CHROMOSOMAL VARIATION AND ITS ADAPTATION IN NATURAL POPULATIONS OF *DROSOPHILA PACHEA*

by

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I hereby recommend that this dissertation prepared under my direction by Garry Alfred Duncan entitled Chromosomal variation and its adaptation in natural populations of Drosophila pachea be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy.

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As members of the Final Examination Committee, we certify that we have read this dissertation and agree that it may be presented for final defense.

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Final approval and acceptance of this dissertation is contingent on the candidate's adequate performance and defense thereof at the final oral examination.

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ABSTRACT

Natural populations of Drosophila pachea were collected from Baja California, Mexico. Only two gene arrangements, '+' and 'A', were observed, as determined by salivary gland polytene chromosome analysis. The 'A' arrangement was fixed in the north and slowly decreased in frequency to the south until an area north of La Paz where it reached its lowest frequency. South of this area the 'A' arrangement rapidly increased in frequency. Temperature, precipitation, and host plant rib number were correlated with this pattern of inversion frequencies. It is argued that the cactus is responding to climatological patterns, whereas the inversions in D. pachea are responding to the cactus and only secondarily to climate.

Computer simulations, laboratory experiments, and field experiments were employed to investigate factors that might influence clinal structure, both the width and the smoothness of the cline. Computer simulations demonstrated that the fitness of the heterozygote (= heterokaryotype) was, for those selective regimes examined, the major influence on clinal width. The influence of gene flow was primarily that of smoothing clines while broadening them only slightly, if at all.

Experiments simulating secondary contact between two populations were performed in the laboratory and by use of the computer. The cline formed between the two populations decayed more rapidly in the laboratory experiment than in the computer analog. Heterozygous advantage and/or negative assortative mating preference among flies in the

laboratory experiment could explain the difference in rates of clinal decay.

A field experiment examining mating preference was conducted by aspirating adult D. pachea directly off a rotting arm of senita cactus, the host plant of D. pachea, and subsequently analyzing the progeny. The data suggest a preference for negative assortative mating and are consistent with previous laboratory results.

Two experiments were designed to test for the fitness of the heterokaryotype in D. pachea, as measured by developmental rate. The first experiment was an interdemic cross between two strains, one homozygous for the '+' arrangement and the other homozygous for the 'A' arrangement. The F_2 results demonstrated a slight excess of heterokaryotypes for the first four days of pupation. A second experiment, again measuring developmental rate, involved intrademic pair matings of flies reared from four senita rots collected at different localities in southern Baja California, Mexico. This experiment was designed to answer the question: Does the heterokaryotype have a developmental advantage in all parts of the species distribution? The data indicate that individuals which develop the fastest carry the inversion that is the most common in the area from which the collection is taken. The presence of modifier genes could explain these results.

The patterns of chromosomal variation in Drosophila pachea on both mainland Mexico and the Baja California peninsula appear to be adaptive. The mechanisms maintaining these patterns are not ones classically thought to promote parapatric speciation.

CHAPTER 1

LITERATURE REVIEW

Since its description by Patterson and Wheeler (1942), a diversity of information has accumulated on Drosophila pachea, a Sonoran Desert fruit fly. The intention of this chapter is to review the literature regarding the taxonomy, ecology, genetics, and reproductive biology of this species.

Taxonomic History

Drosophila pachea is now a member of the nannoptera species group belonging to the subgenus Drosophila. Included in this species group are D. nannoptera Wheeler, D. acanthoptera Wheeler, and an undescribed species, species W. At one time the three described species were classified into three different subgenera. Drosophila acanthoptera was so different morphologically that the subgenus Sordophila was specifically erected for it (Wheeler, 1949), while Drosophila pachea was assigned to the repleta species group of the subgenus Drosophila (Patterson and Wheeler, 1942). Drosophila nannoptera was initially placed into the monotypic nannoptera species group belonging to the subgenus Sophophora (Wheeler, 1949), but Throckmorton (1962) later transferred it to the subgenus Drosophila based on his analysis of the adult internal morphology.

The true phylogenetic relationship among these four species was not exposed until Ward and Heed (1970) examined the salivary gland polytene chromosomes and found them very similar. In fact, the banding sequences of D. nannoptera and species W are identical for all five pairs of chromosomes, although D. nannoptera is heterozygous for one inversion (Russell, Ward, and Heed, 1977b). Banding patterns of D. acanthoptera and D. pachea differ only slightly; D. acanthoptera differs from the two homosequential species by a single fixed inversion, whereas D. pachea differs by three fixed inversions and one which is heterozygous. These dramatic results have once again demonstrated the use of the banding sequences of salivary gland polytene chromosomes as a very powerful tool for elucidating and clarifying phylogenetic relationships.

