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The Historical Turn in the Study of Adaptation

Paul E. Griffiths

ABSTRACT

A number of philosophers and 'evolutionary psychologists' have argued that attacks on adaptationism in contemporary biology are misguided. These thinkers identify anti-adaptationism with advocacy of non-adaptive modes of explanation. They overlook the influence of anti-adaptationism in the development of more rigorous forms of adaptive explanation. Many biologists who reject adaptationism do not reject Darwinism. Instead, they have pioneered the contemporary historical turn in the study of adaptation. One real issue which remains unresolved amongst these methodological advances is the nature of 'phylogenetic inertia'. To what extent is an adaptive explanation needed for the persistence of a trait as well as its origin?

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1 The current state of the adaptationism debate

A number of philosophers have felt the need to defend adaptationism in evolutionary biology against its critics. Prominent examples are Helena Cronin in her widely read book *The Ant and the Peacock* [1991] and Daniel C. Dennett [1983, 1995]. A similar concern to defend adaptationism has been shown by the 'evolutionary psychology' movement (Symons [1992]). These authors interpret the dispute over adaptationism as a dispute between Darwinians and the 'developmental tradition' (Depew and Weber [1995]). Developmentalists seek to explain the range of existent forms in term of some 'internal' factor present in the conditions that set up the evolutionary process. Process structuralists like Brian Goodwin [1994] look for universal developmental laws which define the space of possible organismic forms. They seek to explain the evolution in terms of the

transformations made possible by these laws, rather than the happenstance of history. Complexity theorists of the genome like Stuart Kauffman [1993] aim to explain the orderliness of biological form in terms of the inevitable orderliness of complex systems. Once anti-adaptationism is identified as the view that most traits have non-adaptive explanations, it can be swiftly dismissed. The defenders of adaptationism need only point out that none of the alternative programmes addresses the adaptive fit of organisms to their environment. The other mechanisms explain biological form, but not the adaptedness of biological form.

However, this interpretation of anti-adaptationism is inadequate. The defenders of adaptationism treat Stephen Jay Gould and Richard Lewontin's paper 'The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme' [1979] as the definitive anti-adaptationist statement. Gould and Lewontin discuss alternative, non-adaptive forms of evolutionary explanation, but they also raise issues about the testing of adaptive hypotheses and the relative significance of different evolutionary mechanisms. Elliot Sober interprets the biological literature on adaptationism not as a debate over how many traits are adaptations, but as a dispute about the relative importance of adaptive forces and other evolutionary mechanisms in determining the trajectory and destination of organisms in the space of possible designs (Sober [1987, 1993]). In 'Optimality Models and the Test of Adaptationism' Steve Orzack and Sober [1994] distinguish three claims about adaptation. The first is that it is *ubiquitous*. Most characters are subject to natural selection. The second is that it is *important*. To define this notion more precisely they introduce the idea of a *censored model*. This is a model of evolution from which certain mechanisms have been deliberately omitted. Adaptation is important if a model censored of natural selection would significantly mispredict the actual form of the organism under study. Finally, it might be contended that organisms are *optimal*. Orzack and Sober argue that an organism is optimal if a model censored of all evolutionary mechanisms except natural selection would accurately predict the form of that organism. They suggest that adaptationism is best construed as the claim that most phenotypic traits are locally optimal.

Robert Brandon and Mark Rauscher (forthcoming) argue that some central concerns of the anti-adaptationist literature are omitted from Orzack and Sober's account. As Orzack and Sober make clear, optimality models are only concerned with local optimality. The models rely on a distinction between parameters that are open to optimization and those that can be treated as constraints. It is only because the models are specific to a particular species or group of species at a particular time that it is reasonably clear in practice which traits can be taken as a fixed background against

which others may be optimized. But the anti-adaptationist literature has drawn attention to the explanatory interest of a longer-term perspective on the very same traits. One anti-adaptationist concern mentioned by Brandon and Rauscher is the role of developmental laws in determining which variants are available for natural selection. The ‘phenotype set’ which is assumed by an optimality model is an object of explanation in other approaches. Another central theme of anti-adaptationism is the cumulative effect of history. A character like the pentadactyl forelimb of a penguin has passed through many different selective episodes during its existence. At the grossest level of analysis it has been successively a fin, a leg, a wing, and a flipper. Even if each episode is an example of optimization in Orzack and Sober’s sense, the process as a whole may not be so. Factors whose effects are negligible in any one episode may play a significant overall role when the selective process is iterated many times and its results in each episode fed back as input to the next. These observations are perfectly consistent with Orzack and Sober’s treatment, but suggest that there are aspects of the adaptationism debate where the explanatory focus is significantly different from that treated by Orzack and Sober.

