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NICHE WIDTH AND GENETIC VARIATION IN HAWAIIAN *DROSOPHILA**

WILLIAM W. M. STEINER

Department of Genetics and Development, University of Illinois at Urbana-Champaign,
Urbana, Illinois 61801

In the past decade much attention has been focused on the relationship between genetic variation and niche breadth or niche width, the latter defined by Van Valen (1965) as “the total multidimensional space of limiting resources used by a species or a segment of a community” (p. 378). Van Valen has pointed out why the relationship is of theoretical importance, providing references to the formalization of what has become known as the “niche-variation” model. His paper presents the basic tenets of the model which have been expanded upon or revised by Rothstein (1973), Roughgarden (1974), and others.

Basically the model predicts that the amount of phenotypic variation within any one population should be roughly proportional to the width of the niche exploited by that population. However, the terms of the model can be defined in ways which enable a variety of approaches to be taken in its testing. For example, Roughgarden (1974) recognizes two kinds of measures of niche width utilized in most past studies, the first of which uses morphological variation in traits related to food gathering (i.e., Van Valen 1965; Soule and Stewart 1970). The second uses indices of the dispersion of a population's resource use over its resource categories (i.e., Colwell and Futuyma 1971). Furthermore, wide use has been made of quantitatively varying phenotypic traits to estimate a population's genetic variability. Two assumptions here are that the trait has a polygenic basis susceptible to selection and that it has some relationship to the fitness of the population under study. However, such traits may be susceptible during ontogeny to environmental effects unrelated to their function or their fitness; hence environmental input may affect the trait independently of the role it is being considered for under the niche-variation model. Additionally, determining the extent that variability in a quantitative trait is due to environment and not to genetic heterogeneity has long been an outstanding problem in genetics.

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Nevertheless, a variety of studies have been made, some of which profess to support the niche-variation model and others which do not. The earlier reports used morphological variation primarily in food gathering traits (i.e., bill length, bill depth). Van Valen (1965) found a greater relationship between bill measurement and niche width in six species of birds found in island populations versus continental populations; however, work by Grant (1967), Willson (1969), Soule and Stewart (1970), and others using similar approaches found contradicting evidence.

In the laboratory, two studies have provided some support for the model. Powell (1971) demonstrated that by increasing environmental heterogeneity for *Drosophila willistoni* a concomitant increase in enzyme heterozygosity detected by electrophoresis was obtained as well. Using population density as niche breadth estimators, Shugart and Blaylock (1973) irradiated *D. simulans* males and placed them, with unirradiated females, in competition with *D. melanogaster*. They found that *D. simulans* became a better competitor and increased niche breadth as irradiation dosage increased, fulfilling the expectation that increased mutation rate favored increasing heterozygosity. Thus the latter two studies utilized more direct methods of estimating genetic variability.

In the field, only a few reported studies have been directed at clarifying the relationship between niche width and genetic variation using electrophoresis to estimate directly genetic heterozygosity. Soule and Yang (1973) have concluded that biotic complexity may be more important in promoting increased genetic variation than environmental heterogeneity per se. In a series of multiple-regression analyses, the latter authors found that the number of species of iguanid lizards (*C*) occupying an island accounted for more of the variance in the heterozygosity estimates across 14 islands than did ecological factors such as island area. Prakash (1973) found low gene variation in a narrow-niched species, *D. busckii*. Sabath (1974) investigated genetic variability at five to nine enzyme loci in 11 sympatric *Drosophila* species in central Indiana. Collections were made of *Drosophila* species on 19 quadrats comprised of six habitat types differentiated by plant profile, presence or absence of human habitats, plant densities, etc., with the quadrats defining the resource states and presence or absence of species aiding in defining *Drosophila* niche breadth.

In his final analysis, Sabath (1974) found no relationship between niche breadth and genic heterozygosity. He pointed out four reasons why this might be the case but failed to consider the possibility that the sampling techniques he used may have been directly at fault. For example, the average number of loci sampled per species was seven, with only two (α -glycerophosphate dehydrogenase and esterase-5 [see Sabath 1975]) analyzed in all 11 species. Failure of electrophoretic techniques to expose hidden genetic variability will have a direct consequence on the estimation of electrophoretic variability so important in this study; thus the number of genes analyzed per species should be maximized and similar loci across species studied to obtain an adequate, comparative estimate of heterozygosity per species. In addition, the estimation of niche breadth is based on generalized parameters. This approach would tend to mask direct relationships to elements important in defining the realized or actual

niche of the species (Colwell and Futuyma 1971). Furthermore, it seems plausible that niche breadth over a specific dimension directly related to fitness may be more important than generalized niche breadth over multiple dimensions. Such a dimension, for example, might be the types of substrates used in oviposition, or the number of plant species utilized by the *Drosophilid* in this behavior.

