that in all the studies of homologous pairing cited it is quite possible that homologs had been previously aligned. Pairing of the heterochromatic regions may be observed simply because these are condensed and therefore conspicuous, and perhaps in some cases also because heterochromatic regions tend to adhere, nonspecifically, when they are near each other.

Chromosome regions that have been translocated away from their accustomed centromeres and telomeres and that are devoid of visible heterochromatin have been reported to synapse as capably as they do in their normal locations (*14*). It seems pointless to hypothesize at this time that heterochromatic regions too small to be visible nevertheless serve a pairing function in these cases. Thus although a tendency (which may be erratic) is widely acknowledged for generalized, nonspecific association of heterochromatic regions, a consistent, direct functional role of heterochromatin in pairing of homologous chromosomes currently lacks sound documentation.

MARJORIE P. MAGUIRE
Genetics Foundation,
University of Texas, Austin 78712

References

1. J. J. Yunis and W. G. Yasmineh, *Science* **174**, 1200 (1971).
2. A. Levan, *Hereditas* **32**, 449 (1946).
3. L. Vanderlyn, *Bot. Rev.* **15**, 507 (1949).
4. E. B. Wagenaar, *Chromosoma* **26**, 410 (1969).
5. C. P. Swanson, *Cytology and Cytogenetics* (Prentice-Hall, Englewood Cliffs, N.J., 1957).
6. M. J. D. White, *Animal Cytology and Evolution* (Cambridge Univ. Press, Cambridge, ed. 2, 1954).
7. D. D. Shaw, *Chromosoma* **31**, 421 (1970).
8. S. Ohno, L. C. Christian, C. Stenius, *Exp. Cell Res.* **32**, 590 (1963); S. Ohno and J. B. Smith, *Cytogenetics* **3**, 324 (1964).
9. L. F. LaCour and B. Wells, *J. Cell Sci.* **6**, 655 (1970).
10. M. P. Maguire, *Chromosoma* **21**, 221 (1967).
11. K. P. S. Chauhan and W. O. Abel, *ibid.* **25**, 297 (1968).
12. B. B. Hyde, *Amer. J. Bot.* **40**, 809 (1953).
13. S. S. Stack and W. V. Brown, *Bull. Torrey Bot. Club* **96**, 143 (1969).
14. M. P. Maguire, *Genetics* **51**, 23 (1965).

24 January 1972; revised 10 March 1972 ■

Relative Consumer Species Diversity with Respect to Producer Diversity and Net Productivity

Hurd *et al.* (*1*) present data which purport to indicate that community stability decreased with successional time, and with species diversity, at the consumer trophic levels, particularly the herbivore level. If their published data regarding species diversity and treatment level for producers, herbivores, and carnivores are examined from the point of view of relating the trophic level diversity to producer diversity, it can be seen that such a *relative* index of species diversity (that is, diversity of consumer per unit of producer diversity), as opposed to the absolute comparison used, does not increase by a greater magnitude in the old than in the young (successional) field. On the contrary, in the absence of appropriate statistical analysis the reverse appears to occur, that is, a greater increase in consumer diversity with respect to producer diversity occurs in the case of the young field in response to fertilization (Table 1). Carnivore relative diversity data for old and young fields appear to be approximately equivalent.

It remains true that relative productivity of the herbivore level is elevated by fertilization in the old field, but, as opposed to interpreting this as indicative of instability, an alternative viewpoint might hold that more effective utilization and partitioning of available energy accrues to the older and more diverse community than to the younger and less diverse association, and that this constitutes expression of a stabilizing mechanism.

Relative diversity of the consumers per unit of net primary productivity fell as the result of fertilization in most categories (Table 2); the negative effect was greater in the case of the new-field inhabitants for the first productivity surge and the reverse was true for the second productivity surge. Again no appropriate statistical analysis can be performed with the data as given. The differences as shown in Table 2 are either significant or not significant and in both cases lead to rejection of the hypothesis that instability—as measured either by increase in trophic-level species diversity relative to primary producer species diversity, or by a reduction in trophic-level species diversity relative to net primary producer pro-

Table 1. Relative diversity of consumers, per unit of producer diversity.

	Producer diversity (original data)		Herbivores				Carnivores			
			Early		Late		Early		Late	
	6-year field	17-year field	6-year field	17-year field	6-year field	17-year field	6-year field	17-year field	6-year field	17-year field
Control	10.25	17.5	0.331	0.208	0.326	0.282	0.180	0.100	0.14	0.142
Treatment	9.5	18.0	.442	.305	.573	.247	.247	.169	.13	.113
Magnitude change			+.111	+.097	+.247	−.035	+.067	+.069	−.01	−.029
Relative change with respect to control			+33%	+46%	+75%	−12%	+37%	+69%	−6.4%	−2.0%

Table 2. Relative diversity of consumers, per unit of producer productivity.

	Producer net productivity (original data)		Herbivores				Carnivores			
			Early		Late		Early		Late	
	6-year field	17-year field	6-year field	17-year field	6-year field	17-year field	6-year field	17-year field	6-year field	17-year field
Control	4.46	2.68	0.76	1.36	0.75	1.84	0.41	0.65	0.34	0.93
Treatment	8.76	4.56	.47	1.20	.62	0.97	.27	.66	.15	.45
Magnitude change			−.29	−0.16	−.13	−.87	−.14	+.01	−.29	−.48
Relative change with respect to control			−37%	−11.7%	−17%	−47.16%	−35%	+2.43%	−56%	−52%

ductivity (available energy)—increases with successional age.