The defenders of adaptationism are unimpressed by the fact that the response to one adaptive phase may reflect the historical inheritance with which an organism confronts that phase, as well as the adaptive forces in place. Dennett compares such facts to the constraints imposed on modern design by the adoption of the QWERTY keyboard layout. He remarks that: ‘QWERTY phenomena ... are constraints, but constraints with an adaptive history, and hence an adaptationist explanation’ ([1995], p.279). His mistake is the transition from ‘adaptive history’ to ‘adaptationist explanation’. ‘Adaptive history’ refers to a process of successive adaptive phases, in which the outcome of each phase is partly a function of what happened in the last phase. ‘Adaptationist explanations’ are those which explain an organism’s form in terms of the adaptive problem faced by that organism. QWERTY phenomena cannot be explained in this way. Instead of adaptationist explanations they must receive what I have called adaptive–historical explanations (Griffiths [1994]). These historicized adaptive explanations are the main focus of this paper. A large number of biologists are working on what they see as studies of adaptation that meet the concerns of anti adaptationism.¹ Most of these studies are concerned with the testing of adaptive hypotheses. These biologists are not ‘non-adaptivists’. They do not

¹ Surveys and methodological discussions of work of this kind include: Brooks and MacLennan [1991], Coddington [1988], Felsenstein [1985], Harvey and Pagel [1991], Lauder [1981, 1982, 1990], Lauder, Armand, and Rose [1993], Miles and Dunham [1993], Taylor [1987]. Horan [1989] is an earlier attempt to draw the attention of philosophers to the role of the comparative method in testing claims about adaptation, specifically in sociobiology.

reject natural selection as a major determinant of biological form. Instead, they believe that traditional approaches to testing adaptive hypotheses are woefully inadequate and condemn biology never to go beyond how-possibly explanations. The new methodologies they advocate lead to a new, historicized vision of adaptive explanation.

The interpretation of the adaptationist controversy as a controversy about hypothesis testing contrasts sharply with the interpretation offered by philosophers like Helena Cronin. Cronin sees the problem as a *shortage* of adaptive hypotheses! She suggests that the problem of adaptationism was solved in the 1970s by the development of evolutionary games theory. This fertile source of adaptive hypotheses teaches us 'how resourceful and subtle a tactician natural selection can be' and proves that 'non-adaptive explanations cannot be treated as other than a last resort', ([1991], pp. 109–10). But this interpretation is at odds with the historical sequence of events. It was during this period that adaptationism became such a live issue. The problem of adaptationism was created by the *proliferation* of adaptive hypotheses. The creation of an unstoppable engine of hypothesis generation made it urgent to provide more adequate procedures for hypothesis testing. Biologists were placed in the position of Hume's judge, faced with not one but seven witnesses each identifying a different suspect. The judge did not rejoice in the abundance of evidence, and neither did biologists.

2 What is 'the historical turn'?

Friendly treatments of adaptationism usually identify two components: adaptive thinking and reverse engineering. *Adaptive thinking* is the practice of looking at the structure of the organism and its behavior in the light of the ecological problems which it faces. This is supposed to have a heuristic value. It allows the adaptationist to sort out biologically important features from the mass of empirical detail about the organism in question. It may also lead to the discovery of previously unknown features. *Reverse engineering* is a way to infer the historical causes of biological form. The adaptationist tries to work out what adaptive forces must have produced the existing form by reflecting on the adaptive utility of that form in either the current environment or a postulated ancestral environment. Reverse engineering infers the adaptive problem from the solution which was adopted. Adaptive thinking infers the solution from the adaptive problem. Both practices make use of the strong relationship between biological form and adaptive forces that is the central theoretical commitment of adaptationism. This commitment is identical with the 'optimality' thesis that Orzack and Sober identified. A model of evolution censored of forces

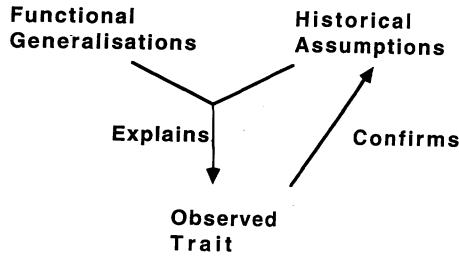


Fig 1. The Adaptationist Abduction. This argument is supposed to avoid the need to independently test postulated adaptive scenarios.

other than natural selection would predict with reasonable accuracy the trajectory and destination of organisms in design space.

The historical turn in the study of adaptation is a rejection of this central adaptationist commitment. The adaptationist supposes that there are adaptive (or ‘functional’ or ‘ecological’) generalizations that can explain the existence of certain biological forms. These generalizations rank alternative traits in terms of their fitness. The actual trait is explained by citing generalizations that assign it a higher fitness than the alternatives. The historical turn is the realization that adaptive generalizations of this sort cannot explain form except in conjunction with a rich set of historical initial conditions. This ‘historicity’ of biology is elevated by G.C. Williams to the status of one of the three guiding insights of modern biology, along with ‘mechanism’ and ‘natural selection’ (Williams 1992). Selection processes are historical because the relative fitness of characters is a function of the historical conditions in which selection takes place and of the complete range of alternative characters present (which is a function of past history), and because selection is stochastic. Successful adaptationist explanations would require adaptive generalizations that are insensitive to historical conditions and to the complete range of characters present, and robust under stochasticity. Only this would make it possible to explain the actual character which results by citing the functional generalizations alone.

