GOULD, S. J., & R. C. LEWONTIN. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc. Roy. Soc. London B 205: 581–598.

GRINNELL, J., & A. H. MILLER. 1944. The birds of California. Pacific Coast Avifauna.

JAMES, F. C. 1983. Environmental component of morphological differences in birds. Science 221: 184–186.

LANDE, R. 1985. Expected time for random genetic drift of a population between stable phenotypic states. Proc. Nat. Acad. Sci. USA 82: 7641–7645.

LANYON, S. M. 1985. Detecting internal inconsistencies in distance data. Syst. Zool. 34: 397–403.

LYNCH, M., & W. G. HILL. 1986. Phenotypic evolution by neutral mutation. Evolution 40: 915–935.

MCKITRICK, M. C., & R. M. ZINK. 1988. Species concepts in ornithology. Condor 90: 1–14.

QUINN, T. W., & B. N. WHITE. 1987. Analysis of DNA sequence variation. Pp. 163–198 *in* Avian genetics (F. Cooke and P. A. Buckley, Eds.). Florida, Academic Press.

RISING, J. D. 1988a. [Review of Zink (1986)]. Auk 105: 217–219.

———. 1988b. Geographic variation in sex ratios and body size in wintering flocks of Savannah Sparrows (*Passerculus sandwichensis*). Wilson Bull. 100: 183–203.

SCHLUTER, D. 1984. Morphological and phylogenetic relations among the Darwin's finches. Evolution 38: 921–930.

ZINK, R. M. 1986. Patterns and evolutionary significance of geographic variation in the Schistacea group of the Fox Sparrow (*Passerella iliaca*). Ornithol. Monogr. 40. Am. Ornithol. Union, Washington, D.C.

Received 26 June 1988, accepted 1 August 1988.

Response to R. M. Zink

J. D. RISING[1]

Zink's study (1986) of geographic variation in the *schistacea* Fox Sparrows (*Passerella iliaca*) of California and Nevada provides us with an excellent opportunity to compare patterns of genetic and morphological variation in a bird species. In my review (Rising 1988a) I found much to praise, but expressed concerns about the morphological analyses and Zink's apparent diffidence about the results. My review stimulated him (1989) to discuss some of these matters in greater depth, and I take this opportunity to respond to his discussion by expanding on my concerns.

Enzymes that are identified by electrophoretic analyses are involved in cell metabolism. These have specific functions, and mutational changes may affect their biochemical effectiveness. Indeed, it seems probable a priori that most "new enzymes," if at all changed, would have reduced activity and be eliminated by natural selection. In a few cases, two or perhaps several different allozymes have optimal catalytic efficiencies in different environments, and *could* be retained in a polymorphic state in populations by natural selection (Koehn et al. 1983); but, for the most part, it is likely that allozymes segregating in populations are selectively equal (i.e. "neutral"). In fact the observed distributions of allele frequencies in natural populations of birds generally are not significantly different from those that would be expected if the allozymes were neutral, their presence and frequency in populations being determined by mutation and stochastic events. Though to my knowledge no one has direct evidence relating the relative fitness of individual birds to different biochemical phenotypes, there is good indirect evidence to support a variant of the neutral hypothesis of genetic variation, the "Infinite allele-Constant mutation rate" model (the IC model; Barrowclough et al. 1985). Barrowclough et al. (1985) argue that the neutral model should be accepted as a "null hypothesis" to explain allozymic variation in birds. While I fully concur with the sentiment of such a suggestion, I have reservations about using the term "null hypothesis" in this way. A null hypothesis is a statistical hypothesis. The IC model predicts a certain distribution of alleles by frequency. The statistical null hypothesis, then, is that the observed distribution of alleles is not different from this predicted frequency. This may seem a semantic quibble, but I am concerned that people will confuse a statistical null hypothesis with that which is biologically reasonable or parsimonious. Neutral hypotheses are not always biologically reasonable, although the mutation-drift hypothesis of allozymic variation is an exception.

To give another example, on the basis of analogy with other sparrows and the theory of sexual selection, one would predict that male Fox Sparrows are larger than females, not the same size. To test this *biological hypothesis*, one would test a statistical *null hypothesis*, namely that there is no difference in size

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between the sexes. Unfortunately, the hypothesis of sexual size dimorphism in *schistacea* Fox Sparrows has not been tested. Zink (1986: 13) merely refers to Linsdale (1928) as having shown that dimorphism occurs in these birds, but this is not entirely accurate. Linsdale, for the most part, sorted his specimens (some of which were collected in winter) by named subspecies rather than by collecting site (a practice rightfully decried by Zink); and he presented tables of measurements (means, ranges, and in some cases standard deviations), but did no statistical analyses. Although Linsdale's data indicate that males are generally larger than females, this has not been tested. A two-way analysis of variance (sex and locality) would have shown whether or not there was sexual dimorphism, geographic variation, and geographic variation in dimorphism for each character.

