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HALDANE'S COINCIDENCE: A REPLY TO BROOKFIELD

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Brookfield (1993) suggests five tests that he claims establish the statistical significance of Haldane's Rule, contrary to our conclusion (Read and Nee 1991). We reject the basis of all five. The first four assume that taxa, branches, or infinitesimally short segments of branches, all have equal and independent probabilities of character change. This is untrue across large phylogenies; indeed, accounting for taxon-specific variation in the likelihood of character change is the central problem for comparative biologists (Harvey and Purvis 1991). If one is willing to make such assumptions, it is far easier to establish the significance of Haldane's Rule by reverting to the discredited practice of treating species as independent.

Brookfield apparently realizes this problem and hence proposes his final test. However, the conclusion he draws from that is critically dependent on the probabilities of change, which he assigns arbitrarily. Ours is not. We compared taxa with female heterogamety to their nearest closest relatives with male heterogamety, and asked in which of those sister taxa is female hybrid inviability more common. Under the null hypothesis of no association, the chance that it should be the taxon with female heterogamety is 0.5. Note that this calculation allows the underlying probability of character change to vary at any point in the tree and does not require that we specify what those probabilities are.

As we pointed out (Read and Nee 1991), only two such comparisons are possible from extant data. Both support the rule, as might be expected by chance alone ($0.5^2 = 0.25$). Thus, far from "neglect[ing] the evidence for a causal link between the characters supplied by the observation that the sex of hybrid fitness loss does change between taxa that differ in their heterogametic sex" (Brookfield 1993, p. 1887), our test makes explicit how few such observations there actually are. (Coyne et al. [1991], Partridge [1993], and Brookfield [1993] suggested that salamanders of the genus *Triturus* provide another relevant comparison. There is some suggestion that male heterogamety in this group is derived [Hillis and Green 1990] and that male hybrids have lower fertility [Spurway 1953]. However, in the absence of data on the fitness of hybrids from a sister taxon with female heterogamety, the *Triturus* data are uninformative.)

Not only has Brookfield based his tests on assumptions that biologists increasingly find unacceptable, but his probability calculations are also flawed. First, the probability given by Brookfield in his initial test, for example, uses a set of possible events that is far too large. Included are the possibilities that all taxa evolved

male hybrid unfitness and that all evolved female hybrid unfitness. But for reasons clearly explained by Fisher (1956, pp. 86–88) in a much earlier debate, rational inference in such cases requires that the set of possible outcomes be restricted to the subset that has five of seven taxa with male hybrid unfitness. Second, in all five of Brookfield's tests, the calculated probability values critically depend on which taxa are specified in the tree. By expanding or collapsing particular parts of the tree, any desired conclusion can be obtained (consider, e.g., adding just those species that are exceptions to the "rule").

Brookfield worries that we regard as irrelevant lineages in which neither the heterogametic sex nor the sex suffering hybrid unfitness has changed. But correlated lack of change in either character could arise either from a causal link between them or, equally, from their independent association with other unchanging, taxon-specific traits. For example, male hybrid unfitness is apparently an ancestral state maintained throughout most of the tree for which there are data (Read and Nee 1991, fig. 1). Even if this is caused by a taxon-specific trait found everywhere except in birds and butterflies, male heterogamety is but one candidate character. Intuition and experimental evidence may support Haldane's inference that that is the relevant trait, but the inference is not supported by the comparative evidence.

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