Unfortunately, for most *Drosophila* species extensive natural breeding substrate information is not yet available, with the recent exception of the Hawaiian *Drosophilidae*. Montgomery (1975) has listed the breeding sites utilized for over 80 species of Hawaiian *Drosophila*, greatly extending the work of Heed (1968). With the availability of this information, an analysis can now be made defining the relationship between niche breadth for a specific ecological feature and genetic variation in 16 endemic and two exotic species of Hawaiian *Drosophila*. The results of that analysis are presented here and provide evidence to favor the niche width-genetic variability hypothesis.

METHODS AND MATERIAL

Genetic variability estimates are taken from studies presently in the literature or in preparation (i.e., Carson and Johnson 1975; Johnson et al. 1975; Steiner et al. 1976; Steiner 1974, 1975; Steiner et al. 1973). Only studies in which a minimum of 12 enzyme loci were analyzed in all species were utilized, although some studies incorporated additional gene loci (i.e., see above studies). The 12 basic loci include alcohol dehydrogenase (*ADH-1*), glutamate oxaloacetate transaminase (*GOT-1*) and (*GOT-2*), α -glycerophosphate dehydrogenase (α -*GPDH-1*), hexokinase (*HK-1*), isocitrate dehydrogenase (*IDH-1*), leucine amino peptidase (*LAP-1*), malate dehydrogenase (*MDH-1*) and (*MDH-2*), malic enzyme (*ME-1*), phosphoglucosmutase (*PGM-1*), and octanol dehydrogenase (*ODH-1*). Numbers for each species and the species studied are indicated in table 1.

The unidimensional niche width estimate is based on species-specific oviposition and larval feeding sites preferred by the study species and is taken from the data of Montgomery (1975). Intuitively, one expects that the greater the number of plant species utilized as oviposition sites the more variable the *Drosophila* species. The null hypothesis used to test this expectation is that there is no relationship between variability and the number of oviposition sites occupied. The regression analysis is after Snedecor and Cochran (1969, p. 150). Here, a word of justification may be in order. Although it might be argued that Montgomery's collection techniques were not intended to allow direct comparisons between localities or even to sample all possible breeding sites at a given locality the data are believed representative for the species of this study for the following reasons. First, repeated sampling of different breeding sites in different plants demonstrated consistently that only certain species of *Drosophila* would be associated with that material (i.e., refer to data of Montgomery [1975]). Second, for breeding purposes the Hawaiian *Drosophila*, like most *Drosophila*, utilize substrates which are most likely to contain bacteria

TABLE 1

GENIC HETEROZYGOSITY AND BREEDING SUBSTRATE DATA FOR SIXTEEN ENDEMIC
AND TWO EXOTIC SPECIES OF HAWAIIAN *Drosophila*

<i>Drosophila</i> Species	Island	No.	<i>H</i>	Plant Species Invaded (No.)	Type of Substrate Invaded*
<i>silvestris</i>	Hawaii	448	.117†	5	S, B, E
<i>heteroneura</i>	Hawaii	> 20	.128†	3	S, B
<i>cyrtoloma</i>	Maui	34	.046†	2	B
<i>melanocephala</i>	Maui	> 20	.076†	1	B
<i>planitibia</i>	Maui	> 20	.045†	3	S
<i>neopicta</i>	Maui	72	.015†	2	S, B
<i>picticornis</i>	Kauai	63	.104†	2	E
<i>orthofascia</i>	Maui	63	.025	2	B
<i>engyochracea</i>	Hawaii	1,026	.128	1	B
<i>silvarentis</i>	Hawaii	97	.080	3	E
<i>sproati</i>	Hawaii	125	.083	1	B
<i>grimsbari</i>	Molokai	72	.129	7	S, B
<i>recticilia</i> ‡	Maui	56	.144	1	E
<i>setosimentum</i> ‡	Hawaii	206	.044	1	S, B, L, Fl, Fr
<i>odontophallus</i> ‡ . . .	Maui	129	.010	1	S
<i>mimica</i>	Hawaii	1,225	.194	5	L, Fr, Fu
<i>immigrans</i>	Hawaii	51	.115	5	E, Fr
<i>simulans</i>	Hawaii	117	.073	2	E, Fr

NOTE.—Genic heterozygosity (*H*) is calculated after Lewontin and Hubby (1966).

* S = stems, B = bark, E = sap exudate, L = leaves, Fl = flowers, Fr = fruit, Fu = fungus.

† Esterases not included, 12 or more loci analyzed in all species.