The research in question would have been strengthened by postulation of specific hypotheses which were then exposed to test rather than by perturbation followed by an attempt to account for resultant differences.

Robin Harger
Institute of Animal Resource Ecology,
University of British Columbia,
Vancouver 8, Canada

Reference

1. L. E. Hurd *et al.*, *Science* **173**, 1134 (1971).

6 December 1971

We have shown that stability, in terms of amplitude of deflection of productivity from ground state, is positively correlated with increasing successional age (and increasing diversity) only at the producer trophic level. The amplitude of deflection for herbivores was indeed greater in the older field than the younger field, thus indicating that stability, as we have defined it, is lower in the older field for that trophic level. The same was shown to be true of the carnivore level.

Harger's "alternative viewpoint" to interpreting the higher productivity response of the older field herbivores as relative instability actually does not differ in the least from our own concept of community stabilizing mechanisms. That is, stability is obviously a function of the characteristic species trophic level relationships, which regulate the partitioning and flow of energy up the trophic levels of natural community ecosystems.

Harger has not been at all clear as to why he has taken the approach of comparing relative consumer diversity to producer diversity and productivity. In addition, it is certainly not clear why, if herbivores are to be compared to producers as a function of the feeding relationships involved, the carnivores are not compared to the herbivores in the same way rather than lumped with the herbivores as "consumers." This would seem to eliminate the inherent value of separating the trophic level responses in the first place. In any case, Harger's own tables disagree with him at a number of points (for example, early peak herbivores and carnivores in his table 1).

Our "specific hypotheses" were clearly provided by current ecological theory (*1*) which asserts that ecosystem stability increases with successional age by virtue of increasing diversity. We have shown that the veracity of this hypothesis rests in how community responses to perturbation are examined.

L. E. Hurd, M. V. Mellinger
L. L. Wolf, S. J. McNaughton
Department of Biology, Syracuse
University, Syracuse, New York 13210

Reference

1. R. Margalef, *Amer. Natur.* **97**, 357 (1963); R. H. MacArthur, *Ecology* **36**, 533 (1955); E. P. Odum, *Science* **164**, 262 (1969).

15 March 1972

■

Genetic Polymorphisms and Environment

Powell (*1*) has demonstrated that the loss of heterozygosity in caged *Drosophila willistoni* populations is less in a varied environment than in a stable environment and thus has provided good evidence for the contribution of niche diversity to the maintenance of polymorphism. Unfortunately it is not possible to determine whether or not the electrophoretic polymorphisms monitored were themselves the direct targets of balancing selection. The experimental populations were undoubtedly highly heterozygous at other closely linked loci, and, apparently, were polymorphic for multiple chromosomal inversions as well.

Purely stochastic models show that alleles of polymorphic loci, in the absence of direct selection, will tend to become nonrandomly associated with closely linked overdominant loci and can be expected to behave as if they were themselves overdominant (*2*). Chromosomal polymorphism greatly increases this effect, as neutral alleles will become associated with "supergene" complexes. There is direct experimental evidence of nonrandom association between chromosomal inversions and electrophoretic alleles in *D. pseudoobscura* (*3*). It is an open question as to whether these associations are due only to stochastic factors or to selection as well.

Powell's observations may be due to a relatively few genes or supergene complexes responding to balancing selection. Most polymorphisms, including those actually monitored directly, may be passively carried along by tight linkage and nonrandom association. In any event this particular experiment does not provide convincing evidence for or against the current hypothesis that most electrophoretic polymorphisms are selectively neutral.

Jack Lester King
Department of Biological Sciences,
University of California,
Santa Barbara, 93106

References

1. J. R. Powell, *Science* **174**, 1035 (1971).
2. T. Ohto and M. Kimura, *Genetical Res.* **16**, 165 (1970).
3. S. Prakash and R. C. Lewontin, *Genetics* **69**, 405 (1971).

17 December 1971

King has brought up two interesting criticisms of my report. First, it is operationally impossible to distinguish between selection at a single locus and selection for closely linked genes. This is admitted; with the possible exception of unconditional lethals, one cannot rule out linkage when testing the fitness effects of a single gene. However, the experiments reported were deliberately begun with as much genetic diversity as possible in that 500 freshly collected single female lines which carry about 2000 genomes from nature were used. This randomization of the genetic background minimizes (but does not eliminate) the effect of linkage.

Second, King asserts that the enzyme loci studied may be involved in inversion supergenes and that the results reflect selection for inversions. Throughout our study of enzyme and chromosomal polymorphisms in the *Drosophila willistoni* group, we have found no correlation either between inversions and enzyme alleles or in the amount of chromosomal heterozygosity and enzyme heterozygosity (*1*).

Further, although we have been unable to detect the association which may exist, this does not vitiate the conclusion drawn in the report. If the enzyme alleles are associated with inversions, they most likely were selected to be coadapted with the rest of the genes in the inversion. The effect reported is still due to the selection of the enzyme alleles, mediated by their inclusion into coadapted supergene complexes. After all, it is not the inversion per se which is adaptive, but the presence of coadapted genes, of which the enzyme alleles may be part.

Jeffrey R. Powell
Department of Genetics,
University of California, Davis 95616

Reference

1. F. J. Ayala, J. R. Powell, Th. Dobzhansky, *Proc. Nat. Acad. Sci. U.S.* **68**, 2480 (1971); J. R. Powell, unpublished data.

18 February 1972