.
5. *Strong heuristic adaptationism*—only by beginning to think of traits as adaptations can we uncover their true status, whether they are adaptations or not.

### C Disciplinary Adaptationism

6. *Explanatory adaptationism*—an evolutionary biologist's proper business is the study of adaptations.

### D Epistemological Adaptationism

7. *Epistemological optimism*—investigators have access to the data that reliably discriminate between conflicting evolutionary hypotheses.

## Empirical adaptationism

### Pan-selectionism

Orzack and Sober (1994a, b, 1996), Sober (1998) have pursued a programme of pinning down what is at stake in part of the adaptationism debate by trying to clearly articulate a testable adaptationist hypothesis. They like to think of adaptationism as the hypothesis that selection is the most important of evolutionary forces. (Strictly speaking, they understand adaptationism as the view that selection is *typically* the most important evolutionary force—their view of what adaptationism is does not entail that other forces never act, only that the action of these other forces is rarely significant.) I call this version of adaptationism 'pan-selectionism'. Its most important element is the view that drift, mutation and migration are in most cases insignificant evolutionary forces. It states little more than this, because many of the views traditionally opposed to adaptationism—e.g., the views that phylogenetic or developmental constraints act to impede or to guide the course of morphological and behavioural change—are irrelevant to the hypothesis that selection is the most important evolutionary force, at least in the way these authors understand that hypothesis.

To say that selection is the only evolutionary force that acts effectively in some series of evolutionary episodes is, for Orzack and Sober, to say that the fittest of the *available* phenotypes in a population goes to fixation. Situations in which drift plays a significant role are often situations in which the fittest phenotype does not go to fixation (often, but not always, as I will shortly explain). If drift frequently has a significant effect, then pan-selectionism is false. Factors that affect which phenotypes are available, on the other hand, are irrelevant to the hypothesis that selection is the most important evolutionary force. Developmental and phylogenetic constraints are typically understood as constraints on phenotype availability. This means, then, that debates about how strong or how weak such constraints might be are irrelevant to the hypothesis of adaptationism as Sober and Orzack understand it. Godfrey-Smith (2001) characterises empirical adaptationism as the view that evolution is comparatively free from constraint. He also suggests that his characterisation is similar to that of Orzack and Sober. We can now see that in fact the characterisations are quite different.

Drift is not the only factor that might render pan-selectionism false. Mutation and migration can also do so: if a population is swamped by migrants, or by mutations, of low fitness, then the fittest available trait may not prevail. One kind of constraint, which Sober and Orzack call ‘genetic constraint’, can also render pan-selectionism false. Such constraints consist in facts about reproductive systems that dictate the proportions in which organisms will produce offspring that resemble them phenotypically. A trait that confers very high reproductive fitness on an organism may fail to reach fixation, because the facts of sexual reproduction dictate that such traits cannot become universal in the population. Cases of heterozygote superiority illustrate this phenomenon. If the fittest trait is coded by a heterozygote, some number of homozygotes will (almost) always be created after these heterozygotes mate.

### Good-designism

The great advantage of Orzack and Sober’s formulation of the adaptationist hypothesis is that it gives a very clear, quantifiable reading of that hypothesis. Even so, there are some important elements of the traditional contours of adaptationism that it fails to capture.

What should be clear from the preceding discussion is there are worlds where pan-selectionism is true, yet because constraints on the availability of variants are so strong, organisms show nothing like ‘good design’ in any traditional senses of the term. It seems to me that many who call themselves adaptationists have wanted to assert that design in nature is good. This is hard to show conclusively; after all, we can consider Richard Dawkins to be an archetypal adaptationist, yet he spends a good part of his time in *The Extended Phenotype* (1982) laying out reasons why we should expect natural design to be poor. On the other hand, much of his energy in *The Blind Watchmaker* (1986) is devoted to marvelling at the excellence of nature’s craftsmanship. Dawkins sees himself as a follower of Paley (1802) in this respect. Orzack and Sober’s characterisation captures only the idea that nature’s designs are the best of what is available; however, if what is available is limited, then design quality may be quite awful—nothing to marvel at after all. If developmental constraints are exceptionally strong, variation will be constrained in such a way that it will be impossible for selection to build anything like an elegant design solution to an environmental problem. Even so, the fittest available trait might go to fixation.

The idea that natural populations are free enough from constraint that they are able to accumulate ‘well-designed’ traits resists precise articulation. But some of the contours of this idea have been captured in work on ‘evolvability’. As Pigliucci (2008) has recently pointed out, some evolvability concepts simply record the range of actual variation existent in a population (e.g. Houle 1992). In contrast to this, Wagner and Altenberg’s (1996) notion of evolvability records what philosophers would refer to as the *disposition* of a population to vary, rather than the actual variation in that population. In this sense, evolvability measures freedom from constraint. Moreover, as Wagner and Altenberg argue, variability in this sense of the term is in part a function of development, for it depends on the ability of new phenotypes to be generated through genetic variation interacting with developmental processes.

As we have seen, Godfrey-Smith takes adaptationism to be the hypothesis that evolution is free from constraint. Even when adaptationists acknowledge the existence of constraints, they sometimes claim that natural selection is a strong enough force that it will tend to overcome these constraints in the long run. This sense of the ‘strength’ of selection cannot be understood as a claim about the likelihood of the fittest available trait going to fixation. Rather, it is a claim about the temporal persistence of limits on trait availability. Although phrased as a hypothesis about the power of selection, this form of adaptationism is in fact committed to various claims about evolvability. That, in turn, shows that this form of adaptationism is committed to claims about the scope for developmental processes to change, as Wagner and Altenberg’s work illustrates.