Subsequent lines of evidence likewise indicate a close relatedness of these four drosophilids. First, comparisons of metaphase chromosomes from larval neuroblasts with the polytene chromosomes revealed that their karyotypes differed only by shifts in amount of heterochromatin (Ward and Heed, 1970). Second, by employing the technique of molecular hybridization, Ward (1975) found that their single-copy DNA sequences were very similar in comparison to drosophilids belonging to different subgenera. Finally, although D. pachea is disjunct from the other three species, which are partially sympatric to one another in southern Mexico (Ward and Heed, 1970), they form the only Drosophila species group to inhabit only the columnar cacti.

Distribution and Ecology

Drosophila pachea is monophagous, or host plant specific, living entirely on the decaying tissues of Lophocereus schottii (Engelmann) Britton and Rose, commonly known as senita cactus. This monophagous behavior dictates the coincident geographic distributions of these two organisms, as collection records have borne out. Senita cactus is distributed from the southern border of Arizona at Organ Pipe National Monument, throughout the western part of the mainland state of Sonora, Mexico, and into the northern part of Sinaloa, Mexico. In addition, senita is found almost entirely throughout Baja California, Mexico (Lindsay, 1963).

A physiological basis for the host plant specificity of Drosophila pachea on senita cactus was demonstrated by Heed and Kircher (1965). They found that a unique sterol in senita cactus, called schottenol, is essential in the diet of D. pachea. More recently, though, Kircher (personal communication, May 1978) has found that the initial methods to isolate schottenol were imprecise. Instead, the isolate solution included not only schottenol but also lophenol and six other unusual sterols. Subsequent tests indicate that two of these unusual sterols, Δ^7 cholesterol and Δ^7 campesterol, rather than schottenol, are more likely responsible for the monophagous behavior of D. pachea.

Although a number of other drosophilids are partially or wholly sympatric with Drosophila pachea, none have been aspirated or reared from the decaying tissues of senita cactus, with the exception of D. mettleri. There are several records of adult D. mettleri being

aspirated from this cactus. Kircher et al. (1967) provided a physiological explanation for the almost complete absence of other drosophilids from senita. One of the alkaloids isolated from senita cactus, called pilocerene, had no effect on D. pachea but was toxic to other co-occurring drosophilids. Ecologically this means that pilocerene has removed D. pachea from extensive competition.

Genetics

Chromosomal Variation

The regular collection record of Drosophila pachea now extends over a period of more than 15 years and covers almost its entire distribution, yet only two gene arrangements, as determined by the banding sequences of salivary gland polytene chromosomes, have been found during this period. These two gene arrangements differ by a paracentric inversion in the number 7 element, the long arm of the number 4 chromosome. One of the two possible gene arrangements in this element has the same banding sequence as all three of its closest relatives. For this reason, this arrangement appears to be the ancestral or standard arrangement and is designated as '+'. The alternate gene arrangement, designated 'A', is not found in any of the three close relatives and is therefore considered to be the more derived of the two (Ward and Heed, 1970).

On the mainland part of Mexico, salivary gland chromosome analysis of collections revealed that the frequencies of the two arrangements form a geographic cline. A cline is simply a gradient in some measurable character. Here, the 'A' arrangement was found to be

fixed, or nearly so, in the northern part of the species range, while the '+' arrangement was fixed in the southern part. A gradual change in frequencies was noted between these two regions (Ward et al., 1974).

Knowledge of the ecology and genetics of Drosophila pachea enabled Ward et al. (1974) to conclude that three forces known to influence inversion polymorphism in other Drosophila species could not be responsible for the cline in D. pachea: (1) the influence of polyphagy; (2) the influence of interspecific competition; and (3) the influence of other inversion systems.

Allozyme Variation

By means of starch gel electrophoresis, Rockwood-Sluss, Johnston, and Heed (1973) examined the allozyme variation in demes of Drosophila pachea from eleven localities. They found very uniform allozyme frequencies both seasonally and geographically for four enzyme loci. Based on the population biology of the fly, they concluded that these similarities could not be due to just dispersal and gene flow but required some selection.