Traditional adaptationists tried to avoid the problem of historicity by conceiving an adaptive explanation as a simultaneous abductive argument for the truth of the historical assumptions which it requires (Figure 1). The adaptive explanation would explain the actual trait, given certain historical assumptions. Therefore, by argument to the best explanation, we have grounds for accepting the historical assumptions. But this defence is unavailable to the modern adaptationist because, as Cronin tells us, we now realize that ‘non-adaptive explanations cannot be treated as other than a last resort’ ([1991], p. 110). Adaptationists are justified in what

Dennett calls their ‘blithe confidence’ that, no matter how obscure the trait, an adaptive explanation will sooner or later be forthcoming. Optimality modelling, evolutionary games theory and the like have created such a powerful engine for generating putative explanations that if we do not have several different potential adaptive explanations for each trait, we can assume that this is because we have not taken the trouble to generate them. Argument to the best explanation becomes impossible in this context, because there is more than one explanation which fits the data. Impressively detailed scenarios exist in which the increase in hominid brain size was caused by the release of a thermoregulatory constraint on brain size, which was itself caused by physiological adaptations to bipedalism (Falk [1990]). The ‘fit’ of this hypothesis to the observed phenomena does not confirm its historical assumptions because the same form of argument would confirm the conflicting historical assumptions of conflicting scenarios. The abduction can be employed to support the machiavellian intelligence hypothesis, according to which brain expansion was driven by the need to manipulate increasingly complex social relationships (Byrne and Whiten [1988]), or to support more traditional accounts of the pressures induced by the move from forest to savannah.

Recent work by Sober and his collaborators has stressed methods for reducing this proliferation of hypotheses by demanding precise quantitative fit with the observed trait (Orzack and Sober [1994]; Sober [forthcoming]). In particular, they have urged attention to the fine detail of the distribution of a trait within individual populations. While this approach can lead to results of the highest interest, it has two limitations. First, it requires extensive experimentation of a kind that is often impractical. Second, because it depends on the current state of a population for its data it is often inapplicable to hypotheses about the origins of a trait in some past period of adaptation. The historical turn in the study of adaptation is an alternative strategy for reducing the proliferation of adaptive hypotheses. Hypotheses can be rejected by directly testing their historical assumptions. Modern versions of the comparative method, inspired by phylogenetic systematics (cladistics), provide convenient tools for testing these assumptions. In the next two sections I want to look in more detail at the two adaptationist activities of adaptive thinking and reverse engineering. I show how both practices can lead us astray and how a comparative approach can put us back on track.

3 Adaptive thinking

The strategy of adaptive thinking faces two main problems. First, it is hard

to characterize an adaptive problem without already knowing the solution. Second, a single problem can be solved in several ways. Dennett says that when I cannot construct an adaptive explanation for something I should remember: 'Orgel's Second Rule: Evolution is cleverer than you are' ([1995], p. 74). I should assume that 'Mother Nature' saw adaptive forces that I missed. This is an excellent injunction, but it needs to be supplemented by the converse rule that 'evolution is more complex than you think'. If I think I can see all the adaptive forces, I am probably wrong. Because of this, few adaptive thinkers would claim to be able to predict the outcomes of selection processes. Most claim only that thinking about adaptive problems has heuristic value. The predictions of adaptive thinking must be tested against the actual results of selection. This is the position adopted by evolutionary psychologists in their investigation of 'the adapted mind' (Barkow, Cosmides, and Tooby [1992]). While enthusiastic about adaptive thinking they are clear that a hypothesis about mental structure cannot be proved merely by producing an adaptive scenario in which that mental structure would be advantageous. An empirical demonstration that the mind is actually structured in that way is also required: 'Although selectional thinking is an important source of inspiration for the evolutionary psychologist, nature always gets the last word' (Symons [1992], pp. 143–4). But although nature gets the last word, the evolutionary psychologist thinks that the fact that a particular feature 'makes evolutionary sense' is a reason for taking seriously even quite marginal data suggesting that it actually exists. If nature disagrees with the adaptationist about what should evolve, then she has to shout. If she agrees, she has only to whisper.

The claim that adaptive thinking has heuristic value is eminently contestable. The passage of Donald Symons from which I just quoted provides a good example. Symons is discussing the claim that the mechanisms of sexual attraction in men are designed to make immediately post-pubertal women maximally attractive. He notes that there is substantial empirical support for the view that men in all cultures are attracted to nubile young girls. But the claim receives additional support from the fact that 'the hypothesised psychological mechanisms that inform the prediction make excellent adaptive sense' (Symons [1992], p. 143). Men who preferentially mated with women who had just begun menstruating and had not yet borne a child would be at an evolutionary advantage. It is at this point that I am sceptical. Suppose the empirical data resolve themselves so as to indicate that more mature young women are maximally attractive. Will it not then 'make excellent adaptive sense' that these older women were better bets in the ancestral environment? They had more skills in foraging, or more resource holding power within the band, or had already proven their fertility by bearing a child. The adaptive story cannot enhance the

credibility of the data because an equally good story would be available for many of the alternative findings.

