

Ecological Specialization of Hawaiian *Drosophila*

II. The Community Matrix, Ecological Complementation, and Phyletic Species Packing*

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Summary. The ecological overlap of three species of Hawaiian *Drosophila*: *D. mimica*, *D. kambysellisi*, and *D. imparisetae*, has been investigated by analysis of the community matrix. The basic model is a Lotka-Volterra formulation, suitably expanded to include sexual dimorphism. We have also investigated equilibrium population sizes and stability properties of all possible communities which might be constructed from these species. Our findings are:

- 1) There is considerable ecological diversification among these species and between sexes of the same species.
- 2) The two sexes of any one species overlap more than does either with other components of the community.
- 3) The two sibling species, *D. mimica* and *D. kambysellisi* overlap the least, and *D. imparisetae* is ecologically intermediate.
- 4) The current three-species community supports greater numbers than would be maintained by any of the one- or two-species alternatives, and appears to make more efficient use of the available resources.
- 5) The present community is numerically stable. Although its taxonomic saturation is difficult to judge with certainty, it appears to be unsaturated.
- 6) The simpler communities would all be invasible by the remaining species. The implications for sympatric speciation of *D. mimica* and *D. kambysellisi* are discussed. It is suggested that *D. imparisetae* might have acted as an ecological wedge, contributing to ecological displacement, reproductive isolation, and further species packing.

Introduction

Richardson and Johnston (1975a) have described the behavioral components of habitat selection in three species of *Drosophila* (*D. mimica*, *D. kambysellisi*, and *D. imparisetae*) in Kipuka Puauulu, Hawaii Volcanoes National Park. Each of the three species is differently cued by food substrates and light intensity, and the three species are spatially somewhat separated as a consequence. Levins (1968) has suggested that habitat separation may serve as a measure of "niche overlap", and has related various measures of overlap to the α -coefficients of the Lotka-Volterra competition equations. Habitat separation in Kipuka Puauulu is a reflection of niche separation, and the purpose of this paper is to quantify the degree

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of ecological overlap among the three species. We shall also attempt to relate competitive interactions among sexes and species to resource utilization and to phyletic species packing in insular communities.

Specifically, we address the following questions:

- 1) To what extent do the three species overlap in this community?
- 2) Is there ecological complementation among sexes of a single species?
- 3) Is taxonomic affinity an accurate predictor of niche diversification?
- 4) Is the current *Drosophila* community more efficiently utilizing the available resources than would any of the component one or two-species communities which might otherwise occupy the habitat?
- 5) Is the current community stable?
- 6) Would any of the component communities be stable in the face of invasive colonization, and is the current community taxonomically saturated?

The Population Model

We take as our basic description of multiple species dynamics the three-species Lotka-Volterra model (Levins, 1968):

$$\begin{aligned}\dot{N}_1 &= r_1 N_1 \left[\frac{K_1 - N_1 - \alpha_{12} N_2 - \alpha_{13} N_3}{K_1} \right] \\ \dot{N}_2 &= r_2 N_2 \left[\frac{K_2 - \alpha_{21} N_1 - N_2 - \alpha_{23} N_3}{K_2} \right] \\ \dot{N}_3 &= r_3 N_3 \left[\frac{K_3 - \alpha_{31} N_1 - \alpha_{32} N_2 - N_3}{K_3} \right].\end{aligned}\tag{1}$$

The r_i are the intrinsic rates of increase; the K_i are the carrying capacities; and the α_{ij} are the competition coefficients. We are deliberately ignoring the many other components in the community, implicitly assuming that "everything else" is constant. The parameters of (1) depend, of course, on "everything else".

Smouse (1971) has extended the model to deal with separate sexes, which leads (in our notation) to:

$$\begin{aligned}\dot{N}_1 &= \frac{r_1 N_1}{K_1} \left[K_1 - N_1 - \sum_{j=2}^6 \alpha_{1j} N_j \right] \\ &\vdots \\ \dot{N}_6 &= \frac{r_6 N_6}{K_6} \left[K_6 - N_6 - \sum_{j=1}^5 \alpha_{6j} N_j \right]\end{aligned}\tag{2}$$

where components 1 and 2 represent males and females of *D. mimica*, components 3 and 4 represent males and females of *D. kambysellisi*, and components 5 and 6 represent males and females of *D. imparisetae*. The r -values for the two sexes of one species depend on the sex ratio, since the sexes are reproductively dependent. The r -values turn out to be irrelevant for what follows, however, and we choose to ignore this minor complication. The K -values for the two sexes should be treated as measures of resource availability for one-sex populations, if such were able to persist in isolation.