What do we learn about the population structure of *schistacea* Fox Sparrows from the genetic data? Zink (1986) found few genetic differences among populations of these sparrows. As he writes (1986: 78), the "... homogeneity of allelic frequencies could be a result of Fox Sparrows occupying a less fragmented range in the near past, with insufficient time for selection to sort out alternative alleles or genetic drift to operate." Alternatively, Zink notes (1986: 78), "A high rate of gene flow is a potential cause of geographic homogeneity of allelic frequencies, as suggested from analysis of the spatial distribution of rare alleles." Zink's (1986) results are in fact those one would expect if there were high gene flow among populations. They do not, however, show that such gene flow is occurring: the existence of genetic dissimilarity among populations points to a "highly substructured population," but the absence of this does not demonstrate gene flow. A very small amount of gene flow can also prevent divergence in gene frequencies among populations if the only factor operating is drift (Lewontin 1974). McKechnie et al. (1975) found a high degree of genetic similarity among populations of *Euphydryas editha* and *E. chalcedona*, even though there is apparently very little gene flow among populations. Additionally, as Zink recognized (above quote), the similarities could be historical. If selection were unimportant (as is probably the case), then only drift or gene flow would operate, in all probability, to change gene frequencies in local populations. If the frequencies are the same in all populations, gene flow could not lead to changes in local populations, and there is no reason to suppose that effective population sizes of local populations have ever been small enough for drift to be a significant factor. Indeed, the existence in Zink's sparrows of more rare alleles than expected specifically indicates that local populations have *not* been recently bottlenecked. Thus, in the absence of selection, we would expect differences among populations of Fox Sparrows to develop only very slowly even if there were little or no gene flow among populations. In any event, even if there were considerable gene flow among populations, natural selection could operate to maintain striking morph-clines, i.e. genetic substructuring at those loci affected by selection (Endler 1977). I do not believe that I underemphasize the value of genetic data sets, and indeed I specifically praised Zink for his presentation of genetic data. I do, however, urge people not to draw conclusions from inconclusive results.

Genetic data may give us valuable information about population structure, but there is no reason to suppose a priori that genes controlling cell metabolism reflect variation in "phenotypic" characteristics such as bill size, body size, or coloration, or vice versa. Such features are influenced by the environment as well as many different genes, each of which may well have numerous pleiotropic effects (Atchley 1983). For this reason, and others (Rising 1988a), I suppose a priori that features such as bill size and coloration would be influenced by natural selection (Zink agrees on coloration). My "null hypothesis," however, is *not* that adaptation *alone* produces geographic variation. My null (statistical) hypothesis is that there are no geographic differences. Zink's analyses reject this hypothesis for the *schistacea* Fox Sparrows. My alternate hypothesis (having rejected the null hypothesis) is that the geographic differences reflect different adaptations, and perhaps "environmental induction" as well. I have never argued that adaptation and adaptation alone is responsible for patterns of geographic variation of such features (cf. Zink 1989), but I suggest that it is highly probable that adaptation *plays a role* in the phenotypic expression of such features. Those of us who speculate about the adaptive nature of structures such as body or bill size should not be ridiculed as purveyors of Panglossian just-so stories, or dismissed as being blinded by "... an adaptationist world view" (Zink 1989). Reasonable scientists are neither "neutralists" nor "adaptationists": they recognize that both selection and stochastic factors play a role in evolution.

Zink (1989) advocates testing "non-adaptationist explanations" such as environmental induction and phenotypic drift prior to testing inferences from correlations about the adaptive maintenance of traits. How does one test these, and how powerful are the tests (Toft and Shea 1983)? Has any ornithologist ever tested for these influences? Should we dismiss "adaptationist" studies such as Boag and Grant (1981) because they did not rule out the possibilities of environmental induction and phenotypic drift? James' landmark research on Red-winged Blackbirds (*Agelaius phoeniceus*), in my opinion, led to the most important paper on geographic variation published in the last 20 years (James 1983). Her results indicate that the role of the environment in determining adult phenotype may be more important than many of us would have predicted. She has *not* shown, however, that environmental induction is the *only* factor in geographic variation. James' results are not straightforward. In most cases, the control birds show the same trends as the transplanted ones (albeit not nearly so strongly), and in all cases the transplanted birds are intermediate between normal offspring from their natural and adoptive populations. Does this not suggest a role for both adaptation and environmental induction? It clearly would be desirable to have more information of the sort that James has given us, both about Red-winged Blackbirds and other species of birds. Yet in the years that have passed since the publication of James' work, no one has followed with a similar study, doubtless because it is extremely difficult to carry out that sort of research on birds. Berven and Gill (1983) found that genetically controlled life-history traits, such as size at metamorphosis and the length of the larval period, may vary geographically in *Rana sylvatica*. In this frog, evidence suggests that development patterns are locally adaptive and reflect the different selection pressures at each environment. If this also holds for Red-winged Blackbirds, James' results are perhaps not so surprising. They certainly do not lead us to the conclusion that the size or shape that a developing bird reaches is not influenced by natural selection. Selection for a developmental rate that results in a particular morphology in a specific environment is still selection.