‡ Previously unpublished data.

and yeast infections as well as provide certain biochemical compounds which furnish nutrition for the developing larvae. Thus, Montgomery would collect this type of material in the field after confirming that *Drosophila* eggs or larvae were present, bring it into the laboratory, and raise the organisms to adulthood (or perform chromosome analysis) to confirm the species present. However, Hawaiian *Drosophila* workers will all attest to the fact that you cannot collect a particular species of adult Hawaiian *Drosophila* unless the plant it prefers for a breeding substrate is in the same locality! This indicates the extent of ecological restriction that Hawaiian *Drosophila* are often subject to. Indeed, Kambysellis and Heed (1971) have demonstrated some of the underlying reproductive basis for this restriction. Finally, Colwell and Futuyma (1971) point out that whether one compares niche metrics among species within a community or between species of different communities (this case) the important point is to standardize the procedure so that measures are comparable for the different species. By using a unidimensional estimate of niche breadth and a direct test of genetic heterogeneity we avoid the problem of standardization of resource states.

In a second regression analysis the data of Carson and Johnson (1975) are analyzed and a relationship between genetic variability (based on the averaged value of both chromosomal and electrophoretic polymorphisms and altitudinal

TABLE 2

GENETIC VARIABILITY AND ALTITUDINAL LOCATION OF EIGHT HAWAII POPULATIONS
OF *Drosophila setosimentum*

Population	Average Number Analyzed/Locus	Altitude (100 Feet)	Average Genetic Variability
Puu Laa Laau	37.8	40	.125*
Puu Ohu	39.4	35	.145*
Kipuka 4,400	50.2	44	.152*
Olaa	364.4	41	.156*
Laupahoehoe	94.3	25	.063†
Puna-Kohala	21.4	< 25	.053†
Mawae	35.0	51	.219‡
Kona	91.9	35	.062‡

* Based on nine polymorphic chromosome inversions and four electrophoretic polymorphisms (see Carson and Johnson 1975). See the latter author for the definition of the average genetic variability.

† Based on nine polymorphic chromosome inversions.

‡ Based on nine polymorphic chromosome inversions and three electrophoretic polymorphisms.

location of populations of *D. setosimentum*) is exposed. In this as in the above analysis the dependent variable is the measure of genetic variability. The rationale here is that the breeding substrate for *D. setosimentum* may increase in numbers and variability with altitude. Degener (1960) describes five species of *Clermontia* on the island of Hawaii with at least one of these, *C. parviflora* (Guadichi), consisting of a species complex of unknown numbers. Further, there appear to be more species of *Clermontia* occurring at higher elevations than at lower elevations. Thus, as a further test, if higher genetic variability is associated with increased numbers of different breeding sites across many species of *Drosophila*, then within one species of *Drosophila* we should expect to see increased genetic variability associated with increasing altitude where a concomitant increase in *Clermontia* diversity may occur. In addition, rainfall in rainforest areas may be higher in the higher altitudes, a climatic factor which should not only enhance overall forest diversity but may also be favorable to *Drosophila setosimentum* reproduction since the wetter the environment the more likely rotting and fermenting *Clermontia* material can be found.

RESULTS

The data used in the analysis are listed in tables 1 and 2. Table 1 lists, in addition to the species and number analyzed, the heterozygosity estimates for each species, the number of plant species recorded to be utilized as an oviposition site and the type(s) of substrate(s) used in which eggs are laid. In those cases involving leaves, bark, stems, and fruit, the substrate is usually in a rotted and fermenting state. An attempt to find a relationship between heterozygosity and these substrate types proved negative. Figure 1, however, demon-

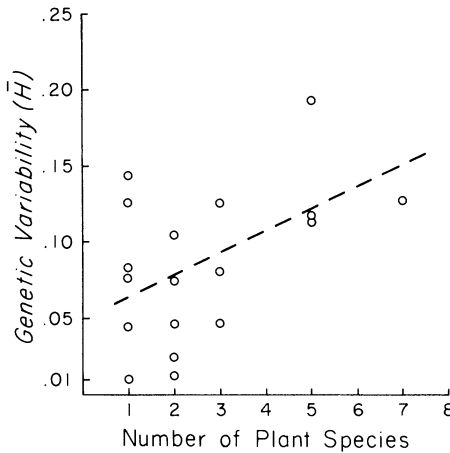


FIG. 1.—The relationship between genetic variability and number of oviposition sites utilized in 18 species of Hawaiian *Drosophila*.

strates the results of the regression of genic heterozygosity on the independent variable—number of plant species used as a breeding substrate. The regression coefficient is significant ($b = 1.45 \pm 1.29$, $p < .05$, $df = 16$), indicating we can reject the null hypothesis of no relationship.

