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Reply from M. Foote and K. Roy

We welcome the perspective Williams *et al.* present on measuring biodiversity. As paleontologists, we emphasize fossilizable traits, but certainly agree that biodiversity measures should consider other traits when possible. Although we agree that different approaches are suited to different questions, the distinction between 'morphological' (in this context, 'phenetic') and 'phylogenetic' measures is not equivalent to that between descriptive and predictive approaches. (This raises a necessary semantic point. Williams *et al.* use observed character data to 'predict' unobserved character diversity. If they are truly foretelling what someone will potentially observe in the future, we can accept this as prediction. However, if, as we suspect, the observed data are used as a proxy for a quantity that is unlikely ever to be observed, the operation in question is estimation.)

In fact, either family of methods can be used to describe or to estimate. One could, for example, use a genealogy as nothing more than a description of evolutionary history. Likewise, one could use phenetic-distance data for more than description. For example, from an observed temporal acceleration in morphological diversity, we may infer that an evolutionary model of variable evolutionary rates is more likely than a constant-rate model¹. Observed phenetic distances could also be used to estimate unobserved character distances if we assumed that all characters followed the same evolutionary model. Such estimation, as Williams *et al.* are aware, naturally requires more burdensome assumptions.

Although we think that diversity exists in its own right, and are uncomfortable in equating it with 'value' (a subjective, human construct), we will accept, for the sake of argument, the importance of Williams *et al.*'s 'applied' (i.e. conservation-related) issue, one aspect of

which is how 'to [estimate] the distribution of richness for the majority of unsampled characters.' The crucial questions here are: (1) How well, for an assumed model of character evolution, do true and estimated character richness correlate? (2) How does the correlation vary with the true model of character evolution and with the deviation between the true and assumed models?

Whether one method is better at estimating total character diversity from sampled character diversity is an open question to be settled empirically. A detailed exploration of which approaches perform better under which evolutionary circumstances would indeed be worthwhile. The problem is very similar to one that exists in the estimation of genealogical relationships². Monte Carlo simulation will likely be useful here just as it is in assessing the accuracy of phylogenetic methods, since, with this approach, we know what we are trying to estimate². There is also a clear need for jackknife-style analyses comparing observed richness of one subset of characters with richness estimated on the basis of a different subset.

Mike Foote

Dept of Geophysical Sciences,
University of Chicago, Chicago,
IL 60637, USA

Kaustuv Roy

Dept of Biology, University of California,
San Diego, La Jolla, CA 92093-0116, USA

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Sperm choice by females

In a recent *TREE* news *2*, comment, Wirtz¹ reported current evidence of assortative use of sperm for fertilization by females. One of the reported studies was our work on the Swedish sand lizard (*Lacerta agilis*), in which we demonstrated negative correlations between parental relatedness and a male's probability of paternity. We interpreted this pattern as evidence that multiply-mated females can select among the sperm of competing males. Wirtz suggested two alternative interpretations: first, that females may selectively abort inbred zygotes; second, zygotes arising from matings between more-related parents may suffer higher mortality.

Our reanalyses refute these interpretations. First, we can show that selective abortion is not important in this system. We have demonstrated that female sand lizards oviposit all ovulated ova irrespective of their fertility and viability^{3,4}, and infertile eggs can be easily identified in this species⁴. Thus, no eggs were lost (i.e. not counted) due to abortion *in utero*. Wirtz's first interpretation can therefore safely be rejected.

Wirtz's second interpretation is more plausible: our earlier work on these lizards has shown that

high relatedness between parents translates into lower offspring viability³. This effect also appears, but does not attain statistical significance, in the smaller present data set. As expected, the number of unhatched eggs in a clutch tended to be higher when parents were more closely related, both in absolute terms and the proportion of these eggs in a clutch. Although neither of these correlations was statistically significant: ($p = 0.12$; $p = 0.20$, respectively), both were in the predicted direction and close to significant with a one-tailed test. Thus, more closely related parents may have higher offspring mortality also in the present data set.

In some species, paternity may be scored soon after fertilization by using PCR-derived markers which require little DNA. However, due to decomposition of tissue, such analyses are problematic when a proportion of the incubation period takes place *in utero* (as in sand lizards⁵). Thus, since this avenue was closed to us, we adopted the most conservative approach by assigning the paternity of all unhatched eggs to the male with the highest genetic similarity with the female, and reanalysing the data in our first contribution². Even after this highly conservative 'correction', band-sharing was negatively correlated with the proportion of the clutch that a male sired ($p = 0.024$). In nine out of 11 clutches, the male with the lowest genetic similarity with the female still sired most of the offspring ($p = 0.032$). Other plausible contributors to fertilization rates, such as time for sperm replenishment and male mass were not correlated with male proportional paternity ($r = 0.26$, $p = 0.63$, respectively), or male relatedness with the female ($r = 0.78$, $p = 0.76$, respectively). Thus, our data provide strong evidence that female sand lizards are able to control the paternity of their offspring by selective use of sperm.

Few studies in natural populations allow researchers to look for negative effects of parental consanguinity on offspring viability; when they do, this relationship has been repeatedly confirmed^{6,7}. This scenario may have important implications for the evolution of female sperm choice and the question 'Why do not the first sperm to arrive at the fertilization site always fertilize the egg?'⁸ Individuals do not carry the same (defect) genes/alleles and, hence, for several reasons the same male may be a good partner for one female and a bad one for another^{9–12}. How females discriminate among sperm is not yet resolved but two possible mechanisms have been described¹: selection by the female reproductive tract, and choice of sperm by ova. In sand lizards, more closely related males also have more similar proportional paternity ($p = 0.033$). Thus, the more similar in chemical structure the sperm membranes, the greater may the difficulty be for maternal immunorecognition systems to distinguish among them.

Mats Olsson
Richard Shine
Thomas Madsen

The University of Sydney,
School of Biological Sciences,
Zoology Building A08,
NSW 2006, Australia