It is not practical to do studies such as James' with most species of birds. Disregarding the thorny issue of whether it is desirable to move large numbers of birds from one place to another, such research requires that nests are easy to find, and that there is substantial geographic variation in morphology. If we wish to study developmental genetics, environmental induction, or phenotypic drift, perhaps we should not study birds. It is possible that all of us who have studied morphological geographic variation of birds have wasted our time (Atchley 1983), but it is not productive to offer platitudes about doing what cannot be done (Zink 1989). Because I feel it is reasonable to think that bill size and shape is influenced by natural selection, I do not think that it is a waste of time to study bill morphology. Of course, I make assumptions: I assume that evolution occurs, and I assume that selection influences bill size and shape. These assumptions cannot be proven by studies of geographic variation, but correlations between bill size and environmental variables can lead to hypotheses about adaptation that can be tested. Correlation does not reveal cause, but it can be suggestive (which is why so many people have stopped smoking). I confess that, after studying Zink's work (1986, 1989), I am mystified as to why *schistacea* Fox Sparrows show so much geographic variation in bill size, and I (1988a) applauded Zink (1986) for *not* offering facile "*ad hoc* hypotheses." Perhaps the assumptions of evolution and adaptation will be shown to be unfounded, but I think that it is premature to accept Zink's proposition (1986: 107) ". . . that local environmental conditions acting during the nesting period shape inherent phenotypic plasticity, effecting spatial patterns." Although possible, absolutely none of this speculation is supported by Zink's work—and I think that such a hypothesis is improbable. If size variation reflected only the local environmental conditions, why do males and females from the same locality on average differ in size (if indeed they do)? Why, other than selection, would the sexes respond differently to the local environmental influences? Environmental induction perhaps does effect geographic variation. But adaptation, too, almost certainly, is reflected in such variation. Perhaps the ultimate challenge is to experimentally identify the variance components associated with each of these alternative hypotheses, but birds may not prove suitable subjects for such research.

Zink (1989) has raised two methodological points that need clarification. Certainly a critical sample size of 10 is not a magic number. I have bootstrapped some measurements of Savannah Sparrows (*Passerculus sandwichensis*), and find that my estimates of averages are "good" with samples of 10 individuals; but estimates of variance do not become consistent until n = 35 or so. Of course, it is not practical, and in some cases would not be possible to obtain samples that large, but such results can be substantiated by examining the F value asymptote at a critical level of say 0.05 with increasing denominator degrees of freedom. Strictly speaking, however, this indicates that we should not be doing statistical analyses that involve estimates of variance (such as ANOVA and product-moment correlations) with samples of fewer than 35 individuals, but I suspect that this is unnecessarily conservative. At least with 10 individuals, we apparently can have some confidence in our estimates of means, but samples of 1, 2, 3, 4, etc. are not satisfactory.

I admit to being among the many sinners who have not bootstrapped principal components loadings, but Zink (1989) appears to have missed my (1988a) point. In his analyses (Zink 1986: table 15) his PC II and PC III explain virtually the same amount of variance, i.e. in three-dimensional space his data form a football-shaped cluster. Thus the two shape axes that are orthogonal to PC I (PC II and PC III) may be arbitrary, and should be jackknifed or bootstrapped to ascertain whether they represent repeatable axes *if* they are to be treated as accurately reflecting character covariation. In my study (Rising 1988b: table 3), PC II explains about twice as much variance as PC III; thus, the distribution of points in three-dimensional space is more like a tongue depressor. Thus, component II would almost certainly have the same loadings even if bootstrapped. It is important to "resample" only when the dimensions have approximately the same eigenvalues (which can be visually assessed from a Scree plot [Cattell 1966] or by direct inspection).