Can we say in more precise terms how pan-selectionism and good-designism are related? Pan-selectionism takes its concerns from those of population genetics. The pan-selectionist wishes to show that some population is optimal, in the sense that it contains only the fittest phenotypes available at some earlier time. Good-designism, as we have seen, is intimately linked to themes in evolutionary developmental biology, particularly themes associated with the notion of evolvability. These ideas of evolvability, which have been thrust into the foreground of evolutionary thinking with work by Wagner and Altenberg (*ibid.*), Kirschner and Gerhart (1998), and many others, were partially foreshadowed in Gould and Lewontin’s own thinking on adaptationism. To give an example, the question of whether an organism exhibits what Lewontin has called *quasi-independence* influences the degree to which ‘good design’ can emerge in a lineage (Lewontin 1984). If organisms are highly integrated, rather than possessing largely independent organisational units, then the chances are lower that sustained cumulative evolution can act on any one of the organism’s features. Quasi-independence is a property of organic development. While the proponent of pan-selectionism need not make any claims about the nature of development, the proponent of good-designism will tend to find herself committed to various substantive claims about the nature of developmental processes, perhaps via an assertion of the ubiquity of quasi-independence.

We have seen that pan-selectionism does not entail good-designism. Neither does good-designism entail pan-selectionism. A functional morphologist, for example, may wish to show the ways in which some trait contributes to the survival and reproduction of an individual organism, where that organism is considered as a representative example, or archetype, of the species as a whole. More ambitiously, the functional morphologist may wish to make some claim that the trait is specially designed for this function, in the sense that it has a history of cumulative modification, throughout which its functional performance improves. Neither claim of functional morphology requires that we show, in addition, that drift has played no role in explaining the presence of this trait in the population. Maynard-Smith (1978, pp. 96, 97) tells us that ‘In general, the structural and behavioural traits chosen for functional analysis are of a kind that rules out neutrality as a plausible explanation’. Selection will have played some role in their explanation—that is true—yet a trait that does its job well may be present in a population in spite of the earlier existence of an alternative trait that did the same job equally well, or even a little better. What

is more, drift might act so as to *increase* the speed with which the fittest available trait reaches fixation, over that which selection would lead us to expect.

I have followed Sober and Orzack in understanding pan-selectionism as a hypothesis about the frequency with which the fittest available trait goes to fixation. Good-designism is a hypothesis about the facts that affect trait availability; hence it is about the facts affecting the prospects of good design emerging in nature. It is time to admit that the distinction between factors affecting trait availability, and factors affecting whether the fittest available trait goes to fixation, is not always clear cut.

Gould and Lewontin, among others, have attacked adaptationism by stressing the high degree of integration of different parts of the organism. Can such claims be understood as attacks on pan-selectionism, or are they better understood as attacks on good designism? It depends on how we answer Gould and Lewontin's question of how to define a trait, as we will shortly see. Gould and Lewontin's question—which they do not answer themselves—has received sustained attention in recent years, especially in a volume edited by Günter Wagner on the *character concept* (Wagner 2001). Much of Wagner's own discussion suggests that facts about development should inform any effort to atomise the organism into traits (e.g. Wagner 1989).

Consider a creature that runs on its hind legs. Let us suppose that long hind-limbs are better than short, for these make the creature run faster. The creature makes no use of its forelimbs. Short forelimbs are consequently better for this creature than long ones, for long forelimbs get in the way. Now suppose that development is set up in such a way that increases in the length of hind-limbs are accompanied by increase in the length of forelimbs. Our creature can have four long limbs, or four short limbs. But it cannot have long hind-limbs and short forelimbs, even though this would be the fittest combination. Suppose, finally, that selection ends up eliminating short forelimbs from the population. The question is whether this is merely a failure of the fittest *properties* to reach fixation, or whether it is also a failure of the fittest *traits* to reach fixation.

One might say that this is a case in which developmental constraints prevent the fittest available trait going to fixation—short forelimbs are fitter than long ones, but long ones go to fixation in virtue of selection acting on length of hind-limbs. Alternatively, one might say that in virtue of the existence of developmental constraint, we should not consider length of forelimbs and length of hind-limbs as independent traits at all. The fact that their development is not independent means we should recognise just two alternative traits here—short limbs and long limbs. Long limbs are the fittest available trait, and they go to fixation. On this understanding, developmental constraints result in a restriction on the availability of traits—they prevent a combination of short forelimbs and long hind-limbs appearing. If development informs our understanding of what a trait is in this way, then facts about the tight integration of organic development will tend to have relevance for 'good-designism', while they will be independent of the truth of 'pan-selectionism'.

In personal communication, Patrick Forber has raised the example of linkage, another problematic case in this context. Suppose the fittest trait in a population

appears only when the linkage between two alleles is broken by segregation. One might naturally think of linkage as constraint acting on trait availability here. Yet even when alleles are at closely linked loci, they can come apart on rare occasions. Under such circumstances, the fittest trait might be available in the population, but it might appear only very rarely. It may even be present so rarely that it disappears from the population instead of going to fixation. In these circumstances, one might choose to regard linkage as a factor that prevents the fittest available trait from going to fixation. Again, there is not always a clear-cut answer to the question of whether some factor affects trait availability, or whether it affects the chances of a trait that is available going to fixation. Once we see this, we also see that if developmental constraints range probabilistically over populations, so that certain traits appear rarely (rather than never), it also becomes problematic to assign developmental constraints to the list of factors affecting trait availability, as opposed to the list of factors affecting the chances of an available trait reaching fixation. These comments reinforce my observation that ‘good designism’ resists precise characterisation, in spite of a strong sense that some commitment to the excellence of design in nature underlies the outlook of many adaptationists.

### Gradualism

A final strand of empirical adaptationism, independent of both pan-selectionism and good-designism, is the claim that all of the apparent design in nature is to be explained in terms of natural selection. This claim might seem like a tautology. After all, adaptations are typically defined as those traits that have been selected for their functions (e.g. Sober, 1984, but see Reeve and Sherman (1993), p. 9 for a non-historical definition that avoids this implication of tautology). Hence if we equate ‘apparent design’ with ‘adaptation’, selection is the only possible explanation for such apparent design.