Adaptive thinking can, in fact, have a substantial negative heuristic effect. It can induce complacency in the face of unreliable or ambiguous data, because those data or the interpretation of the data 'make[s] excellent adaptive sense'. Parent/offspring conflict is a good example. Many sociobiologists were impressed by Robert L. Trivers' demonstration that the long-term interests of parents need not be identical with those of their offspring (Trivers [1974]). There is an appealing story according to which the parent wants to conserve its resources for future offspring, whereas the offspring wants as much as it can get. This model was taken to confirm observations of squabbling between parents and offspring around the time of weaning in primates, including humans. It also created the expectation that offspring would deceive their parents about their needs in an attempt to get more resources. These ideas still have currency in the Darwinian psychology literature. Parent/offspring conflict is 'inherent to the human condition' (Pinker and Bloom [1992], p. 483) and its 'inevitability' reinforces Nesse and Lloyd's [1992] belief in psychodynamic mechanisms of deceit and self-deceit. Yet empirical evidence for parent/offspring squabbling over weaning is very weak. Patrick Bateson [1994] summarizes various studies which failed to find aggressive interactions at weaning in a wide range of species, studies which found offspring weaning themselves, and studies which found both parties engaging in reliable signalling in order to co-ordinate weaning. These behaviours offer rich opportunities for adaptive explanation but their discovery has been hindered by devotion to a simple model of the evolutionary problem that behaviours surrounding weaning were supposed to solve.

The second problem with adaptive thinking is that different lineages solve the same problem in very different ways. Alligators and anacondas are both top-rank fresh-water predators, but they approach the task somewhat differently. They bring to the task very different resources accumulated earlier in their history. There are two different ways to look at this situation. One is to claim that the two lineages face different problems, the problem being partly defined by the resources available to solve it. The other is to maintain that there is one problem, but to say that the same solution characterized in functional terms can be realized by two different mechanisms (Hull [1987]; Griffiths [1994]; Goode and Griffiths [1995]). Both formulations make it clear how comparative considerations can improve the heuristic power of 'adaptive thinking'. Adaptive-historical thinking, as it might be called, would take into account the systematics of the organisms involved as well as the ecology. It would recommend the sort of heuristic that Konrad Lorenz had in mind when he talked of a

'phylogenetic' perspective on behaviour. An example of this heuristic in action is given by John Garcia and Kenneth Rusiniak in their discussion of poison avoidance mechanisms. The coyote's poison avoidance mechanism uses odours to mark foods associated with nausea. The red-tailed hawk faces the same problem on the same prairie, but uses visual cues. The two species solve the adaptive problem in a way that reveals their kinship to the laboratory rat and laboratory pigeon respectively. Garcia and Rusiniak remark that 'learning, like fixed action patterns and morphology, is also a matter of taxonomy' ([1980], p. 153).

Adaptive-historical thinking is also better able to address the first shortcoming of adaptive thinking, the difficulty of accurately characterizing the adaptive problem. A phylogenetic analysis of the species under investigation will often reveal the true nature of the adaptive problem. A simple example is given by Miles and Dunham [1993]. Many studies of migratory nearctic² birds have emphasized their need to avoid harsh conditions in winter. A phylogenetic perspective reveals that many of these species are of tropical origin. Migrating south for the winter is a consequence of migrating north for the summer. This suggests that the adaptive problem is one of obtaining resources for breeding, not of avoiding harsh winters. This puts the behaviour in a quite different perspective, and suggests different hypotheses about its underlying mechanisms.

The anti-adaptationist critique of 'adaptive thinking' does not rest on a rejection of adaptive explanation. It merely requires adaptive explanation to take account of two important features of biology. First, adaptive problems are too complex to be characterized in advance of some descriptive biology of the systems produced by those problems. Attempts to do so are as likely to be misleading as illuminating. Second, the solution adopted is a function of the resources available to the lineage facing the problem, as well as of the problem itself. These two closely linked features mean that a comparative perspective is essential when thinking about adaptation.

4 Reverse engineering

Reverse engineering utilizes the link between adaptive forces and biological form in the opposite direction. It tries to infer the nature of the adaptive problem from the form of the solution. I have already remarked that this presumes the existence of functional generalizations that are insensitive to historical particulars and robust under stochasticity. In his defence of adaptationism Dennett offers the classic argument for the existence of

² The zoogeographic region from Greenland to mid-Mexico.

these generalizations. The existence of adaptive convergence between organisms of different lineages shows that there are some forms, which he calls 'forced moves' and 'good tricks', that will emerge due to their adaptive superiority in a wide range of historical circumstances. Both vertebrates and the invertebrate cephalopoda have developed strikingly similar eyes. Eyes of some form are found in a whole range of taxa. Nocturnal forest-dwelling kiwis have whiskers and produce highly developed young, just like the mammals that occupy similar ecological niches. Surely these cases, and many others, show that there are robust adaptive-generalizations of the sort the adaptationist requires? Discussing Gould's claim that mass extinctions kill lineages at random, Dennett remarks that 'whatever lineages happened to survive would . . . grope towards the Good Tricks in Design Space' ([1995], p. 307).

