

are obtaining extra-pair young' and he suggests that these data disagree with predictions from the good genes hypothesis. However, under the good genes hypothesis, we expect females to base their choice for extra-pair copulations on their assessment of the relative quality of their own mate versus the available extra-pair males (i.e. usually their neighbours). Thus, quality should not be seen in an absolute sense, but relative to other options available for each female. Ideally, pairwise comparisons of the characteristics (quality) of within-pair and extra-pair males from the same nests should be made, such as those in the recent study of great reed warblers (*Acrocephalus arundinaceus*)¹.

We suggested, under the genetic quality hypothesis, that low levels of extra-pair paternity might be expected in populations that had undergone a bottleneck, because genetic quality differences among males would be low. Cordero suggests there are alternative explanations. According to the 'heterozygosity' theory, females choose mates to avoid the expression of lethal or deleterious genes by producing heterozygous rather than homozygous offspring. This theory does make predictions about the frequency of extra-pair copulations in relation to the overall genetic diversity in populations, but in the opposite direction to that expected from genetic quality benefits. In populations with lower genetic diversity, the risks of inbreeding depression are higher and, therefore, females might be more likely to seek extra-pair matings if the main benefit is the production of heterozygous offspring.

We agree that avoiding inbreeding effects or genetic incompatibility is important for a female and might explain some multiple mating patterns (such as when a female has several extra-pair partners). However, it is not yet clear whether these mechanisms, by themselves, can maintain the high variance in male mating success, which is a feature of species with high levels of extra-pair paternity². It is this nonrandom distribution of matings that provides the evolutionary force necessary to produce the sexual ornaments characteristic of populations with extra-pair paternity³ and that is more readily explained by genetic quality benefits.

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Key innovations?

Hunter's *TREE* review⁴ of 'key innovations' raises several concerns:

(1) Most definitions of key innovations portray them as playing a causal role in diversification. They are identified as adaptive features present in all members of a diverse clade and, by implication, in the clade's ancestor. But how is a clade delineated? A clade is diagnosed by synapomorphies implicitly present in a common ancestor. So, the features used to define a clade are also advanced as the explanation for its existence – thereby confusing correlation and causation.

(2) Hunter's terminology ignores the 1980s revolution in macroevolutionary theory – particularly his reference to 'successful' clades seizing 'opportunities' to diversify into new 'adaptive zones'. Hierarchy theorists laboured to expunge such ideological thinking. Vrba's 'effect' hypothesis² argues that apparently 'successful' clades are actually intolerant clades; their members have narrowly defined resource requirements, and environmental change exposes them to negative selection (mortality or reproductive failure). Can such a clade sensibly be labelled more successful than a more tolerant group (which can roll with the punches), which is consequently species-poor and likely to persist in the face of habitat deterioration?

(3) This value-laden terminology points to a confused model of speciation and/or radiation. The most enduring conflict of evolution concerns the role of natural selection in the origin of species. Key innovations imply features that enhance survival or reproduction in the face of competition, predation or environmental challenge. If key innovations are a cause of radiation, it must be in one of these contexts. However, there is little evidence to support such a claim³. Adherents of both the traditional synthesis^{4–6} and the expanded macroevolutionary synthesis^{7,8} argue that radiation is more rapid and more extensive in the absence of competitor and predator pressure, for example on oceanic islands or in the period immediately following a mass extinction. Furthermore, Hunter's review indicates that the role of key innovations is to allow organisms to escape these very sources of selection, leaving environmental challenge as the sole directional pressure driving diversification.

If key innovations allow taxa to invade new adaptive zones, they must arise before such invasions and without the benefit of direct selection by the environment to which they are fortuitously suited. They are true exaptations⁹. We have no difficulty believing the concept that an exaptation might allow a population to persist under altered environmental conditions; this is the essence of Darwin's model. What we fail to see is why an exaptation should 'promote speciation'. Why should the possession of a fortuitous character that has allowed a population to survive one punishing round of selection, provoked by exposure to a novel environment, now inspire its descendants to invade new and different environments with similarly destructive consequences? Isn't it more likely that the real factor promoting speciation is not the key innovation but the same kind of environmental change that destroyed the population's habitat in the first place, forcing it to adapt to a new niche?

The concept of key innovations does more to confuse macroevolution than to clarify it.

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Reply from J.P. Hunter

I agree with Masters and Rayner on three points. First, the search for key innovations might become circular if one merely assumes that synapomorphies of diverse clades are key innovations, which is why I warned against such assumptions (Ref. 1; Box 3). The test of a key innovation lies in its functional attributes and association with radiation in (preferably) multiple replicate lineages and not in its usefulness in reconstructing phylogeny. Some key innovations are indeed rather homoplastic (Ref. 1; Box 4). Second, species richness is not the sole measure of 'success'. Rather, success can be measured in many ways, including species longevity, phenotypic diversity, abundance and even biomass¹, all of which imply expansion in the use and control of energy². Third, I have argued^{1,3} that some key innovations are exaptations that allow a lineage 'to persist under altered environmental conditions'. Enhanced survivorship promotes diversification because extinct species can neither speciate⁴ nor 'invade new and different environments'. Exaptations need not promote speciation when they can operate equally well by lowering extinction rate.

Masters and Rayner oversimplify when they characterize the consensus opinion to be that competition inhibits diversification. Competition is indeed commonly modeled as inhibitory⁵, and exponential diversification is the null expectation in the absence of pre-emptive competition and other constraining factors⁶. However, competition may also escalate adaptation⁷ and drive character evolution during adaptive radiation^{8,9}, particularly in low density environments, such as on oceanic