One might try to define the facts to be explained—the facts of apparent design—in such a way that selection need not be involved in their definition. It then becomes an empirical question as to whether selection is, indeed, the only explanation of this design (see Lewens 2007). Yet even if this approach fails, the issue of whether selection should be credited with the role of ‘shaping’ or ‘designing’ the trait, rather than merely increasing its representation in a population, does make sense. What is distinctive in Darwin’s explanation of the facts of apparent design is not simply the idea that fitter variants will replace the less fit ones in a population. It is the idea that through the accumulation of many small, favourable mutations, the emergence of complex adaptations becomes far more likely than it would be through single saltation. Merely pointing to saltation and subsequent selection would not have counted as an explanation for adaptation in nature, because the appearance of the first token of the adaptive trait in question remains a mystery. So an additional, distinctive commitment of traditional adaptationism is to gradualism.

Suppose we discover that eyes sprang forth fully formed in a single leap, and then swept to fixation. Eyes would be an adaptation by Sober’s definition, they may have a developmental independence from other traits that makes it appropriate to give them a design history of their own, and the optimal phenotype indeed is the one that

goes to fixation. In this case, then, the evolution of the eye counts as an example consonant with both pan-selectionism and good-designism. Yet selection here only answers the question of why eyes exist in such high proportions; it does not tell us why eyes came to exist in the first place. There may be no answer to that question at all—perhaps what explains the appearance of the first eye is nothing short of an extraordinarily unlikely coincidence. On the other hand, an investigator may try to appeal to some set of facts about development. Perhaps it turns out that our intuitive assumption that eyes are unlikely to arise through macromutation is wrong—it is an empirical question, after all. One might show that the nature of certain proteins dictates that they are rather likely to spontaneously form an eye-like structure. This hypothesis hasn't been much defended in the case of eyes, but attention to development has led some to suggest that macromutation did play a role in the generation of two distinctive features of the anatomy of the turtle—its protective shell and the anomalous positioning of the shoulder blade inside the ribcage (see Robert 2002, for further detail and references). Regardless of whether one accepts such empirical claims, the main point of these examples is to illustrate the point that part of the empirical content of adaptationism is the claim that fitness-enhancing saltations are so unlikely to occur that gradualism can offer the only non-miraculous explanation for the emergence of adaptations. Gould and Lewontin's insistence that there are alternative mechanisms to selection in the explanation of adaptation is conceptually intelligible, and not empirically outlandish, so long as we understand it as a reaction against the exclusively gradualist conception of adaptation and selection. And once again, their gesturing towards such possibilities points towards developmental work that might discriminate between different hypotheses for whether some adaptation emerged through macromutation, or a series of gradual changes.

### **Methodological adaptationism**

In practice I think it is quite rare that biologists think of adaptationism as a thesis. Instead, they seem to propose it as a way of doing biology—sometimes as a fruitful one, sometimes, more strongly, as the only way to do biology. So they ask what alternatives there could be to being an adaptationist, while agreeing all the same that such things as drift, constraint and bad design might pervade the organic world. Methodological adaptationism is rarely well-articulated, and as a heuristic there is no reason why it should be. It is worth distinguishing a couple of varieties of methodological adaptationism, although I do not claim that these are the only forms of methodological adaptationism that one might detect.

No one should argue against the view that it is often useful to propose hypotheses that suggest that some trait *T* is an adaptation for *X*. First, proposing such hypotheses will be a good way to discover that *T* is an adaptation in cases when it is. Second, in cases where *T* is not an adaptation, or it is an adaptation for some function other than that hypothesised, the evidence that one gathers in evaluating the hypothesis will point to suggestions about the true function of the trait, about likely constraints and so forth. Not only should no one argue against this form of



adaptationism, so far as I can see no one ever has argued against it (certainly neither Gould nor Lewontin—see Lewontin (1984)). The two more interesting forms of adaptationism I examine here propose, in one case, that only by assuming that all traits are adaptations will genuine adaptations be recognised, in the other that the assumption of adaptation is essential to uncovering the true status and history of traits, whatever that status may be.

### Weak heuristic adaptationism

The first, weaker forms of methodological adaptationism—that is, the view that only by proposing adaptationist hypotheses will we recognise adaptations as such—seem false. If we understand adaptations as those traits selected for their function, then the existence of such adaptations can be uncovered, in principle at least, from the opening assumption that all traits are selectively neutral. Such an assumption leads to predictions for how traits should fluctuate in a population. If these predictions are not met, we have evidence that the trait in question confers some fitness advantage over competitors. In other words, the opening assumption that all traits are selectively neutral can lead to the identification of adaptations.

### Strong heuristic adaptationism

The stronger form of methodological adaptationism also seems false, yet it is worth investigating in more detail. I see Dennett (1995) as a methodological adaptationist *par excellence*. Dennett defends optimality thinking on the grounds that we should always ask why it is right, or best, for organisms to be designed in the ways they are. Dennett's optimality thinking is compatible with all kinds of constraints and terrible design. On Dennett's view we explain this poor design by showing why it was, in fact, the best design in the circumstances. Dennett's view does not assert that populations are free from constraint, nor from drift; indeed, the value of optimality thinking for Dennett is that we show what kinds of constraints and trade-offs need to be posited if some behaviour or trait is to be shown optimal.

Things are not quite as simple as this, of course. Strictly speaking, the form of optimality thinking that Dennett recommends should not always lead us to exclaim at the excellence of Mother Nature's designs. Her designs may be truly awful, yet so long as the fittest overall phenotype goes to fixation we are guaranteed to find some set of constraints and trade-offs that explains why we don't see some better phenotype, hence why the design is the best that could be done given this background. The primary value of the approach consists in using the drive to give a rationalising explanation for the dynamic pattern of evolution as a means to illuminate constraints and trade-offs that can make designs at the same time terrible, yet also the best or most sensible in those circumstance. That is why Dennett talks so much of reading Mother Nature's mind. Someone who travels from Cambridge to London on foot via Edinburgh may strike us as a fool, and indeed this is a truly awful way to make the journey. Yet if we assume that the person is making sensible choices, we are driven by necessity to a richer explanation of his path. We are driven to uncovering the circumstances—terrible memory, inability to read train

timetables, faulty compass—that conspire to make each of his choices rational within those constraints, and hence which make sense of the whole journey in a richer way than if we write the whole thing off as a piece of idiocy. Now while the explanation we end up with is valuable, it hardly shows us that our traveller was a genius after all. Why, then does Dennett tell us that:

Time and again, biologists baffled by some apparently futile or maladroit bit of bad design in nature have eventually come to see that they have underestimated the ingenuity, the sheer brilliance, the depth of insight to be discovered in Mother Nature's creations. (1995, p. 74)

It is true, of course, that many traits turn out to have rather complex functions that a less persistent biologist would never have noticed. Dawkins (1982, p. 31) cites von Frisch's discovery of insect colour vision via the assumption that the bright colours of plants cannot be for nought as an example. Even so, there is an important distinction to be made between an empirical adaptationism that asserts the general excellence of design in nature, and a more Kantian form of methodological adaptationism that backs only the heuristic value of thinking in a certain rationalising style.

The consumer of heuristic adaptationism needs to be wary, then, of inferring from the success of the optimality approach to the thought that there is anything well-designed about nature. Dennett himself seems to swing between both views, and it is not always clear whether his exclamations of design excellence are intended to be understood literally, or merely as performative exemplifications of the optimality heuristic itself. We can return briefly to our toy example of the organisms that run on their back legs, and whose front limbs are used for nothing, to illustrate a more important limitation of strong heuristic adaptationism. Remember that in the example as we left it, small front limbs are better than long front limbs. Yet we imagine that long front limbs go to fixation, because hind-limbs need to be long to enable fast running. It is possible to imagine approaching these organisms from the standpoint of optimality. The biologist examines the obstructive, dangling front limbs and wonders why they are so badly designed. Why on earth are these limbs not shorter? The adaptationist posits some developmental constraint that makes long front limbs the right choice for Mother Nature after all. If they were shorter, then hind-limbs would be shorter, too, and the animal would be a less effective hunter. By investigating the population under the assumption that Mother Nature's choices are always good ones, we thereby expose a constraint that prevents organisms from combining short front limbs and long hind-limbs.

Stephens and Krebs (1986, p. 212) claim in a much-cited sentence: 'Even if they serve no other purpose, well-formulated design models are needed to identify constraints: without a design hypothesis there would be no basis for postulating any kind of constraint!' The example we just looked at suggests that any claim to the effect that such optimality thinking gives the only way of arriving at a perspicuous catalogue of developmental constraints is most likely wrong. In many cases it won't even provide the best way. The constraint in our example can be discovered by direct investigation as much as through the route of questioning why the dominant variety does not have short forelimbs, given that these would appear to confer

greater fitness. The end result of beginning with an investigation of the rules of organic development is also richer, for we understand not only the non-appearance in the population of animals with short forelimbs and long hind-limbs, which would have gone to fixation had they appeared, but also the non-appearance of animals with long forelimbs and short hind-limbs, which would have been strongly selected against. To echo a point made elsewhere by Ron Amundson (1994), while optimality thinking may illuminate the existence of developmental constraints in so far as they restrict adaptation, direct developmental investigation may expose the role of constraints in restricting the appearance of alternative forms that would be less adaptive than the dominant form, as well as those that would be more adaptive. Strong methodological adaptationism, if it argues that optimality thinking is the only basis for discovering constraint, is false.

Both ‘developmentalists’ and ‘adaptationists’ may share a view of the goal of evolutionary biology as the provision of a perspicuous account of how, and why, organic form changes over time. Thinking at first in terms of the demands of environments and about the failures of predicted optimality is not the only method on the market for achieving this programme. There is a coherent developmentalist methodology that urges us to begin instead by attending directly to the rules that define growth patterns. This is how we arrive at an empirically grounded, explanatorily transparent account of what traits we should recognise. The job of attaching functions to those traits and explaining their relative successes at the population level then becomes far easier, for we understand better which shortcomings in function need to be explained through drift, and which through constraint. By asking the question ‘what is a trait?’ Gould and Lewontin point towards one reason for seeking an integration of developmental and evolutionary biology of the kind that is so frequently discussed today.

### **Disciplinary adaptationism**

Methodological adaptationism consists in a recommendation for how to go about investigating nature. Disciplinary adaptationism is a view about what is worth investigating. Here the claim is simply that adaptations should be the prime point of interest for any evolutionary biologist worthy of the name. Maynard-Smith (1969) shows himself to be an adaptationist of this type when he says that ‘The main task of any theory of evolution is to explain adaptive complexity, that is, to explain the same set of facts that Paley used as evidence for the creator.’ Alternatively Dawkins writes, in a revealing quotation that I borrow from Godfrey-Smith:

Large quantities of evolutionary change may be non-adaptive, in which case these alternative theories may well be important in parts of evolution, but only in the boring parts. (Dawkins 1986, p. 303)

For the most part I agree with Godfrey-Smith that there is not much one can do to assess this kind of view, for it is hard to see what makes some set of facts more interesting, or more important, than another. For the likes of Dawkins and Dennett the explanation of adaptation can be given some special importance on the grounds

that if such facts are not accounted for, the creationists will poison our minds with nonsense about God. Yet if we set the creationist agenda aside and look within biology, there are certainly many things that can be explained that lie outside the adaptationist agenda. One can simply trace the history of various physiological mechanisms, without speculating as to their functions. Alternatively, one might be interested to give an account of diversity and nothing more.

