NOTES AND COMMENTS

TESTING WHETHER CERTAIN TRAITS HAVE CAUSED AMPLIFIED DIVERSIFICATION: AN IMPROVED METHOD BASED ON A MODEL OF RANDOM SPECIATION AND EXTINCTION

One of the more striking patterns of organismal diversity is the repeated occurrence of taxonomic groups that are conspicuously large as compared to related groups. Well-known examples include passerine birds and beetles. A common response to such groups by systematists and evolutionary biologists is to invoke one or more intrinsic features of those groups as the causal factors in those groups' evolutionary success. For example, with regard to anoline lizards, Peterson (1983, p. 245) wrote, "The pad complex [the expanded subdigital toe pad] appears to be a key innovation . . . in the successful radiation of the group." The literature is replete with such statements. Traits believed to have caused increased diversification are usually termed "key innovations" or "key adaptations."

However, when a researcher claims that some derived feature of a group is responsible for that group's increased diversity, he or she is making two implicit assumptions: that the group's unusual size must have resulted from an increased probability of speciation and/or a decreased probability of extinction (relative to related groups) and that the specified trait can be identified as the causal factor.

These assumptions are dubious. The problem with the first assumption is made clear by a simple, but strongly counterintuitive, mathematical result: under a simple model of tree growth by random speciation, all possible numerical divisions of a fixed number of species into two disjoint groups of species (representing sister groups) are equiprobable (Farris 1976; Van Pelt and Verwer 1983; Slowinski and Guyer 1989; Maddison and Slatkin 1991; Felsenstein 1992). As Maddison and Slatkin (1991) point out, this result is equivalent to a special case of Polya's urn model (Feller 1957, pp. 109–111), which can be described as follows. An urn initially contains one red ball and one black ball. A ball is drawn at random and replaced into the urn, and another is added of the same color as the one drawn. This is continued until there are n balls in the urn. As is well-known (Feller 1957), it is equally likely that there will be $1, 2, 3, \ldots, n - 1$ red balls in the urn. In phylogenetic terms, the number of balls of one color represents the number of species in one of two sister groups arising from a common ancestral species. Slowinski and and Guyer (1989) found that this result also applies if random extinction is incorporated into the model. We are not arguing that specia-

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tion and extinction have been random but rather that a group's size, no matter how great, is not prima facie evidence that the group arose from nonrandom speciation and/or extinction.

The problem with the second assumption is that, even if it could be assumed that some particular group arose via nonrandom diversification, it would be impossible to identify the responsible trait correctly. How, for example, would one devise a test of the specific hypothesis that the toe pad complex in anoles caused anoles to diversify at a faster rate than related lizards? It seems to us that the traditional process of identifying key innovations simply entails identifying whichever feature of a diverse group seems most distinctive. Seldom is any consideration given to whether there are theoretical reasons to believe that the identified trait would amplify speciation and/or decrease extinction.

Taken together, these criticisms suggest that the common practice of invoking key adaptations to explain the diversity of *individual* groups should be abandoned. Key adaptation scenarios are untestable and, hence, unscientific.

However, the existence of a cause-and-effect relationship between some trait and increased diversity can be tested if several to many groups possessing the trait are considered, not just one. In this note, we discuss this approach as developed in two recent articles (Mitter et al. 1988; Zeh et al. 1989), then suggest improvements to the method.

THE SISTER-GROUP COMPARISON METHOD

Recent articles by Mitter et al. (1988) and Zeh et al. (1989) stand out as major advances over traditional key innovation scenarios. Mitter et al. tested whether phytophagy has promoted increased insect diversity. They compared 13 putatively monophyletic groups of phytophagous insects to their nonphytophagous sister groups. In 11 of the 13 comparisons, the phytophagous clade was larger. Under a null model in which either clade could be larger with a 0.50 probability, the null hypothesis that phytophagy has not promoted increased diversification was strongly rejected using a one-tailed sign test. Zeh et al. (1989) used the same methodology to test whether a suite of derived egg-related characters has promoted increased diversification in insects. In 12 of 14 sister-group comparisons, the group possessing the derived characters was larger, a statistically significant result under a one-tailed sign test.