There are three main problems with this argument. The first is that of converting the striking examples into developed science. I find an analogy to convergence in human history useful here. The great narrative historians of the nineteenth century excelled at providing parallels between modern Europe and the ancient world. They drew lessons for the likely fate of European civilization from Rome and other ancient civilizations. But no one has yet succeeded in converting these striking parables into a set of generalizations about the rise and fall of civilizations. If convergence is to demonstrate the power of adaptation it must do so as part of a robust ecological theory, not as a collection of striking examples. Too many narrative presentations of convergence take traits which are similar in appearance and then argue, by an adaptationist abduction, that they must have the same adaptive cause. But similar traits need not have similar explanations. All eyes are mechanisms for gathering visual information, but that does not give them the same evolutionary rationale. The complex eyes of many invertebrates are far better at detecting movement than at resolving an image. Perhaps they are closer in ecological terms to the ears of many vertebrates. What is needed is, at a minimum, data showing a correlation between the evolution of a trait in different lineages and the presence of some environmental factor. The search for this sort of data has been one element of the historical turn in the study of adaptation.

The second problem lies in Orzack and Sober's distinction between the view that natural selection is important and the adaptationist view that natural selection is a sufficient account of form. The fact that several organisms display the same trait does not show that its emergence is due to a functional generalization that is insensitive to historical factors. Even where a strong correlation exists between the existence of reasons for a trait and the actual emergence of the trait, some historical factor may make the difference between cases where the trait emerges and those where it

does not. This possibility has recently emerged in the most unlikely place, the flagship example of convergence, the eye. Research into the genetic factors in the development of eyes suggests that the eyes of vertebrates and invertebrates rely on the same, ancient genetic sequences (Quiring *et al.* [1994]). Although the eye has undoubtedly evolved in parallel in several lineages, it has done so on the basis of some common resources.

The third problem is that the fact that a character *is* convergent does not explain *why* it is convergent. Many birds fly south for the winter, but this does not stop the adaptationist misidentifying the adaptive nature of this trait. The adaptationist uses convergence to argue that there are some functional generalizations or other which are robust across different historical conditions. She then constructs candidates for these robust generalizations, shows that if true they would explain the convergent character, and argues for their truth by argument to the best explanation (the 'adaptationist abduction'). But this traditional adaptationist approach ignores the methods that offer the best chance of understanding and studying adaptive convergence. The adaptive–historical alternative includes methods that allow us to test whether the appearance of the same trait in many organisms is really an example of convergence, to locate empirically the environmental factors that correlate with the emergence of the character, and to construct tests of hypothesis that these factors were, in fact, the basis of the adaptive forces leading to convergence. These methods, and the other elements of the historical turn, are described in the next section.

5 The comparative method and the adaptive–historical approach

There are two main ways in which historical considerations have been brought to bear on ecology and evolution by the use of modern phylogenetic techniques. Donald Miles and Arthur Dunham [1993] call these the 'statistical' and the 'historical transformation' approaches. Looking at the subject from a more philosophical viewpoint, I think of these as an inductivist, correlational approach to establishing adaptive hypotheses and a falsificationist hypothetico-deductive approach to testing adaptive hypotheses.

The correct insight behind the adaptationist stress on convergent evolution is that the emergence of similar traits in different lineages suggests the presence of a common environmental factor. But the systematic study and validation of convergence requires an extensive use of the comparative method. Without a phylogenetic analysis it is not even possible to tell if something *is* a convergence. Dennett is struck by the fact

that 'so many creatures—from fish to human beings—are equipped with special-purpose hardware that is wonderfully sensitive to visual patterns exhibiting symmetry around a vertical axis . . . The provision is so common that it must have a very general utility' ([1987], p. 303). Dennett endorses the suggestion that this adaptation is a device for detecting other organisms looking straight at the subject, and hence vertically symmetrical. But it has yet to be established that there is any need for a convergence explanation. If this device is a homology in vertebrates, then it has only originated once. Having originated and been passed on by descent, it may serve a dozen functions in different groups, and exist in many others through phylogenetic inertia (a notion discussed at length below).