Upon setting each equation of (2) to zero, we obtain one of seven possible steady-state solutions (ignoring the trivial case, total extinction). We may have

a mixture of all three species, any of three two-species mixtures, or any of three one-species populations. Both sexes of any given species will persist or perish together. The steady-state array for the three-species mixture is given by the matrix equation $\hat{N} = A^{-1} K$, where A is the "community matrix" of α -coefficients. The steady-state array for a two-species mixture is given by the same equation, using the appropriate portions of A and K , and similarly for a one-species array. The size of any one component depends on which other components contribute to the particular steady-state. The stabilities of the various "side solutions" depend upon the eigenstructure of the A matrix.

The mathematical analyses detailed below derive explicitly from the choice of growth model embodied in (2). This second order formulation has the advantages of being ecologically familiar, easily interpretable, and mathematically tractable. It suffers from being somewhat unrealistic. The α -coefficients which we have assumed constant are actually functions of the population composition of the total community, and may even depend upon population densities of the species studied. A more detailed population model would probably improve our inference, but would be totally beyond the available data from natural communities. Lacking a much more elaborate data base, we have opted for simplicity. At the price of a few simplifying assumptions, we are able to extend our inference considerably beyond what is usual for studies of this sort. The numerical results depend, of course, on the assumptions employed. The patterns are clear enough, however, that we suspect the basic conclusions are qualitatively correct, even if numerically approximate.

Sample Characteristics

Our sample consists of flies collected at 151 points within the Kipuka on each of 15 days. A thorough description of sampling procedure is provided in Richardson and Johnston (1975b), but the analysis used here depends on two points which warrant further comment. Repeated sampling of the same 151 locations might introduce serial correlations, due to reductions in population size. The sample sizes for the three species are shown as functions of time in Fig. 1, along with the observed sex ratios of each species. There is day-to-day variation, but no pattern over time, and certainly no general decline in population size.

We also need to consider the impact of sampling at one point on the catch at adjacent points. A single sample covers an area of one square meter, however, and there are several meters between collection points. Moreover, the gentle sweeping involved in collecting flies constitutes a minimal disturbance; the escapees alight in the immediate vicinity, and quickly resume courtship, feeding, and other normal behavior. On the basis of these observations, we shall regard our collections as independent samples.

The spatial distributions of the six components are not stable over time. Substrate location and light intensity form strong bases for habitat selection (Richardson and Johnston, 1975b), but the taxa also respond to a variety of more subtle changes in microenvironment, and their "niches" shift position from day to day. Different taxa may occupy the same location, but generally on different days. We have therefore treated each of our 2265 collections (151 points \times 15 days) as a separate sample.