It is hard to give a clear distinction between disciplinary and methodological questions. On the face of it, the first concern the ends of research—what questions are most important to answer—while the second concern the means—what methods should be employed to answer them. But in many cases a shift of perspective will turn two groups that disagree on disciplinary questions into two groups that share some higher goal, yet think it is best to pursue it through different means. One important element of the *Spandrels* paper consists in putting forward an alternative to the adaptationist programme, and we should not get too distracted by the question of whether this alternative amounts to a different basic goal for biology, or a different set of means for the attainment of traditional goals. The programme which they advocate:

Holdes... that the basic body plans of organisms are so integrated and so replete with constraints upon adaptation... that conventional styles of selective arguments can explain little of interest about them. It does not deny that change, when it occurs, may be mediated by natural selection, but it holds that constraints restrict possible paths and modes of change so strongly that the constraints themselves become much the most interesting aspect of evolution. (p. 594)

It is hard to see on what grounds we can secure the claim that constraints are more *interesting* than the selective retention of variants permitted by those constraints. On the face of it what we are offered here is a picture of evolution where the continental, *structuralist* school focuses on general constraints that tell us what forms are biologically possible, and that investigates the ground in development for such restrictions. Within such permitted forms, some are fitter than others, and the adaptationist simply concentrates on how ecological and population demands ensure that some are selected and others eliminated. The structuralist may claim title to the grander aspects of evolution, for she alone can give a set of mechanistic principles that explain the broad similarities in form across many taxa. On the other hand, the adaptationist may retort that only she is equipped to understand the true ground of those admirable contrivances that result from selection within such taxa. Gould and Lewontin certainly advocate a legitimate refocusing of interest from selection to development, yet it is hard to see how one group can be said to win. A pluralist stance not only on the kinds of forces affecting evolving populations, but on the questions of evolutionary interest and the heuristics used to answer such questions, appears the preferable position.

In spite of all this, some might think that the structuralist ‘alternative’ to the adaptationist programme is really no alternative at all. This move will not try to deny that attending to development is important; rather, it will seek to show that the adaptationist’s concern with selection does not preclude his attending to how

different developmental pathways, and different internal relations between traits, can affect survival and reproduction. This already signals a move away from ‘the conventional styles of selective argument’, for conventional styles of selective argument tend to work by thinking of environments as posing problems for adult organisms to solve. Yet nothing in the logic of selection understood as the differential survival of the fittest type entails this view alone. One type may be fitter than another in virtue of its superior ability to develop.

At this point it becomes even harder to keep score in the debate. I began by noting that the dispute between adaptationism and structuralism looks like nothing more than a difference in interests. But now it appears that even the explanatory interests of the structuralist can be given an adaptationist gloss, with the result that the contrast between the positions disappears altogether. Gould and Lewontin advocate switching attention away from explanations of organic form that cite the superior performance of individual traits in the face of local ecological features, and towards explanations of form in terms of broad structural constraints on the development of the whole, integrated organism. The adaptationist school responds by arguing that selection models can explain the appearance of certain forms in the face of the generic demands of development, just as well as they explain the appearance of certain forms in the face of the specific demands of the environment. This kind of adaptationist cannot deny the importance of direct attention to developmental processes in the explanation of form, any more than he could deny the importance of direct attention to ecological demands in the context of more traditional functional explanations. Perhaps, then, Gould and Lewontin should claim victory since the legitimacy of their advocated refocusing is acknowledged. But the adaptationist might also claim the spoils, in virtue of preserving a basic selection model that admits no non-selective mechanism of evolutionary change of the kind that a full-blooded structuralist *alternative* might require. This difficulty in adjudicating victory is exemplified by the fact that ‘internal selection’, which Schwenk (2001, p.171) describes as ‘the idea that the internal dynamics, or temporal and functional relationships among parts, create selection pressures on character phenotypes independent of the external environment’, is also labelled by Schwenk as a distinctively *structuralist* notion. Yet it is also by stressing the appeal to *selection* in this kind of model that Reeve and Sherman (1993, 2001, p. 21–22) claim that *adaptationism* makes best sense of developmental constraint, with the result that structuralism is either mystical, or a form of adaptationism after all: ‘Phenotypes are developmentally constrained when the alternative phenotypes have lower fitnesses because they depend upon developmental processes that would seriously disrupt the original developmental program, thereby reducing viability.’

Let me give a summary of an intermediate position we have arrived at in this section. Perhaps the fittest organic forms always survive. Perhaps, then, a selectionist argument can always be given for why we see the forms we do. Yet if our goal is to understand why we see the forms we do, the best place for that inquiry to begin might sometimes be to see how traits are produced in development, and how they are related to each other, rather than asking what kinds of demands the external environment lays down. The structuralist programme thereby offers a heuristic focus for investigation on the insides of organisms, which differs from the traditional external, ecological focus of adaptationists. Furthermore, if traits are

highly developmentally integrated, then we should expect external problems to be of little value in predicting organic form compared with an investigation of the means by which these traits are generated. That is so because we should not expect organisms to have the right degree of independence among their parts to be able to evolve over time to acquire complex adaptation. Adaptationists often demand that structuralists explain what novel evolutionary mechanism they are proposing that might counter the action of selection. A fair response is to stress the novel payoff of direct attention to developmental processes in delivering insights that might elude a traditional adaptationism focused on external selection pressures. The value of this reorientation does not depend on the discovery of a non-selective mechanism for evolutionary change, and there is no requirement on the structuralist to deny that such processes can be approached from a broader adaptationist perspective that incorporates ‘internal selection’.

So the structuralist programme does not rely for its value on an ability to elude classification as part of a permissive adaptationist programme that recognises internal selection. Even so, I have not established that all the talk of constraint, or ‘design limitations’, adopted by the structuralist can be given a selectionist gloss. Many *phyletic* constraints (*Spandrels*, p.594) can surely be understood from an adaptationist perspective. We have reason to think that the evolution of lineages will be highly constrained by what has gone before, for if novel functional systems are built on top of structures laid down earlier in phylogeny, and if those systems rely for their operation on features of these ancestral structures, then any alterations to such ancestral structures will tend to be disastrous for the organism itself. They will become progressively more entrenched as new traits are built on top of them. In this way, a selective explanation can be given for the existence of phyletic constraint. (Wimsatt and Schank 1988, but see Raff 1996 for empirical evidence, that, in some cases, ancestral systems can be altered without prohibitive sacrifice of fitness.)

