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Constraints in Evolution: On the Baby and the Bath Water

Author(s): N. Perrin and J. Travis

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Constraints in evolution: on the baby and the bath water

We respond to Perrin & Travis's (1992) comment on our critique (Antonovics & van Tienderen 1991) on the use of constraints in evolutionary biology with some hesitation, as we probably agree with them on the major issues. However, their claim that we want to ban the concept of constraints from evolutionary biology is unjustified and motivated our response. Evolutionary biology indeed studies how changes take place, on the one hand directed by selective forces, and on the other hand by various kinds of limitations. That is 'our baby' and we cherish it. At the same time the literature is polluted with *ad hoc* terminology and the invocation of constraints in many contexts. This is the 'bath water' that we want to throw away. Instead of a Panglossian paradigm (if it ever existed) we seem to have evolved to a (Pan-Gouldian?) paradigm, in which the view of 'the best of all possible worlds' is replaced by 'the only possible in a restricted set of worlds'. This is as unrealistic as the Panglossian paradigm, and it results in the invocation of ill-defined and untested constraints as a causal explanation for every pattern observed.

Our critique on the usage of constraint and its terminology also seems to be shared by Perrin & Travis. In their paragraph 'constraints are diverse', they admit that adjectives are largely arbitrary, and they conclude: 'This is a matter of circumstantial convenience and remains unimportant *as long as the context is explicitly stated*' (our italics). This is indeed similar to our 'We ... urge that authors state the null model explicitly; usually this null-model describes what phenotypic variation to expect given a set of assumptions on the presence and expression of genetic variation'. Our plea for a moratorium on the term constraint was in fact a plea for more explicit specification of what is meant and we hope that most readers understood this message.

Perrin & Travis present an interesting view on constraints. They see evolution as a process of constrained optimization, which gives a formalization of constraints as the limits to the possible states. It follows then that 'the very process of natural selection is that of favouring those character values, from the set of existing values, that maximize fitness'. This is clear, although almost tautological. Option sets are probably seldom directly observable, and may change continuously through mutation, migration, drift, recombination, and indeed selection itself. The spectrum of possible mutations, for instance, may in turn depend on physiological or developmental mecha-

nisms. Separating the laws that limit the set of possible states, and the (optimization) process acting upon them is possible in engineering and optimization theory; however, in evolution there is a constant interaction between constraints and the processes that generate them. The crucial point is that the processes responsible for the actual constraints need to be identified. It is because of this complexity that we advocated the use of clear null models.

We would not have been unduly distressed with Perrin & Travis's contribution had they omitted the paragraph 'Extending the concept'. For instance, in discussing phylogenetic constraints, they state '*Sensu stricto*, these constraints do not refer to actual limits of opportunity sets, but rather to the shape of adaptive landscapes'. Now everything is thrown into confusion. Global instead of local maximization of fitness is now taken as the optimization process, justified by the facile invocation of the teachings of another deity, Sewall Wright. To us, it seems undesirable that a renowned optimization law (i.e. local selection) which we know operates in nature, is labelled as a constraint in a teleological or vaguely stated global optimization law. Furthermore, why is selection the constraint here? Major mutations that allow a jump to another higher peak may simply be neither feasible nor likely (some may call this a genetic or developmental constraint). Or there may be insufficient environmental variation to switch from one peak to another (Kirkpatrick 1982) (an environmental constraint?). The remark that 'non-feasible phenotypes may also be thought of as zero-fitness phenotypes' only adds to the chaos. We would like to see stated exactly why evolution has stopped at the local optimum and, for instance, what is needed to reach another optimum. If these things are stated explicitly the word 'constraint' becomes obsolete and no longer muddies the waters. It is a shame if progress in evolutionary biology is frustrated by sloppy terminology. Let us not forget that TALMUD stems from the Hebrew *lāmadh*, which means 'to learn'; hopefully this is our universal goal.

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P.H. VAN TIENDEREN
Netherlands Institute of Ecology
Department of Plant Population Biology
PO Box 40, 6666 ZG Heteren
The Netherlands

J. ANTONOVICS
Department of Botany
Duke University
Durham
North Carolina 27708, USA

Reply to TALMUD

Our main point (Perrin & Travis 1992) was that the concept of constraint is actually less fuzzy than claimed by TALMUD (Antonovics & van Tienderen 1991), which we illustrated by showing how its frequent uses can be understood by reference to a single conceptual framework borrowed from optimization theory.

Within this framework we distinguished two main current uses of the concept, according to whether it refers (1) to limits on the option set, or (2) to the shape of the adaptive landscape. To type 1 for instance belong the so-called 'physiological' and 'genetic constraints', and to type 2 the so-called 'selective' and 'phylogenetic constraints'.

We considered type 2 and extension of type 1. Whether this extension is justified is, of course, a matter of discussion. There is an important tradition in

this sense in biology, which may result, as TALMUD (van Tienderen & Antonovics 1994) suggests, from the difficulties met by biologists (as opposed to engineers) when trying to separate empirically the laws that limit the set of possible states and the optimization process acting upon them. Because of this tradition we suggest, instead of a moratorium, that biologists make clear statements about whether any current use refers to type 1 (option set) or to type 2 (adaptive landscape).

Apart from this, we are glad to see TALMUD converging on our position.

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N. PERRIN
Department of Behavioural Ecology
Bern University
CH3032 Hinterkappelen
Switzerland

J. TRAVIS
Department of Biological Sciences
Florida State University
Tallahassee
Florida 32306, USA