

long interbirth intervals (IBIs) could just as easily be a consequence of high levels of infectious secondary sterility rather than an adaptive response to local ecological conditions. Placing the !Kung into a wider geographical context thus allowed Pennington and Harpending to identify STD infection as another relevant variable in the analysis of !Kung birth spacing, and to proffer this as an equally valid, nonevolutionary explanation for the patterns shown.

Our second example concerns the issue of appropriate methodology. In a series of celebrated papers, Cosmides (1989; Cosmides & Tooby 1992; Fiddick et al. 2000) has used the Wason selection task as a means of testing whether humans possess a psychological adaptation for “cheat detection.” The central result of these studies is that subjects generally solve a conditional reasoning problem easily when it is presented as a social contract infringement, but they consistently fail to do so when it is presented as an abstract logical problem. According to Cosmides, these results point to the operation of a content-specific mental algorithm devoted to social contract problems.

However, Sperber and colleagues (Sperber et al. 1995; Sperber & Girotto 2002; in press) have argued that Cosmides’ results demonstrate nothing of the sort – not because her notion of a cheat detection algorithm is wrong; indeed, they suggest that it is highly plausible – but because the Wason selection task, and the variants that Cosmides has used, are simply not capable of testing whether such a thing exists. Although lack of space prevents a full discussion, the core of their argument is as follows. First, they consider the value of the selection task as a means of studying human inference to have been grossly overestimated. This is because, as Sperber et al. (1995) have demonstrated, the original Wason selection task is solved by what they call “relevance-guided comprehension processes” that preempt the use of other inferential capacities. In other words, the selection task does not tap into human inference processes in the way that Cosmides has assumed. Secondly, they argue that some of the variants of the Wason task that Cosmides has employed are not actually Wason tasks at all, and are even more inappropriate for the purpose of discovering a competence for social exchange – that is, they do not ask subjects about the truth/falseness or respect/violation of a conditional rule, but merely ask subjects to select cards that define a category (such as “cheater”), and so are trivially easy for subjects to pass. Sometimes this category selection task is mixed with the Wason task, giving rise to a task that is, in Sperber and Girotto’s (2002) opinion, methodologically unsound. Backing this argument with convincing experimental results, they conclude that, to date, Cosmides’ hypothesis has not been properly tested experimentally, least of all by Cosmides herself, and that “further investments of effort” in uses of the task should be discouraged (Sperber & Girotto 2002 p. 289).

Thus, while the adaptationist programme is indeed the best research strategy we have for detecting adaptations and testing for alternative explanations, we need to ensure that, as well as appropriate standards of evidence, we also adopt appropriate methods to provide this evidence and that all of the evidence appropriate to the issue is included in our analyses.

## Use of phylogenetic analysis to distinguish adaptation from exaptation

Daniel G. Blackburn

Department of Biology, Life Sciences Center, Trinity College, Hartford, CT 06106. [daniel.blackburn@trincoll.edu](mailto:daniel.blackburn@trincoll.edu)  
<http://shakti.trincoll.edu/~blackbur/>

**Abstract:** One important difference between adaptive and nonadaptive explanations can be found in the evolutionary sequence of structural and functional modifications. Phylogenetic analysis (cladistics) provides a powerful methodology for distinguishing exaptation from adaptation, by indi-

cating whether character traits have predated, accompanied, or followed evolution of particular functions. Such analysis yields falsifiable hypotheses that can help to distinguish causal relationships from mere correlation.

Critiques of adaptationism (e.g., Gould & Lewontin 1979; Lewontin 1978; Williams 1966) have focused on the scarcity of good criteria for recognizing adaptations, and on untested assumptions that natural selection optimizes structural features. Other work has developed alternative explanations for structural-functional correlations – notably exaptation and formation of architectural by-products (spandrels) (Gould 1991a; 1997e; 2002; Gould & Lewontin 1979; Gould & Vrba 1982). Although adaptationism gained a pejorative connotation in some circles (see Rose & Lauder 1996b, p. 2), adaptation remains a central concept in evolutionary biology (Gans 1988; Mayr 1982; 1988).

Andrews et al. have contributed usefully to ongoing dialogues by reviewing and refining criteria for the recognition of adaptations. Their analysis emphasizes the importance of rigorously testing adaptationist hypotheses, and of rejecting them in favor of alternatives when adaptationist explanations fail to conform to predictions. However, if exaptation and spandrel formation are to be treated seriously as evolutionary explanations, they too must be defined in falsifiable terms, and ideally, tested against adaptationist hypotheses. Otherwise, exaptation itself may become an untested assumption or a default explanation, despite other nonadaptive explanations for structural-functional relationships.

