The exquisite corpse: a shifting view of the shifting balance

> 'What exalted us in these productions was…that they were endowed, in much greater measures, with a power of drift, that poetry cannot value too highly. With the exquisite corpse, we had at our disposal – at last – an infallible means of temporarily dismissing the critical mind and fully freeing metaphoric activity.'[1]

In 1925, a game called 'exquisite corpse' was invented by a group of surrealists to harness the random power of imagination through collaboration. Working either with words or drawings, an exquisite corpse was begun by one member of the group, who then folded the paper so that his or her contribution was obscured and then passed it to the next member. The game (named after one of their first results – *Le cadavre exquis boira le vin nouveau*) allowed the random words or images to be combined, followed by selection of the best results for preservation and dissemination (although they de-emphasized the latter). Therefore, the game serves as an acceptable metaphor for the shifting-balance process. After a recent flurry of papers[2–7], we might pronounce the strict adaptationist version of the shifting-balance theory (SBT) both 'exquisite' and a 'corpse', although the authors of these papers would probably only agree with one or the other of these assessments.

In 1931, Sewall Wright[8] proposed a theory, which would come to be known as his shifting-balance theory. This began with the idea that interactions among loci could result in populations achieving a genotypic state that was locally relatively fit (a 'peak'), but was not as fit as possible because of intervening unfit genotypes ('valleys'). Wright[9] suggested several mechanisms by which evolution might allow a population to reach higher adaptive peaks, including novel favorable mutations, relaxation of selection, qualitative changes in the environment and the model now known as the shifting-balance theory.

The shifting-balance process, in its strict interpretation, imagined that species were subdivided into many demes weakly connected by migration. Demes might be small enough that genetic drift can sometimes overwhelm the effects of natural selection and take the population to the domain of attraction of a new peak (i.e. the allele frequencies can drift to a point where the deterministic effects of selection would be expected to take the population to a new peak; this is referred to as Phase I). Individual selection could then take that population near to the height of the new peak (Phase II), at which time Wright envisioned intergroup selection would act to pull the whole species towards the new peak (Phase III). This story has served as a significant theory of adaptive evolution for the greater part of the 20th century.

Three years ago, a significant challenge to the SBT came from Jerry Coyne, Michael Turelli and Nick Barton[2], in the longest paper ever published in *Evolution*, where they reviewed the evidence against SBT. At the risk of oversimplification, their main arguments were: (1) Phases I and II are possible, but drift is often not necessary for peak shifts; (2) Phase III is unlikely to successfully spread new adaptive peaks to other demes; and (3) there are no known examples of the shifting-balance process going through all the steps envisioned by Wright. Furthermore, none of the partial examples can demonstrate an increase in adaptation as a result of shifting balance. They argue that parsimony would lead one to choose Fisherian mass selection as the simpler, and experimentally confirmed, explanation for the majority of adaptations. Although Coyne *et al.* allow for the potential occurrence of the SBT, they strongly reject it as an explanation for a significant proportion of adaptation. Coyne *et al.*[2] is also notable for its appendix, in which the distribution of allele frequencies among populations with drift, selection, mutation and migration, one of Wright's most enduring contributions to population genetics[10], was used to address the plausibility of the SBT itself.

Subsequently, Michael Wade and Charles Goodnight[3] have, in the same forum, published a defense of Wright's perspective on evolution. Although not a direct response to Coyne *et al.*, Wade and Goodnight argue that evolution is most effective 'when nature does many small experiments'; that is, when species are subdivided into a metapopulation. This perspective has prompted a debate[5,6] over the adaptive importance of epistasis, group selection, population structure and drift. Wade and Goodnight argue that the evolutionary process is strongly affected by epistasis; that group selection is much more effective than additive models would predict; and that population subdivision allows for multiple semi-independent evolutionary trials and for more effective adaptation and speciation.

These papers, and the recent round of rebuttals and responses[5–7], disagree greatly; however, they largely address different questions. Coyne *et al.*[2,5] are focused on the plausibility of a narrowly defined version of SBT, while Wade and Goodnight[3,6] have more broadly considered the role of 'Wrightian' modes of evolution without addressing important criticisms of the SBT. To some extent, the two sides are talking past each other and reading them sequentially is a bit like viewing the unfolded picture after drawing an exquisite corpse. We agree with Coyne *et al.* that showing that each of the components of SBT is plausible is not equivalent to showing that SBT is a major factor in adaptation, but it would be premature to entirely dismiss the possibility of the SBT (indeed, as Coyne *et al.*[2] have not done; see their final paragraph).

