Is There a Relationship between Multilocus Homozygosity and Dominance Rank in Sea Anemones? A Reply to Zeh and Zeh

Richard K. Grosberg; David J. Ayre

The American Naturalist, Vol. 149, No. 4 (Apr., 1997), 790-793.

The American Naturalist is currently published by The University of Chicago Press.

IS THERE A RELATIONSHIP BETWEEN MULTILOCUS HOMOZYGOSITY AND DOMINANCE RANK IN SEA ANEMONES? A REPLY TO ZEH AND ZEH

Richard K. Grosberg[1,*] and David J. Ayre[2,†]

[1]Division of Biological Sciences, Section of Evolution and Ecology, University of California, Davis, California 95616; [2]Department of Biological Sciences, University of Wollongong, Wollongong NSW 2522, Australia

In an earlier article (Ayre and Grosberg 1995), we documented a consistent and transitive dominance hierarchy for a set of seven clones. We also showed that dominance rank was statistically correlated with variation in the number of fighting tentacles per polyp, and we used these data plus later experiments to argue that variation in the number of fighting tentacles provides a simple causal explanation for variation in dominance rank (Ayre and Grosberg 1996).

Using linear regression analysis, Zeh and Zeh (1997) provide an intriguing comment on the nature of this dominance hierarchy by noting that dominance rank is also statistically associated with homozygosity at the 11 allozyme loci that we used to distinguish the seven clones in our original study. As an alternative functional explanation for this association, they propose the homozygote aggressive superiority hypothesis. The hypothesis assumes that "numerous loci contribute in an additive fashion to allorecognition" (p. 788). It predicts that dominance rank will depend on relative homozygosity at these allorecognition loci, because individuals that are highly homozygous will be better able to distinguish self from nonself. Zeh and Zeh (1997) conclude that the correlation of dominance rank with number of acrorhagi per polyp may "simply be a by-product of the positive correlation between acrorhagi and multilocus homozygosity" (p. 787).

From a statistical perspective, there can be little doubt of the association between dominance rank and homozygosity at the allozyme loci that we assayed. However, in the absence of any direct information concerning the genetics and mechanisms of allorecognition in *Anthopleura elegantissima*, the plausibility of the homozygote aggressive superiority hypothesis rests on the crucial premise that there is a strong statistical association between homozygosities estimated from 11 polymorphic allozyme loci and homozygosities at putative allorecognition loci.

---

* To whom correspondence should be addressed; E-mail: rkgrosberg@ucdavis.edu.
† E-mail: d.ayre@uow.edu.au.

There are at least two reasons not to expect such an association. First, unless there is substantial inbreeding (or multilocus underdominant selection), it is highly unlikely that homozygosities at allozyme loci will be significantly correlated with homozygosities at other loci (Mitton and Pierce 1980; Chakraborty 1981). The available data (Smith and Potts 1987; McFadden et al., in press) provide little evidence for inbreeding at any spatial scale in populations of *A. elegantissima*. In each of 13 local populations surveyed by McFadden et al. (1996), genotypic frequencies at nearly all allozyme loci that we used (Ayre and Grosberg 1995) match expectations for Hardy-Weinberg equilibria, and neither of the estimators f (corresponding to F_{IS}, or total inbreeding) or F (corresponding to F_{IT}, or inbreeding within each sampled population) differ significantly from 0 (Weir and Cockerham 1984).

Second, theoretical analyses have demonstrated that there are potentially serious problems in the statistical analysis of relationships between multilocus heterozygosity and traits such as dominance rank (Mitton and Pierce 1980; Chakraborty 1981). These problems arise because estimates of heterozygosities based on a relatively small sample of the genome usually have large associated measurement errors. If the errors in measuring the independent variable (homozygosity) are so great that individual observations cannot be statistically distinguished (i.e., the ratio of measurement error variance to variance of the independent variable is large), then regression analysis cannot be reliably used to establish whether a general statistical relationship exists between the two variables (Fuller 1987; Neter et al. 1996).

To assess whether the estimates of homozygosity from the 11 allozyme loci could be used to predict a statistical relationship between homozygosities at other loci and dominance rank, we calculated the upper and lower 95% binomial confidence intervals (CIs) of estimates of homozygosity for each of the seven clones used in our original study. The plot of estimated homozygosity ($\pm$ 95% CI) versus dominance rank shows that the 11 loci are very poor predictors of overall homozygosity (fig. 1). The considerable overlap of confidence intervals demonstrates that even the two most extreme values of homozygosity do not significantly differ. Thus, it is impossible to predict whether any of the seven clones have different overall homozygosities at allozyme, or any other, loci.