Does the adaptationist programme incorporate in this way the study of *all* supposed constraints? Gould and Lewontin (1979, p. 594) consider *developmental constraint* to be a type of phyletic constraint. These constraints are limitations on the range of alternative traits that can be generated, which are imposed by the processes of development themselves. Williams (1985, p.20) rightly stresses that the structuralist needs to be just as wary of telling ‘just-so stories’ as the adaptationist here. One cannot infer from the repeated appearance of some structure across several related taxa that the taxa in question are constrained in such a way that alternative structures cannot be built, any more than one can infer from the repeated appearance of round car tyres across all car manufacturers that tyre factories cannot produce tyres of any other shape. The reason why one always sees the same structure may be that alternative structures are inferior at performing some job, and they are selected against.<sup>1</sup>

Williams’ point is an epistemological one, but it suggests, first, a genuine difference between selective and structural hypotheses for the non-appearance of some form, and second, a method for determining which hypothesis we should

<sup>1</sup> Thanks to Paul Sherman for pointing me in the direction of Williams’ paper, and for penetrating criticisms of the following paragraphs.

prefer. There is, after all, a difference between a world in which factories cannot be easily modified to produce different shapes of tyre, and a world in which they can be so modified, but cars with different tyre shapes go off the road. Looking at the distribution of tyre shapes on cars that run smoothly will not tell us which world we are in. One way to find out whether factories are constrained so that only one kind of tyre can be produced is to look at the factory itself, the materials that the tyres are made from, and how these could easily be modified. Analogously, if we are presented with the regular appearance of some morphological structure across a range of related taxa, then attention to how the structure develops will help us to understand whether it is likely that alternative structures can be produced. In neither case is the structuralist's appeal to constraint mystical. It is a given of neo-Darwinism that different structures have different chances of arising through mutation, depending on the probabilities of various genetic mutations, and the developmental processes that exist to be coopted by those mutations. Note, also, that this kind of structuralist is not restricted to pointing out that certain forms are universally (nominally) impossible given generic laws of nature; since evolution occurs through mutations to existing lineages, the structuralist can also point out how particular forms will have quite different chances of arising through mutation in different species, depending on what structures exist to be modified. That is why direct attention to development can tell us why we see some forms regularly in certain taxa, and others not at all.

So it seems that explanations for non-appearance offered by adaptationists really are quite different to those offered by structuralists. One school explains the non-appearance of form  $F^*$  by pointing out that it is less fit than the actual  $F$ . The other explains this non-appearance by claiming that  $F^*$  cannot arise (or is very unlikely to arise) by mutation from the existing system. One hypothesis is about the fitnesses of possible forms, and makes no comment on how likely they may be to arise through mutation; the other is about the probabilities of possible forms, and makes no comment about their relative fitnesses. (This is an alternative way of making the point that underlies Amundson's important (1994) distinction between two concepts of constraint.) Note that if it is true both that  $F$  is fitter than  $F^*$ , and that  $F^*$  cannot arise by mutation, then the second explanation trumps the first one. If some form  $F^*$  never arose in a population as a variant, then this is what explains its non-appearance. The further fact that had  $F^*$  appeared nonetheless, it would have been selected against, is irrelevant in this world. Equally, if a man dies from poisoning, then it is poisoning that explains his death. His death is not explained by the further fact that had he survived the poisoning, someone else would have shot him, and he would have died too.

All we have shown so far is that some structuralist hypotheses are different from some selectionist hypotheses. We have not established that we cannot find some selectionist gloss on every well-articulated structuralist hypothesis, for maybe even facts about the likelihoods of certain variants arising through mutation can be cast, ultimately, as selectionist claims of sorts. Reeve and Sherman (1993) try to give just such a selectionist reading of Wake's (1991) discussion of constraint in salamanders. Wake argues that the repeated, independent evolution of small body size and four-toed feet from larger five-toed ancestors is the result of developmental



constraint. Wake suggests that ‘selection for very small size may have, as an incidental side-effect, the loss of a toe’ (Wake 1991, p. 549). Informally, Wake is suggesting that development is set up in such a way that small size and five toes don’t go together, with the result that selection for small size brings four-toedness along with it. Reeve and Sherman press the legitimate epistemological complaint that observing four-toedness regularly does not by itself tell us the causes of this appearance. We have just used Williams’ example to show how we could give either a selectionist hypothesis, or a structuralist hypothesis, for an analogous pattern in observed car tyres. But Reeve and Sherman (1993), p. 22 instead give only selectionist options:

It is possible that four-toedness evolved in small individuals because either (1) the production of four toes minimally disrupts the development of small individuals (an example of our selective version of developmental constraints), or (2) for small individuals, locomotion, clinging, and foraging, for example, are more efficient with four toes than with five toes. Both hypotheses (1) and (2) are functional explanations, and neither has apparently been explored. The difference between them is that the selective context for (1) involves the internal environment (the developmental pathway leading to a small individual), while the selective context for (2) involves the external (physical and biotic) environment.

The moral, for Reeve and Sherman, is that on close inspection all structuralist hypotheses will turn out to be selection hypotheses in disguise. One problem in evaluating their approach here is that we can compare the fitnesses of two phenotypes even in situations where one is merely hypothetical. Indeed, their definition of adaptation (Reeve and Sherman 1993, p. 9) allows that some trait is an adaptation just in case it is the fittest of some range of phenotypes, where the alternatives in that range need not include phenotypes that have actually appeared in the population. It is because Amundson (2001) thinks that the selectionist reading of constraint demands that alternative variants have truly existed that he dismisses Reeve and Sherman’s suggested equivalence of developmental constraint and embryonic selection. Amundson thinks that Reeve and Sherman are positing embryonic five-toed variants without evidence that they exist. Reeve and Sherman, on the other hand, may believe that one can give a functional explanation of the existence of four-toedness in spite of the non-existence of any alternative to the four-toed variant—it is enough that five-toed salamanders would be less fit, were they to exist. Here I am with Amundson: if there are no such five-toed variants, then the counterfactual statement that had they been present in the population, they would have been selected against, is not, in fact, explanatorily relevant to their non-appearance.