The methodology employed by these authors represents a significant advance for two reasons. First, they directly considered phylogenetic information by comparing the sizes of sister groups. Comparing sister groups redefines evolutionary success in terms of relative size rather than absolute size. The traditional approach has been to evaluate a group's evolutionary success in terms of its absolute size, which is unacceptable because the amount of time that it has taken for the group to evolve is not considered. Sister groups, on the other hand, arose from the same ancestor and, therefore, are equally old (Cracraft 1981).

Second, these authors, in examining multiple, independent groups, have introduced testability to questions of evolutionary success resulting from key innovations. As previously mentioned, under a simple model of random speciation and

extinction, large groups are as probable as small groups. Therefore, there is no justification for assuming that a particular group represents the result of nonrandom diversification. The solution, as adopted by Mitter et al. (1988) and Zeh et al. (1989), is to compare the size distribution of several pairs of sister groups to the predictions of some null model.

Despite these advances, we feel that the methodology of Mitter et al. and Zeh et al. suffers from two flaws. First, both biased their results by choosing traits to test that they knew to be associated with diverse groups, a practice that introduces problems with Type I statistical error (rejecting a null hypothesis that is correct). Ideally, traits should be chosen in ignorance of the diversity of the groups possessing them and because there are theoretical reasons to believe that they would cause amplified diversity.

The second problem with their methodology lies in the null model employed, in which either of two sister groups could be larger with a 0.50 probability. Statistical tests based on this null model will lack power for the simple reason that the model fails to consider the absolute difference in the sizes of sister groups, only whether one is larger than the other. For example, consider a hypothetical trait with a genuine potential to cause increased diversification; if several of the groups possessing that trait have responded strongly to it (have many more species than their sister groups) but most have not, a sign test or binomial test would probably be nonsignificant.

We feel that a more powerful approach combines Mitter et al.'s and Zeh et al.'s sister-group comparison method with a more sophisticated null model, namely one based on random speciation and extinction.

AN IMPROVED APPROACH

A model of tree growth by random speciation was originally formalized by Harding (1971), under which every tip of a growing phylogeny has an equal probability of speciating. Speciation events are constrained to be dichotomous. We (Slowinski and Guyer 1989) found that random extinction could be incorporated without changing the model's predictions. The following expressions give the conditional probability under this model that some number n of species will be divided into sister groups of $r \geq n/2$ and $n - r$ species:

$$p(r|n) = 2(n - 1)^{-1} \quad \text{if } r > n/2 \tag{1}$$

or

$$p(r|n) = (n - 1)^{-1} \quad \text{if } r = n/2 \tag{2}$$

(Farris 1976; Van Pelt and Verwer 1983; Slowinski and Guyer 1989; Maddison and Slatkin 1991; Felsenstein 1992). As discussed above, this result is equivalent to a special case of Polya's well-known urn model (Maddison and Slatkin 1991). These equations made the surprising and strongly counterintuitive prediction that all possible divisions of n into sister groups of size r and $n - r$ are equiprobable.

Equations (1) and (2) can be modified to use for testing whether certain traits have caused amplified diversity. Two modifications are necessary. First, r is

redefined as the size of the group possessing the trait being tested, rather than arbitrarily as the size of the larger sister group. Second, for statistical testing, it is necessary to convert equations (1) and (2) to a cumulative form expressing the probability that a group possessing a particular trait is of size r or greater. This is

$$p_c(r|n) = p(r|n) + p(r + 1|n) + \ldots + p(n - 1|n) = n - r/(n - 1). \quad (3)$$

To test a trait using equation (3), the groups possessing the trait are compared to their sister groups, and the cumulative probability of each comparison is calculated using equation (3). The resulting series of independent probabilities can be tested with Fisher's combined probability test (Sokal and Rohlf 1981), which is calculated as $-2\Sigma \ln p_i$, where p_i is the ith probability as calculated from equation (3). The statistic is distributed as a χ^2 with $2k$ degrees of freedom, where k is the number of probabilities.