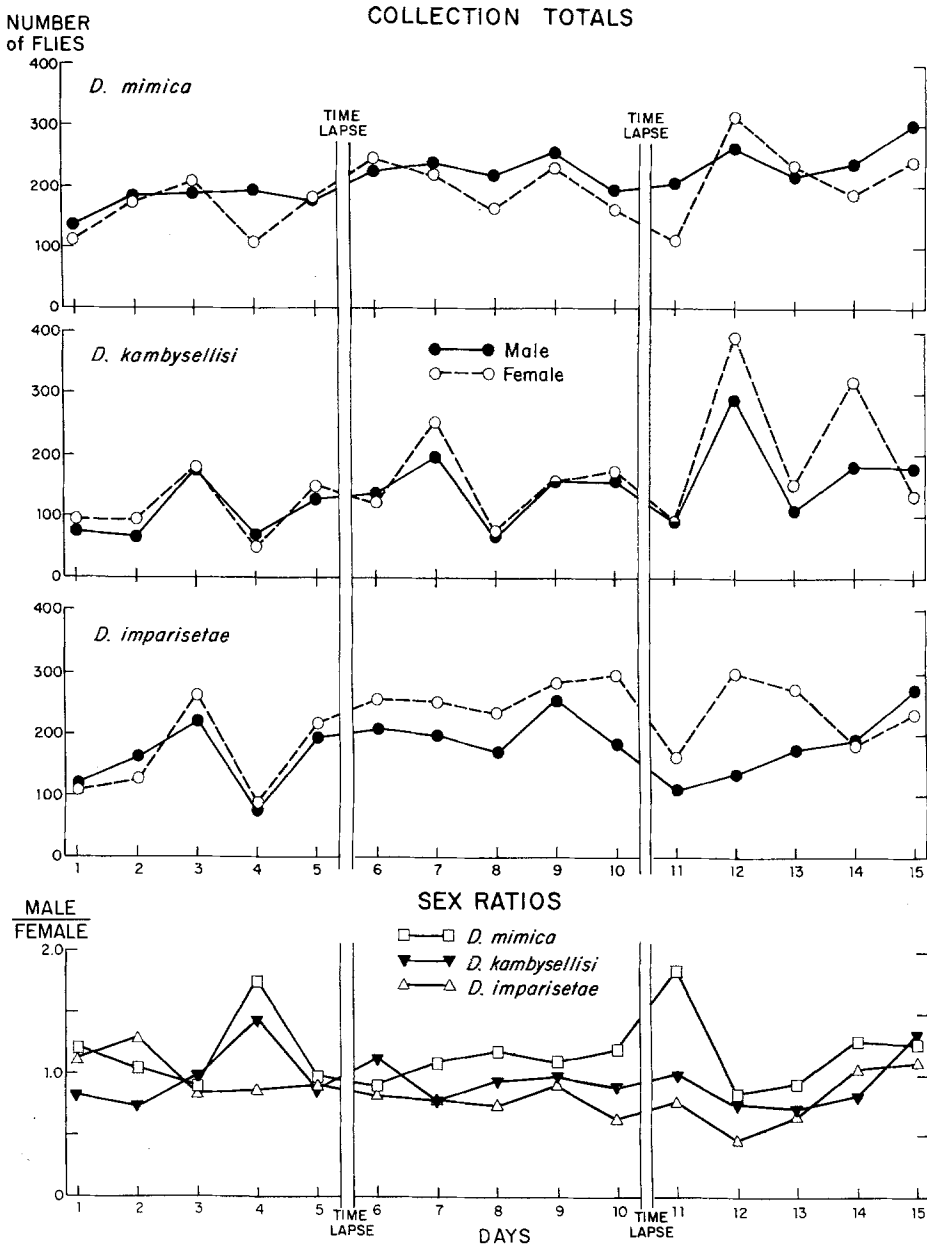


Fig. 1. Daily collection totals and sex ratios during study. Time lapse between days 5 and 6 was 1 day, and between days 10 and 11 was 2 days

The Community Matrix

We denote the fraction of the i -th component recovered from the h -th collection by Q_{ih} , and we use these measures to describe the distributions of the

various components over time and space. Levins (1968) has suggested two different (but analogous) measures of niche breadth (in our notation)

$$B_i = \left[\sum_{h=1}^H Q_{ih}^2 \right]^{-1} \quad \beta_i = \left[- \sum_{h=1}^H Q_{ih} \log Q_{ih} \right]. \quad (3)$$

Corresponding to the B-measure, Levins (1968) has defined elements of the community matrix A

$$a_{ij} = \frac{\sum_{h=1}^H Q_{ih} Q_{jh}}{\sum_{h=1}^H Q_{ih}^2} \mp \frac{\sum_{h=1}^H Q_{ih} Q_{jh}}{\sum_{h=1}^H Q_{jh}^2} = a_{ji}. \quad (4)$$

The resulting A -matrix is asymmetric, but May (1974, p. 195) has shown that the essential stability features of the matrix can be captured by

$$a_{ji}^* = [a_{ij} \times a_{ji}]^{\frac{1}{2}} = a_{ij}^*.$$

It is also possible to devise a measure of "niche overlap" corresponding to the "niche breadth" measure (β_i), using the sort of conditional information argument employed by MacArthur (1965), Colwell and Futuyma (1971) and Pielou (1972). The measure can also be derived from sampling considerations, and has immediate analogues in statistical contingency analysis. The details are shown in Appendix A. Here, we simply state the result. For each pair of components, we define