The need to treat multiple examples of a trait with a single evolutionary origin as a single data point in an analysis of convergence has been known for many years (e.g. Maynard-Smith [1978]). But techniques for correlating evolutionary change with environmental variables have undergone a great deal of recent development. A study of convergences due to shared feeding mode in *Anseriformes* (ducks, geese, etc.) by Daniel Faith provides a good example. Faith [1989] used a phylogenetic analysis of the group to find how much of the resemblance between species could be accounted for by common descent. He then mapped the species into a space defined by the shared features not due to descent. Various axes through this space corresponded to axes of variation in the feeding mode of the species falling along those axes. The result of this analysis was a set of characters with the potential to be explained adaptively, and a set of environmental variables correlated with the emergence of those characters. Like other examples of the inductivist use of the comparative method, Faith's work provides the sort of data that would allow the transition from anecdotal presentations of convergence to an investigation of the adaptive forces that produce it.

The other way in which historical and phylogenetic considerations have been brought to bear on adaptation is a falsificationist approach which targets the historical assumptions of adaptive scenarios. Comparative testing of this sort is the necessary counterpart to the extraordinary ingenuity in hypothesis generation made possible by modern evolutionary theory. The testing of the historical presuppositions of each model provides the necessary engine of hypothesis pruning to complement the engine of hypothesis generation. The simplest tests make sure that the actual sequence of evolutionary change is the one presumed by the adaptive hypothesis. Jonathan Coddington provides a simple example ([1988], pp. 10–11). Living species of rhinoceros have either one or two horns. As both horn numbers are 'strategies' demonstrably available to the evolving rhinoceros, it is natural to invent an adaptive scenario in which both

horn conditions are evolutionarily stable strategies (e.g. Lewontin [1978]). Once a population contains a large proportion of individuals with one number of horns it cannot be invaded by a mutant with the other number of horns. Victory goes to whichever strategy gets in first in a particular population. Various sexual selection scenarios would fit these requirements. However, a cladistic analysis of the rhinocerotid group shows that the two-horned condition preceded the one-horned in the phylogenetic tree. This suggests that at some point or other, in some environment, the one-horned form was adaptively superior. To sustain the existing proposal it would be necessary to add an auxiliary hypothesis such as the claim that a small population containing one-horned mutants was isolated and the one-horned form drifted to a frequency from which it could become an ESS. This claim could also be tested using cladistic biogeographic methods which associate taxa with habitats and allow inferences about ancestral habitat associations.

Slightly more complex tests compare the distribution of two or more characters which play a role in one another's adaptive explanations. Mary McKittrick [1993] provides a simple example. It has been suggested that the low birthweight characteristic of the genus *Ursa* is the result of an adaptive trade-off. It is the price bears pay for altering their physiology in order to allow hibernation. But a mapping of the two characters on to the relevant portion of the phylogenetic tree shows that this cannot be the case. Low birthweight emerges before hibernation, and exists on branches on which hibernation never originated. Tests of this sort have wide application. The 'aquatic ape' hypothesis (Morgan [1973]) claims as a particular strength its ability to explain a wide range of human characters. It suggests that these characters emerged together in a single phase of hominid evolution. The theory can be tested by mapping these traits on to a tree for hominids and their relatives.

Other tests look at the implications of an adaptive scenario for the historical relationship between a lineage and its habitat. These tests are simplest when the habitat factor is another lineage of organisms. Hypotheses of co-evolution should be reflected in congruences between the trees for the co-evolving species. Many studies of parasite-host co-evolution have shown that when a host species splits into separate species, so do the parasite species it carries. Cladistic biogeography offers opportunities to make tests on a much wider range of habitat factors. Habitat associations can be treated as characters and used to infer the ancestral habitat association in earlier portions of the tree. It was a study of this sort that suggested the neotropical origins of various nearctic migrant birds described above. The migrant forms are related to groups most of whose members are tropical, suggesting that the ancestor in whom migration evolved was

tropical. Biogeographic studies might also help test the auxiliary hypothesis, put forward above, that the one-horned rhinoceros evolved by drift in a small, isolated population. Cladistic biogeographic methods could be used to associate a geographic region with this origination event, and the genetic distance between the modern species could be used to establish a rough date of separation. If these studies suggested that the one-horned form split off in a large, undifferentiated land mass, this would tell against the defensive hypothesis.

The anti-adaptationist critique of ‘reverse-engineering’ is not a rejection of adaptive explanation. It is a recognition that adaptive processes and their results typically do not correspond one-to-one. The same feature may serve different ends and the same end may be served by different features. In order to ‘infer the problem from the solution’ more constraints must be added in order to create a unique correspondence. These constraints can be obtained from the reconstruction of evolutionary history. The scientific breakthroughs that have made this possible are the development of cladistic methods for reconstructing phylogeny and the availability of molecular data as a convenient source of data for cladistic analysis.³