Intergroup selection can be a weak force, thus making Phase III difficult, but Coyne *et al.* have not presented a convincing case that it is impossible – in fact, most of the papers cited by Coyne *et al.*[2] have shown the efficacy of Phase III. Goodnight and Wade[6] point out that there are many effective demonstrations of the efficacy of group selection; but, Coyne *et al.*[5] argue that these studies are not controlled for individual selection. However, all that is required for SBT to function is that interdemic selection is possible – it is not necessary for interdemic selection to be faster than individual selection.

Perhaps more germane is that group selection might not be sufficient to overwhelm the effects of back-migration of old peak genotypes into the newly shifted population[11,12]. This causes a particular difficulty of Phase III in the island model, where a newly shifted deme has only a weak influence on all other demes, but collectively the other demes can exert strong pressure via migration for that deme to return to the original genotype. (Note, that Wright's distribution assumes an island model, thus the case explicitly modeled by the appendix[1] is certainly not the most probable scenario for the SBT to work. Strangely, given their interpretation, the calculations in the appendix of Coyne *et al.*[2] demonstrate a substantial parameter range under which SBT would be effective.) As others have pointed out[4,7,13], models of population structure with isolation by distance are

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much more conducive to effective export of adaptive peaks by group selection.

However, more convincing is Coyne *et al.*'s claim[2] that SBT is not necessary to explain any known biological phenomenon. Wright's alternative models of peak shifts, particularly changing environments and selection pressures, are much more plausible and more probable than peak shifts by genetic drift[14].

Moreover, as Coyne *et al.* argue, there is no known example of evolution for which we have a demonstration of each of the phases of the SBT. There are examples of evolution that require population structure, examples that require genetic drift, those that involve epistasis and, arguably, some that involve group selection[3,6]; however, none demonstrably involve all of these processes jointly, as invoked by strict versions of the SBT. Importantly, none of the examples provided of shifting balance have demonstrated an increase in fitness as a result of peak shifts. Thus, the SBT has not succeeded in predicting patterns of adaptation in nature. We see this as the primary challenge to the supporters of the SBT – to produce an example of adaptation that cannot have proceeded except by shifting balance. Indeed, Wade and Goodnight have failed to point to such an example. As Wright[9] said: 'How far do the observations of actual species and their subdivisions conform to this picture?'

However, we should not throw out the baby with the bath water. Although the SBT has not yet been shown to succeed as a theory of adaptation, a diversity of evolutionary processes has been informed by elements of Wright's model. As Wade and Goodnight[3] point out, there is a wealth of evidence about the existence and importance of genetic drift, epistasis and population structure. These processes would not have been studied nearly as much without the framework of the SBT. Indeed, many evolutionary stories, including those reviewed by Coyne *et al.*[2] (such as RNA evolution, evolution of mimicry in *Heliconius* butterflies, tristyly in *Eichhornia*, coiling in snails and chromosome evolution), are better understood as a direct result of work on the SBT. Nevertheless, these cases are limited in number and the proponents of SBT, such as Wade and Goodnight, have yet to demonstrate that SBT-related processes, even when they are present, play a central and necessary role in explaining many existing evolutionary patterns.

Coyne *et al.* are trying to bury the corpse of the SBT. Why its enduring attraction? First, Wright's metaphor of evolution on an adaptive landscape is one of the most compelling in evolutionary biology. Seemingly, it reduces a complex set of interacting forces to a simple graphical form. However, multidimensional landscapes are likely to be quite complicated and to possess emergent properties not easily represented in simple diagrams. For instance, adaptive peaks in two dimensions might be spanned by ridges of higher fitness in other dimensions, therefore, not requiring drift for evolution on a rugged landscape[15,16]. Second, the SBT directly confronts the evolution of complexity. The basic mechanisms of biological systems suggest that they are composed of complexes of interacting components whose individual roles seem crucial to the successful functioning of the whole. Complexity in, and of, itself does not necessitate a shifting-balance process; components can be added to complex systems independently, as long as they exhibit some initial advantageous function. It is also possible that many parts of existing systems are stuck at local optima as Wright envisioned, but that overall evolutionary change does not cease because there is nearly always some dimension in which the system as a whole can improve[1]. Third, the SBT is the most synthetic theory of evolutionary change ever formulated. Of the major forces on evolution, only mutation does not play a central and determinative role in Wright's account of the theory[17], although it is included in the equilibrium solutions. The SBT is a powerful pedagogical tool because it forces one to appreciate the potential importance of the balance and tradeoffs among evolutionary forces.

The SBT has been extremely valuable as a means of focusing attention on the diversity of processes that can affect the trajectory of evolution. Our view is that the SBT is plausible but not necessary; other forms of evolution on adaptive landscapes are theoretically and empirically better supported. The SBT might be important for many examples of nonadaptive evolution, such as chromosomal rearrangements or tRNA evolution; however, as a model of adaptation it has little empirical or theoretical support. As an exquisite corpse, the themes SBT embrace continue to have great relevance to modern evolutionary theory.

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