We conclude that the data presented in our original article lack the power to reveal whether there is a positive, negative, or any statistical relationship between homozygosities at other loci—including putative allorecognition loci—and dominance rank. The relationship reported by Zeh and Zeh (1997) therefore does not provide support for the central genetic assumption of the homozygote aggressive superiority hypothesis. As such, the predictions and merits of the homozygote aggressive superiority hypothesis ultimately await an explicit test, using a cnidarian in which the formal genetics of allorecognition can be directly ascertained (e.g., Mokady and Buss 1996; Grosberg et al. 1996).
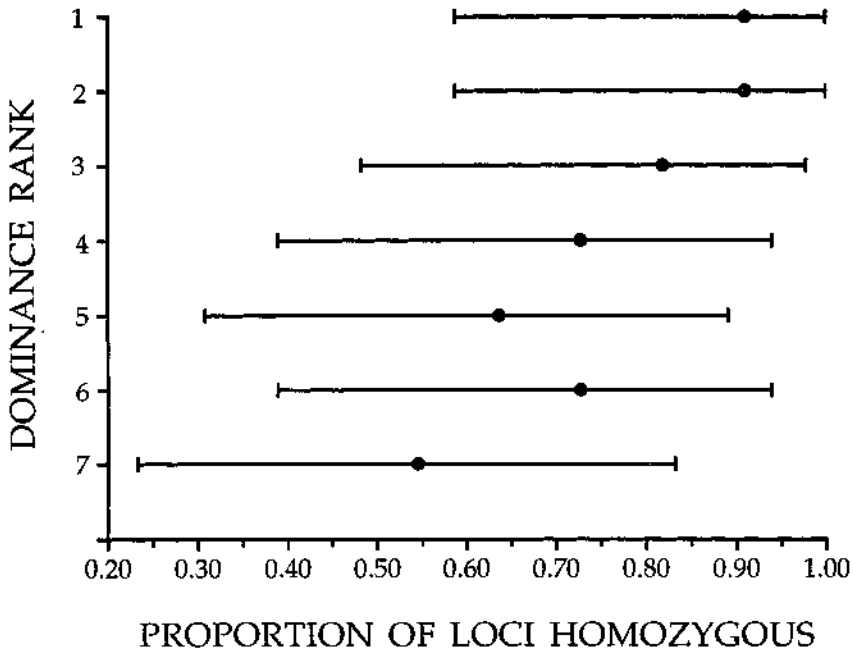
Fig. 1.—Dominance rank (medal play-ranking procedure; Ayre and Grosberg 1995) versus proportion of homozygous allozyme loci, estimated from the 11 polymorphic allozyme loci that we assayed earlier (Ayre and Grosberg 1995). Error bars show upper and lower 95% binomial confidence intervals of estimates of homozygosity.

LITERATURE CITED

Ayre, D. J., and R. K. Grosberg. 1995. Aggression, habituation, and clonal coexistence in the sea anemone *Anthopleura elegantissima*. American Naturalist 146:427–453.

———. 1996. Effects of social organization on inter-clonal dominance relationships in the sea anemone *Anthopleura elegantissima*. Animal Behaviour 51:1233–1245.

Chakraborty, R. 1981. The distribution of the number of heterozygous loci in an individual in natural populations. Genetics 98:461–466.

Fuller, W. A. 1987. Measurement error models. Wiley, New York.

Grosberg, R. K., D. R. Levitan, and B. B. Cameron. 1996. Evolutionary genetics of allorecognition specificity in the colonial hydroid *Hydractinia symbiolongicarpus*. Evolution 50:2221–2240.

McFadden, C. S., R. K. Grosberg, B. B. Cameron, D. P. Karlton, and D. A. Secord. 1996. Genetic relationships within and between solitary and clonal forms of the sea anemone *Anthopleura elegantissima* revisited: evidence for the existence of two species. Marine Biology (in press).

Mitton, J. B., and B. A. Pierce. 1980. The distribution of individual heterozygosity in natural populations. Genetics 95:1043–1054.

Mokady, O., and L. W. Buss. 1996. Transmission genetics of allorecognition in *Hydractinia symbiolongicarpus* (Cnidaria: Hydrozoa). Genetics 143:823–827.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models. Irwin, Chicago.

Smith, B. L., and D. C. Potts. 1987. Clonal and solitary anemones (*Anthopleura*) of western North America: population genetics and systematics. Marine Biology 94:537–546.

Weir, B. S., and C. C. Cockerham. 1984. Estimating F-statistics for the analysis of population structure. Evolution 38:1358–1370.

Zeh, J. A., and D. W. Zeh. 1997. Homozygosity, self-recognition, and aggressive ability in the sea anemone, *Anthopleura elegantissima*. American Naturalist 149:785–789.

Associate Editor: C. Drew Harvell