$$M_{ij} = P_i \cdot \left[\sum_{h=1}^H Q_{ih} \log Q_{ih} \right] + P_j \cdot \left[\sum_{h=1}^H Q_{jh} \log Q_{jh} \right] - \sum_{h=1}^H P_{\cdot h} \log P_{\cdot h} \quad (5)$$

where P_i and P_j are the fractions of the total sample ascribable to the i -th and j -th components, respectively, and $P_{\cdot h}$ is the fraction of the total sample recovered from the h -th collection. We then define a standardized symmetric α -value

$$\alpha_{ij} = \frac{M_{\max} - M_{ij}}{M_{\max}} = \alpha_{ji} \quad (6)$$

where $M_{\max} = -P_i \cdot \log P_i - P_j \cdot \log P_j$. We have elected to use this alternative form, and the estimated A -matrix is shown in Table 1.

The ecological separation of the three species is considerable, in accord with the observations of Richardson (1974) and Richardson and Johnston (1975 b). It is also evident that the two sexes of any single species are ecologically more similar than is either with any other component of the community. Nevertheless, they are still rather separated compared to the non-Hawaiian species of this genus we have observed. Generally the feeding, breeding, and oviposition sites of *Drosophila* appear to be interspersed for the two sexes. In Hawaiian species, on the other hand, Spieth (1966) has described many instances of vertical separation of sexes by lek behavior (including *D. kambysellisi* and *D. imparisetae*). Several cases of horizontal separation are also known (including *D. mimica*). If the community is not saturated (tightly packed), then ecological diversification along sexual lines would reduce competition within a species. Other examples of sexually based ecological variation are known in Anolis lizards (Schoener, 1967) and in *Rumex* (Putwain and Harper, 1971).

Table 1. Estimated community matrix A of Kipuka Puau

	<i>D. mimica</i>		<i>D. kambysellisi</i>		<i>D. imparisetae</i>	
	Males	Females	Males	Females	Males	Females
<i>D. mimica</i>						
Males	1.0000	0.6616	0.4601	0.3605	0.4901	0.4975
Females	0.6616	1.0000	0.4958	0.4302	0.5608	0.6106
<i>D. kambysellisi</i>						
Males	0.4601	0.4958	1.0000	0.6964	0.4987	0.4969
Females	0.3605	0.4302	0.6964	1.0000	0.4825	0.4674
<i>D. imparisetae</i>						
Males	0.4901	0.5608	0.4987	0.4825	1.0000	0.7226
Females	0.4975	0.6106	0.4969	0.4674	0.7226	1.0000

The trio of species consists of a pair of siblings (*D. mimica* and *D. kambysellisi*) and the more distantly related *D. imparisetae*. In view of the possibility that the siblings emerged *in situ* (Richardson, 1974), it is noteworthy that this pair of species exhibits the least overlap. Whether this inverse relation between taxonomic affinity and ecological overlap is a general phenomenon or a consequence of habitat displacement is not clear. The fact that both *D. mimica* and *D. imparisetae* use *Sapindus* fruit for a larval substrate, while *D. kambysellisi* utilizes *Pisonia* leaves suggests the latter view.

Carrying Capacity and Community Composition

A primary objective of our analysis is to compare the characteristics of the three-species community with those of simpler communities of one or two species. We are concerned in this section with the total population sizes attainable by the various possible *Drosophila* communities. In particular, we wish to determine whether the three species community is larger than any community of fewer species which might occupy the habitat. If so, we have an indication that the current community is more efficiently utilizing the available resources than would any of the alternatives.

Given the A -matrix of Table 1, and a vector of sample sizes \hat{N} for the six components of the community, we can estimate the six K -values by the relation $\hat{K} = \hat{A}\hat{N}$. The observed sample sizes are listed in the first row of Table 2, and the estimated K -values are listed in the last row. The total observed density (16,454) is considerably less than the sum of the K -values (60,053), due to competition among components.