We also need to be mindful of two different situations that might underpin a model of developmental constraint that appeals to internal selection. Selection early in ontogeny might consist in, for example, small embryonic salamanders with five toes aborting owing to the interference in other elements of growth caused by five toes. This is indeed a selection process, and a functional explanation to boot. Alternatively, embryonic five-toed salamanders might be perfectly viable, yet such salamanders do not exist at any stage of development. What might explain this?



Perhaps a single mutation from four to five toes is prohibitively unlikely, while intermediate forms between the two always abort through disruption of an alternative growth field. Embryonic selection is again at work, but only on those forms that show tendencies of some kind towards the possession of five toes. Here we appeal to a *fitness trench*, of non-viable, or highly unfit, forms, lying between four and five-toed forms. (The notion of a fitness trench is exploited in many of Sterelny's recent papers on evolvability. See, e.g., Sterelny (2003)). In the first case we explain the non-appearance of five-toed salamanders by pointing to the existence of such salamanders at an early stage of development. In the second case five-toed salamanders need never exist—we simply point out that salamander development is such that no five-toed salamander would be constructed. Yet even in the second case we rely on a logical leap—we cannot be sure that if some form occurs regularly, then that must be because it is surrounded by fitness trenches. Hence it is not a matter of logic that structuralist explanations will always be reducible to selection explanations. Even if these nearby alternatives have lower fitness than the actual form, the facts that explain the regular re-appearance of a single form might relate simply to the very low chances of *any* alternative being generated in mutation, perhaps given the high degree of canalisation of the trait in question.

The first case of embryonic selection on five-toed salamanders would enable the adaptationist to claim a victory of sorts, subject to the caveats already laid out above about whether serious attendance to development is not already enough for Gould and Lewontin's alternative. I am much less sure about casting an appeal to fitness trenches as a *reduction* of developmental constraint to selection pressure. In this scenario we agree that development makes the appearance of a five-toed form highly unlikely, regardless of its fitness with respect to the four-toed form. We supplement this with further facts about the workings of developmental pathways that explain why they either cannot be perturbed at all, or why it is the case that if they are perturbed, the knock-on effects to other pathways are so severe as to result in no development at all. Of course this second option, at least, could be represented as a fitness landscape in which alternative forms have fitness zero, and this could therefore be thought of in terms of a form of selection. But it is the facts of development themselves that explain the shape of the fitness landscape. The nature of developmental processes is what dictates that departures from such processes will result in non-viable forms. Landscapes with fitness trenches are representations of developmental constraints, not reductions of them to some more basic, selectionist model.

It may well be the language of function and optimality that is confusing us here. Wake wishes to augment the 'functionalist' approach of adaptationism with a 'structuralist' approach. As we have seen, Reeve and Sherman respond with the claim that Wake's apparently anti-adaptationist alternative *is* a functional explanation, or if it is not, then it is wholly mysterious. In many cases the developmental explanation for the non-appearance of some trait will certainly not be a functional explanation in the 'selected effects' account's sense of that phrase.<sup>2</sup> That account of

<sup>2</sup> There are many proponents of the selected effects account. Most of the contributors to Buller (1999) defend a view of this form, although the tide may be turning against it (e.g. Davies, 2001, Boorse, 2002, Lewens, 2004).

functional explanation demands competition between actual variants—in this case, variants with four and five toes. But the developmentalist may be proposing an explanation that explains why small five-toed salamanders fail to exist at any stage of development.

Suppose, instead, that we move to a weaker conception of functional explanation that allows that any explanation of the presence of a form A over some alternative form B in terms of the likely lower stability of some of the required intermediaries between A and B, is a functional explanation for the non-appearance of B. Even the explanation for the reliable appearance of A that appeals to its high degree of canalisation may count as a functional explanation here, for canalised systems may themselves be explained as systems in which the canalised trait is one of particularly low energy in comparison to other structural alternatives. On this kind of view, functional explanations lose any claim to being distinctively adaptationist, and the adaptationist reduction of structuralist explanation again fails. Optimality analyses can be used to explain stability of forms—even of purely physical forms—by appealing to the costs and benefits to the overall system of certain kinds of modification. Again, there is nothing mysterious about this kind of explanation. We can explain the rare appearance of carbon in the ‘buckyball’ form, for example, in terms of the constraints and energetic tradeoffs that mean that more usual forms of carbon will rarely be stably transformed into that allotrope. Is this a functional explanation for the existence of graphite versus the buckyball? Perhaps, but if so, then that only reminds us that we should not propose a strict contrast between functional and structural explanations—structural explanations for stability can be recast as functional explanations of sorts by pointing out the consequences of perturbation from structural equilibrium. We also show that talk of functions, trade-offs and optimality is not, at this level of abstraction, the preserve of the adaptationist. The adaptationist cannot use the difficulty of distinguishing functional and structural explanation to dismiss the thought that the study of development—and of developmental constraint—has something distinctive to offer evolutionary biology.

### **Epistemological optimism**

*Epistemological optimism* is the view that our capacities for gathering evidence and comparing hypotheses about the functions and origins of organic traits are good enough to be able to provide strong support for these hypotheses. It would be quite legitimate to deny that this view is strictly a part of the adaptationist programme at all. That is because an optimism regarding our abilities to reconstruct the evolutionary past (and present) need not play into the hands of those who assert the importance of selection, or the relative lack of constraint, in the evolutionary process. We need evidence to say whether drift has played an important role—we need to establish that population sizes have been small, for example, or that selectively neutral variants have existed in ancestral populations. In spite of this, we can include epistemological optimism as a form of adaptationism on historical

grounds. Many of the criticisms of adaptationism—most obviously *Spandrels'* own caution about evolutionary just-so stories—have consisted in highlighting the complexities of the evolutionary process and expressing scepticism over our abilities to satisfactorily confirm our best hypotheses about it. But this favourite slur of anti-adaptationists is an epistemological grumble, and one that could, in theory, be made about drift as much as it is made about selection.