The principles and methods of cladistics (phylogenetic analysis) offer a powerful way to distinguish adaptation from exaptation. Cladistic methodology originally was developed to analyze phylogenetic relationships (Hennig 1950). In cladistics, lineages are recognized by presence of shared, derived (advanced) characteristics (Brooks & McLennan 1991; Eldredge & Cracraft 1980). Thus, derived neural and skeletomuscular features define bats (Baker et al. 1991), whereas hair defines the more inclusive mammalian group to which these chiropterans belong. The cladistic approach contrasts markedly with older approaches, in which organisms are grouped by overall similarity and taxa are defined by subjective criteria. Cladistics has revolutionized systematics, overturning some traditional taxonomic categories and firmly establishing others.

Phylogenetic analysis has also proven valuable as a means of reconstructing evolutionary history. By superimposing phenotypic features over accepted phylogenies, one can adopt parsimonious interpretations of evolutionary change. For example, application of cladistic principles has facilitated analyses of reproductive evolution in vertebrates (Blackburn 1992; 1999; Mess et al. 2003), as well as reconstruction of fetal membrane evolution in mammals (Freyer & Zeller 2001; Lockett 1977; Mess 2003) and reptiles (Blackburn 1998; Stewart 1997; Stewart & Thompson 1996; 2003). Cladistics requires us to document carefully the evolutionary sequences through which features evolve, with reference to particular phylogenies. Resultant evolutionary explanations therefore are testable, parsimonious, and relatively free from preconceptions about the nature and direction of evolutionary transformations.

One crucial difference between adaptation and exaptation lies in the chronological sequence of structural and functional modification. In adaptation, the modification of a phenotypic feature (e.g., a structure or behavioral trait) accompanies or parallels its evolutionary acquisition of a function. However, in exaptation, the feature originates first (either as a selected or nonselected attribute) and only later is coopted for the function in question. For example, the presence of elongate, vaned feathers in terrestrial saurischians (Qiang et al. 1998; 2001) implies that they are adaptations for endothermy or display, that only later became exaptations for avian flight. Likewise, mammary secretions may originally have functioned in immunological protection of offspring, and were exapted and secondarily adapted for nutrient provision (Blackburn 1993).

Phylogenetic analysis provides powerful methods for distin-

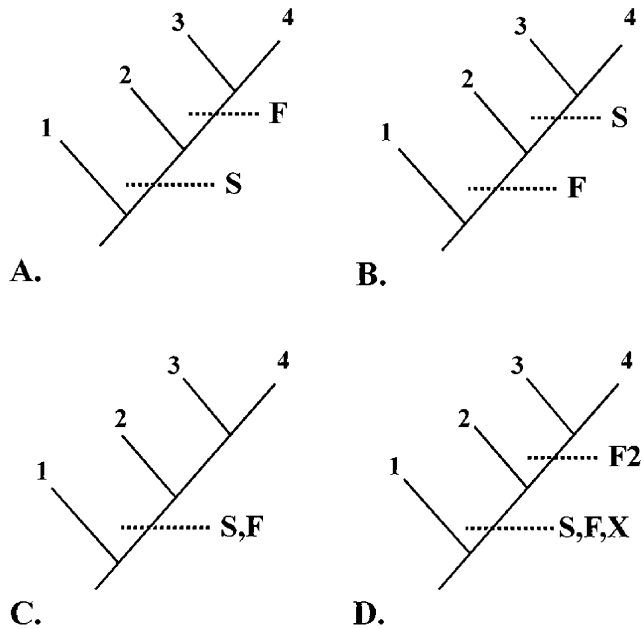


Figure 1 (Blackburn). Cladograms of four taxa, showing the timing of evolution of a given structure (“S”) and function (“F”), as inferred from characteristics of the taxa. In A, the structure evolutionarily predates a function that it serves, indicating exaptation. In B and C, the function respectively predates or accompanies evolution of the structure; such sequences are necessary (but not entirely sufficient) indicators of adaptation. In D, a spandrel (X) has accompanied evolution of an adapted structure (S) as an architectural byproduct; here, the structure subsequently is exapted for a new function (F2).