AN EXAMPLE FROM ACTINOPTERYGIAN FISHES

In this section, we illustrate our method using data from Lydeard (1993). Lydeard compared 12 groups of viviparous actinopterygian fishes to their nonviviparous sister groups to test whether viviparity has amplified diversity in actinopterygian fishes. The evolution of viviparity has been suggested as a possible reason for the success of poeciliid fishes (Rosen 1962; Meffe and Snelson 1989), a group of approximately 200 species whose sister group is either the monotypic subfamily Fluviphylacinae or the subfamily Aplocheilichthyinae with over 100 species (Parenti 1981). Several aspects of viviparous reproduction are thought to have enhanced the probability of speciation in poeciliids (see Lydeard 1993). Given this, Lydeard was interested in applying the sister-group comparison method to test whether viviparity is a key innovation acting to increase diversity in actinopterygians. He compared 10 groups of viviparous fishes to their nonviviparous sister groups and applied a sign test to the results. In six of the 10 sister-group comparisons, the viviparous group was larger, a nonsignificant result using a sign test ($P = .38$). We reanalyzed his data using the method detailed in this note to determine whether the increased power of our test could detect a nonrandom pattern not identified by the sign test. The results are tabulated in table 1. The combined probability test is narrowly significant if the Fluviphylacinae are considered the sister group of the Poeciliinae ($\chi^2 = 31.88$, $P < .05$), but if the Apocheilichthyinae are considered the sister group of the Poeciliinae, the result is not significant ($\chi^2 = 23.43$, $P \sim .32$).

Thus, our method has identified a possibly nonrandom pattern of increased diversity in viviparous actinopterygian fishes not recoverable using the sign test. However, the result is only narrowly significant, and then only if the Fluviphylacinae are considered the correct sister group to the Poeciliinae. Nonetheless, this example illustrates the superiority of our method.

We feel that one of the significant problems that can be addressed with the method described here is the extent to which variation in rates of speciation and extinction has been determined by intrinsic versus extrinsic factors. We find it

TABLE 1

LIST OF VIVIPAROUS ACTINOPTERYGIAN FISHES AND THEIR RESPECTIVE OVIPAROUS SISTER GROUPS (MODIFIED FROM LYDEARD 1993)

VIVIPAROUS		OVIPAROUS		
Taxon	No. of Species	Taxon	No. of Species	PROBABILITY*
Osteichthyes:				
Actinopterygii:				
Ophidiiformes:				
Bythitodei	98	Ophidioidei	234	.707
Atheriniformes:				
Dermogenys				
Normorhamphus				
Hemirhamphodon	8	*Zenarchopterus*	17	.708
Cyprinodontiformes:				
Poeciliinae	193	Apocheilichthyinae	100	.343
		or Fluviphylacinae	1	.005
Goodeinae	36	Empetrichthyinae	4	.103
Anablepinae	7	Oxyzygonectinae	1	.143
Scorpaeniformes:				
Sebastinae	128	Neosebatinae	12	.086
Comephoridae	2	*Batrachocottus*, *Cottocomephorus*	6	.857
Perciformes:				
Zoarces	3	*Macrozoarces*	1	.333
Embiotocidae	23	Labridae, Odacidae, Scaridae	481	.956
Ophiclinini, Clinini	70	Myxodini	11	.138

* The cumulative probability of each comparison.

odd that extrinsic factors, such as climatic change, tectonic activity, and so forth, are seldom invoked to explain variation in rates of speciation and extinction. Explanations of diverse groups in the literature usually invoke intrinsic causes. Cracraft (1982, 1985) has suggested that extrinsic factors, especially tectonic activity, are the major determinants of nonrandom diversification. This idea can be tested with the method outlined above.

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JOSEPH B. SLOWINSKI

MUSEUM OF NATURAL SCIENCE
LOUISIANA STATE UNIVERSITY
BATON ROUGE, LOUISIANA 70803

CRAIG GUYER

DEPARTMENT OF ZOOLOGY AND WILDLIFE SCIENCE
AUBURN UNIVERSITY
AUBURN, ALABAMA 36849-4201

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