

RESPONSE TO WAPLES'S COMMENT ON HETEROZYGOSITY AND
LIFE-HISTORY VARIATION IN BONY FISHES

JEFFRY B. MITTON AND WILLIAM M. LEWIS, JR.

*Department of Environmental, Population, and Organismic Biology, University of Colorado,
Boulder, CO 80309-0334 USA*

Key words.—Bony fishes, genetic variation, heterozygosity, life-history variation.

Received April 15, 1991. Accepted August 16, 1991.

Waples (1991) has commented on our study of genetic and life-history variation of bony fishes (Mitton and Lewis, 1989), and has presented the results of his reanalysis of some of our data. We agree with some of the points that Waples has made, but we disagree with others, and we differ from him on the interpretation of his reanalysis.

Waples points out that the data set upon which our analysis is based does not constitute a random sample of the bony fishes. This is correct; the data set, which reflects the vagaries of data availability, omits numerous important groups, and places heaviest emphasis on freshwater taxa. However, the data set does have a very broad scope taxonomically and, most importantly for present purposes, covers much of the full range of easily quantifiable life-history characteristics. Therefore, any conclusions that we might be able to justify could probably be best characterized as representing a taxonomically and ecologically diverse assemblage of primarily freshwater taxa of the bony fishes. This would leave open the possibility that a truly random sampling of all of the bony fishes would show a different result, although it is clear that very few biological generalizations of great taxonomic breadth are based upon random sampling of the taxa to which they are considered to apply.

One problem cited by Waples is the proportionately heavy weighting that is placed on relatively few families of fishes in the data set. We agree that this creates some interpretational uncertainties that would not be present if all families of fishes were represented at random.

However, we disagree with Waples about the degree of difficulty that this taxonomic clumping provides for interpretation.

Homogeneity of heterozygosity among families is a testable proposition. The heterozygosities among the four most heavily represented families (10 centrarchids, 11 catostomids, 11 cyprinids, 14 salmonids) are homogeneous (ANOVA; $P > 0.10$). Therefore, this data set does not seem to show the problem of clustering in heterozygosities that Waples mentions, although data sets of other types or for other families might possibly show this effect.

Waples points out that we have not made allowances for reduction in effective confidence levels when several different correlations are tested. This does indeed add a valid caution to interpretation, but is most likely to be important in cases for which a few significant correlations are found among many separate tests for correlation. This is not the case for our interpretation because the number of a priori tests was small, and the number of significant results is well above the proportion that would be likely at alpha probabilities below 0.05. Intercorrelation of life-history variables is a more serious problem, and we basically agree with Waples: a single alpha error for one variable could be carried through to other variables because of the correlation of variables. While this could occur, it is not very probable given the few correlations that have been tested.

A very important point of difference between our own interpretations and those of Waples has to do with the strength of correlation. Waples notes that the cor-

relations supporting our interpretation are small, even when they are nominally significant, and suggests that this is an indication of relationships that are not likely to be important, even when they can be demonstrated statistically. We believe that relationships between heterozygosity and other variables have proven to be elusive precisely because they are weak in the sense that they account for a relatively small proportion of total variance in heterozygosity. However, this does not mean that they are unimportant. In fact, a persistent trend based on life-history variables across taxonomically divergent groups would be quite significant if statistically valid. This is derivative of the more general and widely accepted viewpoint that sustained directional selection can be quite significant in the evolutionary sense, even if it is quantitatively weak.

The premise of our analysis is that evolutionarily important relationships between heterozygosity and other quantifiable variables may have been overlooked because the associations, although evolutionarily significant, are statistically weak. Given that the independent variables cannot be quantified very exactly, it is a foregone conclusion that any such relationship cannot be found in a small data set or in a data set that has a narrow range of independent variables. This brings us to a general objection concerning Waples's reanalysis of our data. The reanalysis is based upon small data subsets that are taxonomically more homogeneous than the main data set. The power of any statistical test to demonstrate significant relationships in these data subsets is very low because of the small sizes of the data sets and the small range of life-history variables. Therefore, Waples's failure to find these relationships in the small data sets is not surprising and does not reduce our interest in the possibility that a weak but potentially very important relationship exists between life-history variables and heterozygosity in the bony fishes generally. We accept Waples's methodology in subsampling the main data set, but we do not believe that this is a meaningful exercise, nor does it contradict the tentative conclusions that we have reached concerning the main data set.

We also have some differences with Waples in the interpretation of his own reanalysis. Waples's interpretation of small data sets is subject to much the same interpretational difficulties as our interpretation of the larger data set. In analyzing a particular family, for

example, Waples is not randomly sampling the genera within the family. Nonrandom weighting of genera obviously presents the possibility of clustered heterozygosities based on the proximity of the taxa in the evolutionary line. Because numerous correlations are performed, arbitrary selection of one or two relationships for special attention obviously poses an increased risk of alpha error. Finally, the life-history variables are no less intercorrelated for small data sets than they are for large data sets, and in fact may be more so because of close evolutionary relationships. Finally, although Waples puts interpretational weight on one high correlation in particular (heterozygosity versus egg diameter in marine taxa), it is in fact a substantially weaker correlation than the strongest correlations in our own data sets because the sample size is small, and the nominal probability is therefore marginal. Marginally significant correlations based on very small sample sets can be easily accounted for by a single observation. For example, Waples discusses a "strong trend" in the correlation ($r_s = 0.63$, $P = 0.04$) between heterozygosity and egg size in marine taxa, but removal of any one of 6 of 11 data points eliminates the statistical significance.

In summary, we would agree with Waples that the reanalysis shows no evidence of consistent relationships between heterozygosity and life-history variables within families. However, we believe that this result does not carry implications for larger data sets, insofar as the only relationships detectable in small data sets would be very strong and therefore probably would be evident in large data sets even without statistical analysis. Relationships between heterozygosity and controlling variables are obviously subtle, and can be studied most effectively across the broadest possible range of independent variables, and only with large sample sizes.

LITERATURE CITED

- MITTON, J. B., AND W. M. LEWIS, JR. 1989. Relationships between genetic variability and life-history features of bony fishes. *Evolution* 43:1712-1723.
- WAPLES, R. S. 1991. Heterozygosity and life-history variation in bony fishes. *Evolution* 45:1275-1280.

Corresponding Editor: J. Arnold