Zink's monograph on geographic variation in *schistacea* Fox Sparrows is an important contribution that contains much that is valuable and original, and very little that should be criticized. In a short review it is perhaps inevitable that disproportionate emphasis is given to criticism, and if my review of Zink's paper gave the impression that his work was seriously flawed, I am guilty of failing to have achieved a reasonable balance. Zink's work is innovative and thought-provoking, and I urge everyone interested in geographic variation to study it.

LITERATURE CITED

ATCHLEY, W. R. 1983. Some genetic aspects of morphometric variation. Pp. 346-363 *in* Numerical taxonomy (J. Felsenstein, Ed.). NATO AS1 Ser., Ser. G, Ecol. Sci., No. 1. Berlin, Springer-Verlag.

BARROWCLOUGH, G. F., N. K. JOHNSON, & R. M. ZINK. 1985. On the nature of genic variation in birds. Curr. Ornithol. 2: 135-154.

BERVEN, K. A., & D. E. GILL. 1983. Interpreting geographic variation in life-history traits. Am. Zool. 23: 85-97.

BOAG, P. T., & P. R. GRANT. 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galápagos. Science 214: 82-85.

CATTELL, R. B. 1966. The Scree test for the number of factors. Multivar. Behav. Res. 1: 245-276.

ENDLER, J. A. 1977. Geographic variation, speciation, and clines. Monogr. Pop. Biol. 10. Princeton, New Jersey, Princeton Univ. Press.

JAMES, F. C. 1983. Environmental component of morphological differences in birds. Science 221: 184-186.

KOEHN, R. K., A. J. ZERA, & J. G. HALL. 1983. Enzyme polymorphism and natural selection. Pp. 115-136 *in* Evolution of genes and proteins (M. Nei & R. K. Koehn, Eds.). Sunderland, Massachusetts, Sinauer Associates, Inc.

LEWONTIN, R. C. 1974. The genetic basis of evolutionary change. New York, Columbia Univ. Press.

LINSDALE, J. M. 1928. Variation in the Fox Sparrow (*Passerella iliaca*) with reference to natural history and osteology. Univ. California Publ. Zool. 30: 251-392.

MCKECHNIE, S. W., P. R. EHRLICH, & R. B. WHITE. 1975. Population genetics of *Euphydryas* butterflies. I. Genetic variation and the neutrality hypothesis. Genetics 81: 571-594.

RISING, J. D. 1988a. [Review of Zink (1986)]. Auk 105: 217-219.

———. 1988b. Geographic variation in sex ratios and body size in wintering flocks of Savannah Sparrows (*Passerculus sandwichensis*). Wilson Bull. 100: 183-203.

TOFT, C. A., & P. J. SHEA. 1983. Detecting community-wide patterns: estimating power strengthens statistical inference. Am Nat. 122: 618-625.

ZINK, R. M. 1986. Patterns and evolutionary significance of geographic variation in the *Schistacea* group of the Fox Sparrow (*Passerella iliaca*). Ornithol. Monogr. 40. Am. Ornithol. Union, Washington, D.C.

———. 1989. The study of geographic variation. Auk 106: 157-160.

Received 23 September 1988, accepted 23 September 1988.

Response to P. R. Ehrlich, D. S. Dobkin, and D. Wheye

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Ehrlich, Dobkin, and Wheye (1986) provided a useful service by bringing to the attention of ornithologists Beattie's (1985) evidence that metapleural glands of ants produce secretions that include antibiotic plant auxins and that ants spread these secretions over their entire bodies. The suggestion that secondary acquisition of those antibiotic secretions would be an "important reason" for anting by birds is appropriate and worthy of further investigation. However, I submit that Ehrlich et al. (1986) have no scientific basis for their opinion that certain hypotheses pertaining to the adaptive significance of anting are "more reasonably" acceptable than others. Unfortunately the authors failed to read and consider Potter and Hauser (1974), the most recent paper on anting that has appeared in *The Auk*.

Potter and Hauser (1974) determined that anting was most frequently reported from those portions of the United States where thunderstorms occur 30 to 50 times per year. These are places where the weather is alternately dry and wet during the summer and early fall. Such conditions promote the simultaneous loss, and thus the simultaneous replacement, of feathers that would have dropped gradually in dry weather or in a climate with rain daily throughout the molting period.

Potter and Hauser (1974) documented the correlation of anting and sunbathing in wild birds with the rapid loss and replacement of feathers in particular feather tracts. The birds studied ant while replacing feathers in the wing, the tail, and the lower underparts. All of these parts of the body are readily accessible to the bill. Birds sunbathe while replacing feathers on the head, the back, the neck, and the upper breast. These parts of the body are not readily accessible to the bill.

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