Anti-adaptationists who stress this epistemological attack on claims made about the selective forces acting on organisms should, if they are to be consistent, express a similar scepticism about drift. Indeed, this is what they do. So, while pointing to the possibility of the action of many evolutionary forces, Lewontin (2000) is a sceptic about our abilities to decisively confirm any of these stories—not only the selectionist ones. I don't want to investigate this form of adaptationism, or anti-adaptationism, in great detail in this paper. There are two important points to note for our purposes. First, what I have elsewhere called 'evolutionary scepticism' (Lewens 2002), and what might here be called 'epistemological pessimism', is not merely the claim familiar from elsewhere in philosophy of science that there may be some alternative hypothesis that is consistent with our data and incompatible with the hypothesis we do, in fact, believe. There are special reasons to be sceptical of many historical hypotheses, for the data we would need to access in order to confirm or disconfirm them may be inaccessible, given our best methods. The evolutionary sceptic can agree on what data would decisively confirm or disconfirm some hypothesis, while expressing doubt that such data (e.g. data regarding the size of ancestral populations, or patterns of variance in local ecological variables) can ever be reliably retrieved.

Second, the method of inference to the best explanation most favoured by many adaptationists is best supplemented by looking to independent support for the explanatory propositions that we infer on the basis of their fit with data. The claim that fairies come in the middle of the night and steal cheese from my fridge would, if true, offer a good explanation of the regular disappearance of cheese. Yet we prefer the claim that a mouse is the culprit because, to take one example, we have direct observational evidence that mice exist, yet we have none for fairies. In evolutionary explanation there are also many alternative sets of selection pressures, population sizes, and developmental and other constraints, that would, if true, offer a good explanation for the form and distribution of traits we see in organic populations. Here, again, to answer the evolutionary sceptic we would do well to look to data not merely regarding ancestral selection pressures and population sizes, but also constraints themselves, if we are to say which of these explanations should be preferred. If there are no such data regarding constraint we need to generate them. Such talk of constraint is, as we have seen, simply another way of talking about how phenotypic properties arise through development, how they are, and are not, able to vary independently of each other, and hence what should be regarded as a natural trait or character. So if the evolutionary sceptic is to be answered, the adaptationist needs to attend directly to work in developmental biology that will yield an empirically rigorous method of atomising the phenotype, hence which promises independent support for what

otherwise constitutes an unmanageable proliferation of competing models of trait evolution.<sup>3</sup>

## Conclusion

### Atomising the phenotype

I have tried to show in this paper that one of the most significant lessons that the *Spandrels* paper teaches is about the importance for evolutionary biology of an empirically grounded account of what is, and what is not, a trait. Such an account can be derived in part from looking at the behaviour of traits under selection and the failures of expected adaptive pathways, yet it can just as well be generated by direct investigation of development.

Perhaps the most frequent criticism of the *Spandrels* paper from those with adaptationist inclinations goes like this: “True, things were getting a bit out of hand in the seventies, and many biologists were prepared to tolerate rather lazy tests of their hypotheses that consisted in little more than a decent qualitative fit between observed behaviour or form, and a set of posited adaptive pressures and constraints. However, the import of *Spandrels* consists only in this reminder to biologists to test their theories, and such a reminder hardly shows that the adaptationist programme needs to be abandoned. The positive alternative that Gould and Lewontin tried to offer in its place was mystical, ill-articulated, and has had no influence. This is borne out by the continuing stream of research work in broadly adaptationist disciplines. Journals with titles like *Functional Ecology* and *Behavioural Ecology*, and the disciplines of evolutionary psychology and functional morphology, continue to thrive. Dialectical biology, on the other hand, has seen little serious takeup.”

This is to look in the wrong place for the influence of *Spandrels*. The paper does articulate a constructive research programme, and one that has seen considerable uptake among a variety of evolutionary developmental biologists, and developmental evolutionary biologists. In studying the transformations of basic body plans in terms of variations on commonly held developmental pathways, the programme of evolutionary developmental biology achieves just what Gould and Lewontin expressed a desire for in their advocacy of the investigation of the transformation and conservation of basic organic baupläne. And while it might be true that there has been little call for journals with titles like *Dialectical Biology*, there has been considerable call for journals in evolutionary developmental biology. True enough,

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<sup>3</sup> In fact, things are more complex than this. Just-so stories typically relate the ecological pressures that have acted on organisms to determine their fitness. Drift hypotheses instead rely on data about the size of populations and the difference in fitness between variants that suggest actual trait frequencies may not match expected trait frequencies. Stories about the determinants of fitness are at a different level of explanation to stories about both drift and selection, for while drift hypotheses concern the likelihood of actual frequencies not matching expected frequencies in virtue of the differences in fitness between variants and the size of populations, stories about the determinants of fitness instead tell us what gives the different variants the fitnesses they have. Drift may occur in a population with two variants of equal fitness. A further ecological story is needed to explain why those variants were able to survive and reproduce in the ways they did, and with the same expected values of survival and reproduction.

there is no radical new mechanism for evolution posited here. All we have is more mutation and selective retention, and, as always, we should expect the fitter variants to survive. Nevertheless, if our idea is to understand what kinds of variants are likely to arise and why, then direct attention to development, rather than an attempt to provide ecological rationales for the forms we encounter, provides a bona-fide, alternative focus for evolutionary inquiry.

Of course showing that the *Spandrels* paper advocated a successful research programme distinct from traditional adaptationism does not establish that the paper caused the success of that programme. The fact that Gould, Lewontin and current virtuosos in the field like Wagner and Müller were all influenced by Riedl suggests that the intellectual interest in evolutionary developmental biology whose fruits we reap today was sown by Riedl directly. Nor can Gould and Lewontin take the whole credit for early advocacy of the study of development and evolution in the North America. David Wake had advocated something similar in California at around the same time. Finally, many leading proponents of evolutionary developmental approaches have been sparing in citing the *Spandrels* paper. Brian Hall has written to me that he first cited that paper in 1999. Tracing the historical influence of *Spandrels* is a different project. It is enough for now to understand the conceptual importance of what lies within it.

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