6 Phylogenetic inertia: explaining origin vs. explaining maintenance

The historical turn has emphasized explanations of the origin of traits. The implication is that once a trait has evolved its existence needs no explanation beyond the mechanisms of inheritance. This idea is enshrined in Stephen J. Gould and Elizabeth Vrba’s concept of ‘exaptation’. A trait is an exaptation for some function if it now serves that function, but was not originally designed to serve that function. If feathers were originally selected for their insulation value, then they are an exaptation for flight. Several authors have noticed a fundamental flaw in Gould and Vrba’s definition of exaptation (Griffiths [1992]; Reeve and Sherman [1993]; Dennett [1995]). This definition seems to make *everything* an exaptation. All traits originate by undirected mutation, so the process of natural selection is *always* one in which an existing trait spreads through a population because it is found to be useful. A slightly more charitable reading of Gould and Vrba says that each trait is an adaptation for what it was *first* selected for. What justifies this special status for the first of many selection pressures? The underlying thought behind Gould and Vrba’s work seems to be that once a trait has evolved, no further explanation is needed

³ For a very brief introduction to cladistics, see Griffiths ([1994], pp. 207–10). For an in-depth analysis, see Sober [1988]. For a history of the cladistics revolution, see Hull [1988].

of its presence in descendants. It exists there by 'phylogenetic inertia'. A principled definition of exaptation would distinguish those selection pressures that took a trait to fixation in a population from those that applied later on. These later selective forces do not help to define the traits function. They do not explain why the trait exists.

The exaptation concept suggests what I call a 'Newtonian' picture of phylogenetic inertia. An organism subject to selective forces continues in a uniform state until acted on by contrary forces. The Newtonian picture seems to underly a great deal of thought about evolutionary explanation, but it has only to be clearly stated for its problems to become apparent. Robert Brandon ([1990], p. 172) observes that Gould and Vrba have taken no account of the role of stabilizing selection in maintaining traits at fixation. In the absence of continued selection, other traits should enter the population by mutation and spread by drift. In my [1992] I pointed out that it is generally assumed that a complex structure which serves no useful function will tend to become vestigial ('regressive evolution'). The loss of pigmentation and sight in cave-dwelling species does not reflect some special feature of the cave environment that favours being blind and transparent. It reflects the lack of any advantage in being sighted and coloured. There are two common explanations of regressive evolution. The first is the straightforward accumulation of deleterious mutations when there is no selection against them. My dictionary of biology takes this mechanism to be so obvious that it builds it into its definition of a vestigial organ—'an organ whose size and structure have diminished over evolutionary time due to reduced selection pressure' (Abercrombie *et al.* [1990]). The second mechanism is Weissman's 'competition of parts'. This is the economic competition between organ systems for resources during development. The suggestion is that any economy made in the development of useless structures will give the individual an advantage in the development of useful structures. There is therefore automatic selection against any structure which no longer functions to increase an organism's fitness. The need for stabilizing selection and the possibility of regressive evolution suggest that the continued existence of a trait in a population is not explained by mere phylogenetic inertia. A trait must be *maintained* at fixation by some selective force or another. The need for maintenance creates an 'Aristotelian' picture of phylogenetic inertia. Like a body in Aristotle's theory of motion, an organism subject to selective forces gains a certain quantity of 'inertia'. When the selective force is removed this inertia maintains the organism in its current, adapted state. The inertia eventually runs down, and the organism reverts to an undifferentiated state.

Neither the Aristotelian nor the Newtonian picture need be true for all traits. Systematists have long been accustomed to divide traits into those

which are highly conserved, and thus good systematic characters, and those which are more variable. Polygenic and variable traits such as colour may 'run down' relatively rapidly. Phylogenetic inertia may also be quite weak for the functionality of a complex structure like the eye.⁴ This might be impaired by the smallest developmental deficits. The relatively small quantity of phylogenetic 'inertia' possessed by these traits would explain the striking pattern of regressive evolution in troglodytic species. A trait like the pentadactyl limb of tetrapods, however, seems to have an enormous amount of inertia. The relative positions of its parts are preserved in everything from a frog's leg to a bat's wing. This seems to be a 'Newtonian' trait. Apparent 'Newtonian' traits have been the focus of research by process structuralists and other members of the developmentalist tradition. They have offered explanations of phylogenetically stable traits similar to C.H. Waddington's concept of 'developmental canalisation' (Waddington [1959]). Waddington argued that the developmental system of these traits is such that any minor perturbation in a developmental input, such as a gene product, will merely cause a different route to be taken to the same developmental outcome. The recent work of process structuralists centers on the existence of 'generic forms'. If the developmental system of an organism is conceived as a complex system, generic forms are attractors into which that system will fall from a large range of starting configurations (Goodwin, Kauffman, and Murray, [1993]).