Although we cannot directly observe the other possible communities in identical habitats, we can estimate what such "gedanken" experiments would yield. For example, the first four K -values and the appropriate minor of the community matrix A can be used to compute the equilibrium array for a mixed population of *D. mimica* and *D. kambysellisi*. The N -values will be different from those of the three-species community, because the competition from *D. imparisetae* has

Table 2. Equilibrium population sizes for seven potential *Drosophila* communities

Species composition	<i>D. mimica</i>		<i>D. kambysellisi</i>		<i>D. imparisetae</i>		Total numbers
	Males	Females	Males	Females	Males	Females	
M + K + I	3217 ^a	2888 ^a	2069 ^a	2317 ^a	2678 ^a	3285 ^a	16454 ^a
M + K	3996	5020	2880	3381	—	—	15277
M + I	3684	3600	—	—	3679	4006	14969
K + I	—	—	3501	2309	3864	5084	14758
M	5129	7153	—	—	—	—	12282
K	—	—	6414	4521	—	—	10935
I	—	—	—	—	5587	6658	12245
K-values	9862	10547	9563	8988	10398	10695	—

^a The observed numbers.

been “removed”. A similar strategy yields the N-values for single-species populations as well. The predicted population arrays for different sorts of communities are listed in Table 2.

The three-species community supports greater total numbers than would any of the two-species communities, and the latter would support greater total numbers than would any one-species community. The total size of each one-species community would exceed the K-value of either sex. Thus, appreciable ecological complementation exists within and among species.

Community Stability

Turning to an examination of the stability of the various communities, we describe two different sorts of stability. The first is the tendency of a mixed population to revert to mixed equilibrium after numerical perturbation, denoted “*numeric stability*”. The second type of stability is the tendency of a community to resist invasive colonization, denoted “*saturation*”. The first type is included within the second, and the two are mathematically related.

Levins (1968) and Vandermeer (1970) have shown that the *numeric stability* of a community may be determined from the eigenvalues of the community matrix A , but Strobeck (1973) has demonstrated that the usual procedure is valid only under certain circumstances. One such circumstance is that the A -matrix is symmetric, in which case the steady-state is numerically stable if and only if all eigenvalues of A have positive real parts. The numeric stability of each community of one or two species may be investigated in the same manner. The eigenvalues for all seven communities are listed in Table 3, and it is clear that any of these communities would be numerically stable, if it existed.

Each of the one- and two-species communities also constitutes a “side solution” of the three-species model, and might be achieved through extinction of the appropriate components of the three-species community. More probably, the three-species community was formed by invasive colonization of one of the simpler communities. If a particular side solution is *saturated*, however, no colonization could take place. We now wish to investigate the saturation of all side solutions, to determine the possible course(s) of successive colonizations. The method of

Jacobians described by Strobeck (1973) can be used for this purpose. For the special case of a symmetric \mathbf{A} -matrix, the method leads to straightforward criteria, detailed in Appendix B, which we shall simply state here.

Consider first the side solution consisting solely of *D. mimica*. Saturation requires that the eigenvalues of the appropriate (2×2) portion of \mathbf{A} (listed in Table 3) be positive (as for numeric stability). In addition, it is necessary to have positive real parts for all eigenvalues (λ) of the eigenequation.

$$\prod_{i=3}^6 [-K_i^{-1}(K_i - \alpha_{i1} \hat{N}_1 - \alpha_{i2} \hat{N}_2) - \lambda] = 0 \quad (7)$$

where \hat{N}_1 and \hat{N}_2 are the equilibrium densities for the one-species solution. Next, consider the community containing only *D. mimica* and *D. kambysellisi*. Saturation requires numeric stability of the two-species community, and also requires positive real parts for the eigenvalues (λ) of

$$\prod_{i=5}^6 [-\tilde{K}_i^{-1}(\tilde{K}_i - \alpha_{i1} \tilde{N}_1 - \alpha_{i2} \tilde{N}_2 - \alpha_{i3} \tilde{N}_3 - \alpha_{i4} \tilde{N}_4) - \lambda] = 0 \quad (8)$$

where $\tilde{N}_1, \tilde{N}_2, \tilde{N}_3, \tilde{N}_4$ are the equilibrium densities of the two-species community. The saturation of the other one and two-species communities may be examined in similar fashion.

We have determined the eigenvalues (λ) of the counterparts of (7) and (8) for all side solutions, using α values from Table 1 and K- and N-values from Table 2. The results are presented below the divider in Table 3. Since all of these latter eigenvalues are negative, *none* of the one or two-species communities would be saturated, and *all* would be open to invasive colonization by the remaining species.