guishing exaptation from adaptation by determining whether character traits have predated, accompanied, or followed evolution of their functional attributes (e.g., see Blackburn 2000; Larsen & Losos 1996). The enclosed figures illustrate a cladogram of hypothetical taxa, with various possible phylogenetic distributions of a particular structure (or other phenotypic characteristic) and a function superimposed. The timing of evolution of a feature is inferred from its taxonomic distribution (Brooks & McLennan 1991). Thus, in Figure 1A, the presence of a derived structure (“S”) in three of the taxa indicates that it probably characterized their common ancestor. When the structure originates first and only later takes on the function in question (as in the mammary example above), exaptation is indicated (Fig. 1A). When a function either predates (Fig. 1B) or accompanies (Fig. 1C) evolution of a structural feature, it may represent a case of adaptation. Phylogenetic analysis also may facilitate recognition of spandrels. An architectural byproduct should originate as an unselected correlate of a particular structure, regardless of whether the structure itself is selected (Fig. 1D).

In phylogenetic analysis, adaptation and exaptation have the status of mutually exclusive, competing hypotheses, each of which can be falsified or supported according to the sequence of evolutionary modification. That a structure antedated the function it performs, offers a sufficient criterion for recognition of exaptation. However, a function predating or accompanying evolution of a given structure is a necessary but insufficient criterion for recognition of adaptation; therefore, other criteria (such as those discussed by Andrews et al.) must also be brought to bear. In effect, phylogenetic analysis allows us to address, in an evolutionary context, difficult issues whose recognition dates to the writings of David Hume – notably the difficulty of distinguishing causation from correlation.

As a practical matter, phylogenetic analysis is useful chiefly where a robust cladogram can be constructed from taxa that vary

in structural and functional features of interest. It therefore offers no panacea to evolutionary psychology, where inferences of genetically based behavioral attributes are problematic, particularly as applied to extinct hominids. However, in principle, phylogenetic approaches offer ways to analyze evolutionary sequences and transformations in historical contexts, and where sufficient data are available, they can provide clear evidentiary standards for distinguishing exaptation from adaptation.

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**There is no evidentiary silver bullet for the frequency adaptation hypothesis**

Gary L. Brase

*Division of Psychology, Sunderland Business School, University of Sunderland, Sunderland, SR6 0DD United Kingdom.*

[gary.braser@sunderland.ac.uk](mailto:gary.braser@sunderland.ac.uk)

<http://www.sunderland.ac.uk/~bs0gba>

**Abstract:** Special design criteria are largely unable to discriminate between claims that specific competencies in judgements under uncertainty are a result of an adaptation for representing naturally sampled frequencies, or due only to inherent properties of such a format. Because divisions between these perspectives are thin, evidence via additional criteria are persuasive only in combination, using inference to the best available explanation.

Andrews et al. point out, quite correctly, that different traits may require satisfaction of different evidentiary criteria in reaching some consensus on whether it is an adaptation. This may actually not be a strong enough statement of the case: In many situations, one or more of the usual evidentiary criteria may be used to argue against the case for adaptation. A case in point is the recent debates on the nature of statistical judgements under uncertainty.

The claim has been made that information in the form of frequencies, and in particular frequencies in a natural sampling framework, is privileged representational format (i.e., that it is the proper domain for a cognitive adaptation for making statistical judgements; Cosmides & Tooby 1996; Gigerenzer & Hoffrage 1995). Those in opposition to this claim have pointed out that naturally sampled frequencies create computationally less complicated situations simply by virtue of their inherent properties and they reject the claim of a specific adaptation (e.g., Evans et al. 2000; Girotto & Gonzalez 2001; Johnson-Laird et al. 1999). In particular, the counter-hypothesis to an adaptationist explanation is that, because the frequencies within a natural sampling system inherently preserve base-rate information, the set/subset relationships between classes of events become much more easily perceived (see Fig. 1). Instead of an adaptation for understanding and using frequencies, this explanation rests on claims for a basic appreciation of set relations (which happen to be expressible almost exclusively in frequentist terms).

In the context of this debate, criteria such as proficiency, efficiency, economy, and reliable production are unable to discriminate between these two explanations; and in fact, the presence of these features – attributed to the nature of the inputs (natural frequencies per se) – have been used to argue against an adaptationist interpretation. One can argue that the proficiency, efficiency, and economy of the behavior when using natural frequencies is purely the result of the properties of the numbers themselves (natural frequencies are simply easier), or one can argue that these characteristics are a result of a cognitive mechanism that is preferentially tuned to using these numerical formats in the first place (natural frequencies are particularly easy because the mind is designed to work with them).

Discriminating between these two theoretical perspectives is difficult because the divisions between them have become thin,