Process structuralists hope to classify traits by their generic form and return biology to a 'rational morphology' based on universal laws of development (Smith [1992]). The process structuralist programme is thus opposed to the traditional Darwinian approach to morphology which classifies traits on the basis of their descent from common ancestral forms. It is possible, however, to treat 'Newtonian' traits in a manner entirely consistent with Darwinism. One obvious way to do this is to historicize the idea of a generic form. The generic forms divide the overall space of biological possibility into regions available to a particular type of organism. The process structuralists view this structuring of the space of biological possibility as part of the fundamental structure of nature. There is little evidence, however, to back up this interpretation. The generic forms that exist in nature may be a small subset of the possible generic forms that could have been created by the historical design of alternative developmental systems (Griffiths [forthcoming]). Something like this was envisaged by Waddington in his original vision of developmental canalisation. William C. Wimsatt has also written extensively about a Darwinian

⁴ The use of an item's function, as opposed to its structure, as a taxonomic character is central to the Lorenzian tradition in ethology. A description of the use of function characters in more anatomical contexts can be found in the work of George V. Lauder [1990].

mechanism that could divide the space of biological possibility in the manner of generic forms. This mechanism is 'generative entrenchment' (Wimsatt [1985]; Schank and Wimsatt [1986]; Wimsatt [forthcoming]). Wimsatt notes that the key to natural selection is the possibility of incremental design. Very unlikely forms can be produced by a simple generate and test procedure because they can be produced a piece at a time. The improbability of the overall design is the product of the improbability of its components. These component improbabilities can be relatively small. In incremental design a later modification is generated against the background of the existing developmental system. The removal of ancient elements of the developmental system is likely to remove the presuppositions of later modifications and to disrupt the development of those modifications. Element of the developmental system therefore tend to become increasingly generatively entrenched as more is built on top of them. The existing developmental system of the organism comes to shape the space of possibilities available to the organism.

If some traits are Aristotelian rather than Newtonian, then the maintenance of these traits can be explained as well as their origins. Adaptive forces can be postulated to explain why the trait has not become vestigial, or declined in frequency in the population. The possibility of explaining maintenance necessitates some changes in the anti-adaptationist critique. That critique suggested two ways in which the comparative method might be used to improve the study of adaptation: inductivist methods for generating adaptive explanations and falsificationist methods for testing adaptive explanations. The role of both these techniques can be brought into sharper focus by the distinction between explanations of the origins of traits and explanations of the maintenance of traits.

It is universally accepted that when correlating traits with the ecological factors that may be responsible for them, all examples of a trait that result from one evolutionary origination count as one example of that trait. This principle remains sound when the aim is to understand the conditions under which the trait originated. If, however, the aim is to understand the conditions under which the trait has recently been maintained, then all existing populations are potentially relevant. Populations should be weighted according to the length of time for which they have existed as separate evolutionary units. The shorter the time since the population separated from other populations, the less the maintenance of a character in that population calls for an explanation in terms of current environmental conditions. A third possibility is that the explanatory focus is neither on origins nor on recent maintenance, but on maintenance at earlier stages in evolution. In that case, populations which separated from one another after the period in question must be treated as one,

but populations separated at the period in question constitute independent data points even if they derive the trait from a common ancestor.

Another difference between studies of origin and studies of maintenance will be in the way traits are classified. In most comparative studies traits are classified by homology. All traits which descend from a single ancestral origination event are considered to be of one, homologous type. This means that vestigial examples of the trait are counted along with all other examples. This is clearly appropriate when looking at existing populations for evidence of a past event. In studies of recent maintenance, however, the aim is to understand recent processes. Only populations in which the trait exists in an unreduced form will be counted as possessing that trait.

The falsificationist version of the comparative method is currently used to test adaptive claims about origins. The method makes adaptive scenarios yield predictions about the phylogeny of the trait under study, the phylogeny of related traits and the biogeography of the trait. The failure of these predictions suggests that the trait did not originate in the proposed adaptive scenario. The very same methods will be useful in addressing some questions of maintenance. An adaptive scenario might try to explain why a character was maintained in some distant period. This scenario will concern some portion of the phylogenetic tree and should yield predictions about the distribution of characters in existing populations. Ethologists have always explained the possession of phylogenetically ancient behaviours in current species in terms of secondary functions quite distinct from those for which the behaviours originally evolved (e.g. Tinbergen [1952]; Hinde [1966]). Many of these explanations have been supported by appeal to character distributions amongst existing populations. However, where the maintenance explanation concerns the recent past, falsificationist versions of the comparative method will not be relevant. Hypotheses about events in the immediate evolutionary past do not yield predictions about character distribution other than that the character will be associated with the proposed causal factor. These associations are assessed by the 'inductive' use of comparative data.

7 Conclusion

Anti-adaptationism in biology has been widely interpreted as a rejection of natural selection. I have tried to show it was also a call for reform in the methods by which adaptation is studied. The disciplinary angst about adaptationism in the 1980s, like the disciplinary angst about group selection hypotheses in the 1970s, was caused by widespread concern about what felt like a shaky game. Like the group selection debate, it led to a very considerable tightening up of both theory and practice. The historical

turn in the study of adaptation has led to the development of powerful empirical methods for the generation and testing of adaptive hypotheses. These are an essential supplement to the existing methods of hypothesis generation.

One way in which the historical turn may have gone too far is by suggesting that the only interesting questions about adaptation concern the ultimate origin of traits. Criticisms of this view have recently begun to emerge (Griffiths [1992]; Reeve and Sherman [1993]). These critics have argued that adaptive considerations can explain how traits have been maintained, as well as how they originated.

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