We are inclined to speculate that colonization of Kipuka Puauulu proceeded in three stages, each of which resulted in an overall improvement in resource utilization by the *Drosophila* component of the community. Based upon analysis of the present population, it appears that the order of colonization would not have mattered, since each of the possible simpler communities would have been invisable by the remaining species. The analysis was performed on the species as they presently exist. The invaders must necessarily have had similar attributes to their descendants, but the ecological complementation itself could have increased by the process of competitive co-evolution (Lawlor and Maynard-Smith, in press).

Numeric stability of the three species community does not imply saturation. In fact, additional diversity exists, but we have deliberately ignored several rarer *Drosophila* species in the Kipuka. The current three-species community represents a "side-solution" for any more inclusive community which might exist, but lacking α and K values for the other species, we have no direct way of dealing with current saturation. It is worthy of note, however, that none of the eigenvalues of \mathbf{A} is small, and the three-species community is not "tightly packed" in the sense of MacArthur (1970) and Vandermeer (1970). A careful examination of the smallest positive eigenvalues of Table 3 (above the divider) will show that the smallest eigenvalue decreases only slightly with the addition of another species to the community. If the pattern were to persist, then the community might be able to absorb several additional species.

Table 3. Eigenvalues for all possible combinations of species, both as self-contained communities (above divider) and as side solutions of more inclusive communities (below divider)

Species in com- munity	Eigenvalues (in decreasing order)					
	1	2	3	4	5	6
M + K + I	3.6504	0.8364	0.6209	0.3344	0.2938	0.2640
M + K	2.5546	0.8154	0.3389	0.2911	-0.2456	-0.2459
M + I	2.7740	0.6269	0.3332	0.2659	-0.2361	-0.2741
K + I	2.6825	0.7372	0.3045	0.2758	-0.2415	-0.3038
M	1.6616	0.3384	-0.3530	-0.3725	-0.3824	-0.4519
K	1.6964	0.3036	-0.4826	-0.5044	-0.5141	-0.5355
I	1.7226	0.2774	-0.3175	-0.3538	-0.3627	-0.3865

Phyletic Species Packing

Biogeographers since Darwin have been intrigued by the dynamics of insular communities. Taxonomic diversity has been related to the interplay of many factors. The rate of community development has been postulated to be determined by the relative rates of species colonization and extinction. The equilibrium complexity of the biotic community is thought to be determined by the ecological diversity of the habitat, which determines the degree of species packing possible in a saturated community (MacArthur and Wilson, 1967).

The initial progress of species packing would largely depend upon rare colonizations. On isolated archipelagoes, the number of taxa represented by colonizers would be small; colonization of the Hawaiian archipelago probably occurred only once for the *Drosophilidae* (Spieth, 1966; Throckmorton, 1966). Few of the available resources would be utilized by an initially depauperate biota, and further species packing would proceed primarily by adaptive radiation and speciation. The current taxonomic diversity of Hawaiian *Drosophila* has presumably arisen from inter-island colonization, adaptive radiation, and speciation (Carson, 1970). Most of the speciation has been interpreted as allopatric in nature (Carson *et al.*, 1970), but an isolated instance of probable sympatric speciation has been identified (Richardson, 1974). This latter process is possible whenever isolating mechanisms accompany habitat diversification within a local population of a single species (Maynard-Smith, 1966). The ecological work of Heed (1968), the behavioral studies of Spieth (1966) and Grossfield (1968), the cytological studies of Yoon *et al.* (1972), and our own studies of dispersal behavior (Richardson and Johnston, 1975a) all point to the conclusion that *D. kambysellisi* and *D. mimica* arose *in situ* within the last 2000 years.

The transfer of a part of the population from *Sapindus* fruit to *Pisonia* leaves would have been a major ecological event, simultaneously opening up a previously unutilized resource and providing considerable niche displacement. It would have been unlikely, however, to have resulted in instantaneous reproductive isolation, and even limited gene flow between the incipient "species" would have retarded adaptation to *Pisonia*. The imposition of a third competitor into an intermediate

niche would have a tendency to further isolate the incipient species by reducing hybrid survival. *Drosophila imparisetae* is environmentally intermediate between the sibling species. It might well have contributed to both habitat displacement and reproductive isolation by acting as an ecological wedge. Under such circumstances, a relatively few genetic changes affecting habitat selection and mating behavior would be sufficient to insure speciation.