In the second analysis we are interested in determining if genetic variation in one species, *Drosophila setosimentum*, is associated with the location of the population of an altitudinal basis. The data for the second analysis are listed in table 2, while figure 2 displays the results. In this study, altitudinal values have been divided by 100 to facilitate analysis. Again, a significant regression coefficient is observed ($b = 0.59 \pm 0.27$, $p < .005$, $df = 6$), and the null hypothesis—that no relationships exist between the independent variable, altitude, and the dependent variable, genetic variability—can be rejected. The relationship holds up even if the polymorphic enzyme systems used in estimating the average genetic variability in the populations are removed from the samples leaving only the polymorphic chromosome inversions (i.e., see original data of Carson and Johnson 1975).

DISCUSSION

The demonstration of a positive relationship between genic heterozygosity and the number of oviposition (larval feeding) sites occupied by Hawaiian *Drosophila* species provides strong evidence to favor the niche-variation hypothesis. Examination of the data, however, reveals that at least two species do not fit the hypothesis: *D. recticilia* of Maui and *D. engyochracea* of Hawaii. Both species have high levels of variability yet oviposit in extremely narrow niches; the latter in the rotting bark of the endemic tree, *Sapindus saponaria* and the former in sap exudates (fluxes) of the endemic tree *Acacia koa*. Obviously this indicates that other factors are acting to maintain genetic variability

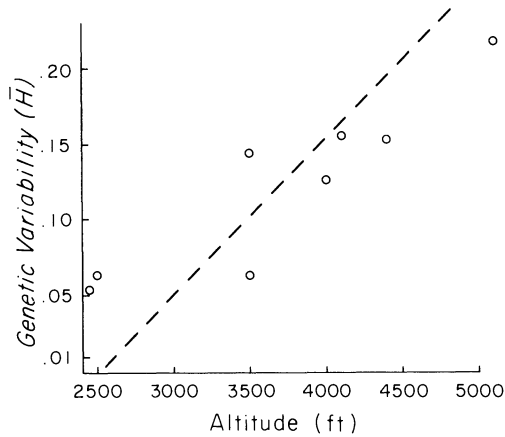


FIG. 2.—The relationship between genetic variability and altitude in eight Hawaii populations of *Drosophila setosimentum*.

as well, and at least for *D. engyochracea* a large outbreeding population size may play a role (Steiner 1974).

The availability and condition of breeding sites must be important for wild *Drosophila* populations since these will, to a certain extent, determine the density of the local breeding population. In this analysis, and in fact in most studies of Hawaiian *Drosophila*, it is difficult to determine population density. Density is an important consideration in this study because small, finite populations may undergo inbreeding effects, thus lowering the overall variability.

The strength of the relationship between altitude and genetic variability for *D. setosimentum* is somewhat surprising. Carson and Johnson (1975) have suggested that these populations are subject to repeated isolation and hybridization with formation of specific ecotypes, factors which would explain in part the strength of the regression analysis in this case.

It is interesting to note that no association was found between the parts of the plant used for oviposition and genetic variability. To a certain extent this is expected, since there are probably more biochemical differences between species of plants than between parts of the same plant. For this reason genetic variability would be expected to be associated with the number of plant species utilized for breeding sites rather than the parts of a plant, although invasion into the latter certainly would increase the chances of a gravid female finding a breeding site. The fact that it is an ecological or environmental factor demonstrating the relationships in each case would appear to argue against the idea of increased biotic complexity providing the basis for the observed relationship. However, biotic complexity can play a role if, in the first case, interspecific competition is occurring for or within the breeding sites and if, in the case for *D. setosimentum*, the number of competing *Drosophila* species or the number of different species of *Clermontia* increases with altitude. I have no solid information

on these points yet. Obviously, the situation calls for an in-depth analysis. For example, an approach can be utilized where species occupying more than one breeding substrate (i.e., *D. mimica*) can be raised directly from the substrate type and the genetic profile of the inhabitants of that substrate type can be determined and compared. In addition, one could control for any effects due to biotic complexity by recording the types and numbers of other larval species occupying the same substrate simultaneously. A similar study of species occupying a single breeding substrate could be done with the substrates drawn from different altitudes or otherwise differing environments. Such studies are needed to confirm the idea that utilization of different breeding substrates requires a genetic adjustment in any one species.

SUMMARY

With the use of regression techniques, associations are found between genetic variability and the number of oviposition sites utilized by two exotic and 16 endemic species of Hawaiian *Drosophila*. An additional association is found for altitudinal location of populations of *D. setosimentum* and genetic variability. These findings are interpreted as providing support for the niche width-genetic variability hypothesis. Additional studies to confirm these findings and establish their genetic basis are suggested.

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