If sympatric speciation were common, we would expect to encounter clusters of sibling species in close proximity. Most such clusters would have been overlooked, however, since their detection would have required detailed knowledge of their genetic and reproductive relationships. For the case at hand, *D. mimica* was originally thought to occur on most of the main islands (Hardy, 1965), but Yoon *et al.* (1972) have since shown these different insular populations to be different species. Moreover, in the original collections from Kipuka Puauulu, no distinction was made between *D. mimica* and *D. kambysellisi* (Spieth, 1966; Heed, 1968). It was only after detailed studies of anatomy and larval substrates were undertaken that Hardy and Kaneshiro (1969) separated the two. We have subsequently found that specimens identified as *D. mimica* from elsewhere on the island of Hawaii are sibling species instead, and it is probable that there is at least one more mimica-like species in Kipuka Puauulu (Richardson, unpublished). In the absence of such detailed ecological and genetic analysis, the subtle differences which distinguish recently separated sibling species go undetected. We are in a particularly fortunate position *vis-à-vis* the Hawaiian *Drosophilidae*, where an enormous backlog of investigation may soon permit such detailed analysis in a number of cases.

Appendix A

The purpose of this appendix is to derive a measure of ecological overlap from information criteria. If there exist I taxa, dispersed over H habitats, one may define the probability that an individual encountered in habitat (h) is of type (i) as P_{ih} , where

$$\begin{aligned} \sum_{h=1}^H P_{ih} &= P_{i.}, \text{ the relative frequency of taxon (i),} \\ \sum_{i=1}^I P_{ih} &= P_{.h}, \text{ the relative frequency of individuals in habitat (h), and} \\ \sum_{i=1}^I \sum_{h=1}^H P_{ih} &= 1. \end{aligned} \quad (1)$$

The probability distribution of a series of independent samples drawn from the H habitats is (except for a constant)

$$\begin{aligned} f(\mathbf{N}, \mathbf{P}) &\propto \prod_{h=1}^H [P_{.h}^{N_{.h}}] \left\{ \prod_{i=1}^I \left[\frac{P_{ih}}{P_{.h}} \right]^{N_{ih}} \right\} = \prod_{h=1}^H \prod_{i=1}^I P_{ih}^{N_{ih}} \\ &= \prod_{i=1}^I [P_i^{N_i}] \left\{ \prod_{h=1}^H \left[\frac{P_{ih}}{P_{i.}} \right]^{N_{ih}} \right\}. \end{aligned} \quad (2)$$

If overlap is total, each taxon has the same distribution across habitats and

$$P_{ih} = P_{i.} \cdot P_{.h}. \quad (3)$$

If overlap is less than complete, then we may use the deviation from condition (3) as a measure of ecological separation (non-overlap).

The maximum likelihood estimate of P_{ih} , under the null hypothesis of independence (total overlap), is

$$\hat{P}_{ih} = \frac{N_{i\cdot}}{N} \cdot \frac{N_{\cdot h}}{N} = \tilde{P}_i \cdot \tilde{P}_{\cdot h}. \quad (4)$$

Under the non-independence hypothesis, the estimate is

$$\tilde{P}_{ih} = N_{ih}/N. \quad (5)$$

One may test the independence hypothesis against the alternative by recourse to the likelihood ratio test criterion \mathcal{A}

$$\mathcal{A} = 2N \left[\sum_{i=1}^I \sum_{h=1}^H (\tilde{P}_{ih} \log \tilde{P}_{ih} - \tilde{P}_{\cdot h} \log \tilde{P}_{\cdot h} - \tilde{P}_i \log \tilde{P}_i) \right] \quad (6)$$

which is asymptotically distributed as χ^2 with $(I-1)(H-1)$ degrees of freedom.

Except for the factor of $2N$, \mathcal{A} is a measure of the redundancy of information, and may be rewritten

$$\tilde{M} = \sum_{i=1}^I \tilde{P}_i \cdot \left[\sum_{h=1}^H \tilde{Q}_{ih} \log \tilde{Q}_{ih} \right] - \sum_{h=1}^H \tilde{P}_{\cdot h} \log \tilde{P}_{\cdot h} \quad (7)$$

where $\tilde{Q}_{ih} = \tilde{P}_{ih}/\tilde{P}_i$. . . The maximum value attainable by \tilde{M} is

$$\tilde{M}_{\max} = \sum_{i=1}^I \tilde{P}_i \cdot \log \tilde{P}_i. \quad (8)$$

and we may define an overlap measure $\tilde{\alpha}$

$$\tilde{\alpha} = \frac{\tilde{M}_{\max} - \tilde{M}}{\tilde{M}_{\max}} \quad (9)$$

which ranges from zero (no overlap) to unity (total overlap).

The value of $\tilde{\alpha}$, as defined in Eq. (9), applies to the overlap of a set of taxa, and we are primarily interested in a set of overlap measures for pairs of taxa. If we simply set $I = 2$, then Eq. (9) becomes the required measure.

Appendix B

We are here concerned with the strategy for evaluating the stability of steady-state solutions of the Lotka-Volterra equations. We shall require such partial derivatives as

$$\begin{aligned} \frac{\delta}{\delta N_i} \left[\frac{dN_i}{dt} \right] &= \frac{r_i}{K_i} \left\{ \left[K_i - N_i - \sum_{j \neq i}^6 \alpha_{ij} N_j \right] - N_i \right\} \\ \frac{\delta}{\delta N_i} \left[\frac{dN_j}{dt} \right] &= \frac{r_j}{K_j} (-\alpha_{ji} N_j) \end{aligned} \quad (1)$$

and we define the Jacobian matrix \mathbf{J}

$$\mathbf{J} = \left\{ \frac{\delta}{\delta N_i} \left[\frac{dN_j}{dt} \right] \right\}. \quad (2)$$

To determine whether a particular steady-state solution is stable, we substitute the N_i of that solution into (2), and evaluate the characteristic roots (λ) of the equation

$$|\mathbf{J} - \lambda \mathbf{I}|. \quad (3)$$

If the real parts of all six roots are negative, the solution is stable (Gantmacher, 1959). In practice, the matrix \mathbf{J} may be simplified. In view of Eq. (1), we define $\mathbf{J} = \mathbf{RC}$, where

$\mathbf{R} = \text{diag}\{r_i/K_i\}$, and

$$\mathbf{C} = \begin{bmatrix} C_1 - N_1 & -\alpha_{12} N_1 & -\alpha_{13} N_1 & \dots & -\alpha_{16} N_1 \\ -\alpha_{21} N_2 & C_2 - N_2 & -\alpha_{23} N_2 & \dots & -\alpha_{26} N_2 \\ -\alpha_{31} N_3 & -\alpha_{32} N_3 & C_3 - N_3 & \dots & -\alpha_{36} N_3 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ -\alpha_{61} N_6 & -\alpha_{62} N_6 & -\alpha_{63} N_6 & \dots & C_6 - N_6 \end{bmatrix} \quad (4)$$

where

$$C_i = \left[K_i - N_i - \sum_{j \neq i}^6 \alpha_{ij} N_j \right].$$

For the three-species steady-state, $C_i = 0$ for $i = 1, \dots, 6$, and one may also factor out $\mathbf{D} = \text{diag}\{N_i\}$, writing $\mathbf{J} = -\mathbf{RDA}$, where \mathbf{A} is the community matrix. For the case where \mathbf{A} is symmetric and positive, if \mathbf{RD} is positive definite and diagonal, the characteristic roots of \mathbf{J} have the same signs as the roots of $-\mathbf{A}$, and we may investigate instead

$$|-\mathbf{A} - \lambda \mathbf{I}| = 0. \quad (5)$$

For the steady-states with some species absent, alternative simplifications of \mathbf{C} are also possible. For example, the solution with *Drosophila mimica* present and *D. kambysellisi* and *D. imparisetae* absent may be investigated by evaluating the roots of

$$|\mathbf{C} - \lambda \mathbf{I}| = 0 \quad (6)$$

which may be reduced to the product of

$$\begin{vmatrix} -1 - \lambda & \alpha_{12} \\ \alpha_{21} & -1 - \lambda \end{vmatrix} = |-\mathbf{A}_{12} - \lambda \mathbf{I}| = 0 \quad (7)$$

and

$$\prod_{i=3}^6 [-K_i^{-1}(K_i - \alpha_{i1} \hat{N}_1 - \alpha_{i2} \hat{N}_2) - \lambda] = 0. \quad (8)$$

Similar treatment is possible for the two-species steady-states.

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