Reproductive Biology

The reproductive biology of Drosophila pachea is unusual in many respects. For instance, most drosophilid females store sperm in both the spermathecae and the ventral receptacle. On the other hand, Drosophila pachea females store sperm only in the spermathecae even though they have what appears to be a normal ventral receptacle (Russell, Ward, and Heed, 1977a). Secondly, the copulation time of D. pachea is unusually long, lasting for an average of about one-half hour (Jefferson,

1977). These two unusual features may in part be due to the atypical sperm produced by D. pachea males. These sperm have tails that are highly coiled, as opposed to the more typical uncoiled tails of other drosophilids (Jefferson, 1977). Perhaps these highly coiled sperm take longer for transmission from the male sperm storage organ to the female sperm storage organ; in addition, they may need to be stored in a more sac-like structure such as the spermatheca, rather than the very long and highly coiled but unused ventral receptacle.

Another reproductive anomaly in Drosophila pachea is the high degree of inbreeding depression that has been observed in the laboratory. This is best exemplified by the difficulty in maintaining isofemale lines and in the low success rate of matings between paired individuals, particularly those between siblings. For this reason, Jefferson (1977) examined a number of reproductive components that could contribute to overall fitness and found that inbreeding lowers the effectiveness of chiefly the following reproductive components: (1) fecundity of the female; (2) quantity of sperm stored by the female; (3) egg hatchability (i.e., the fertility component); (4) egg to adult developmental time; and (5) egg to adult viability.

Inbreeding depression may not be a serious problem in natural populations of Drosophila pachea as suggested by the following features of its reproductive biology and its host plant: (1) in the laboratory individuals of D. pachea prefer to mate with individuals from different strains when given a choice; (2) the sexes show a differential maturation, with females maturing about five days earlier than males; (3) for continued fertility there is an absolute requirement for multiple

matings (Jefferson, 1977); and (4) the ephemeral nature of the rotting substrate dictates the necessity to disperse in search of new breeding sites (such dispersal tends to decrease the probability of inbred matings).

Purpose and Uniqueness of Study

This dissertation was initiated with a plan to augment our understanding of the pattern of chromosomal variation in Drosophila pachea. A combination of field collections and studies, laboratory experiments, and computer simulations were carried out to accomplish this goal. The following chapters focus individually on particular aspects of the problem. The final chapter summarizes and synthesizes this information.

Two advantages of working with this particular system are obvious. First, the size of the polytene chromosomes in dipterans makes karyotype analysis comparatively easy and highly accurate. This is especially true in Drosophila pachea for which only two gene arrangements and three karyotypes are known. Second, knowledge of the ecology of D. pachea is essential to an understanding of the pattern of chromosomal variation in this species.

CHAPTER 2

PATTERNS OF CHROMOSOME VARIATION

Introduction

Prior to this study populations of Drosophila pachea had been sampled rather extensively throughout Sonora, Mexico, for over a decade (Ward et al., 1974), but only three collections had been recorded for the Baja California peninsula: Bahia de los Angeles, Comondú, and Cuñaño (see Table 1 and Figures 1 and 2 for locations). Bahia de los Angeles, the most northern of the three localities, was found to be fixed for the 'A' arrangement. Comondú, south of Bahia de Los Angeles, had a frequency of 0.83 for the 'A' arrangement, while Cuñaño, the most southern of the three, had a frequency of 0.30. These results suggested that the same latitudinal cline of inversion frequencies existed in Baja California as in Sonora.

The intention of this investigation was to confirm or reject the hypothesized similarity in pattern of variation between the two land areas. To accomplish this, extensive collections had to be made throughout Baja California over a period of several years. Also, it was planned to attempt to correlate the observed variation pattern(s) in gene arrangement frequencies with vegetational and/or climatological patterns in Baja California. Several such correlations have been noted by Ward et al. (1974) for Sonoran populations of D. pachea (latitude, mean seasonal temperature and precipitation, mean monthly temperature

Table 1. Collection records and polytene karyotypes of D. pachea from Baja California, Mexico, for three years, March 1976, March 1977, and January 1978.[1]

Site Number[2]	Weather Stations	Collection Number	Collection Date	Type of Collection[3]	Number of Karyotypes Observed +/+	+/A	A/A	Freq. 7+
1	Bahia de los Angeles	A191	3/68		0	0	17	.00
2	Bahia de los Angeles	A606	3/76	PM7	0	0	13	.00
3	San Borja	A605	3/76	PM7	0	0	16	.00
4	Bahia Tortugas	A608	3/76	RL	0	0	34	.00
5	Mulegé	A603	3/76	PM7	0	1	31	.02
6	Mulegé	A607	3/76	PM1	1	19	33	.20
7	Comondú	A62.2	3/62		1	6	16	.17
8	San Agustín	A720	1/78	FCF7,PM1	9	7	1	.74
9	San Agustín	A719	1/78	PM1	3	6	2	.55
10	La Paz	A596	3/76	PM7	7	12	5	.54
11	La Paz	A679	3/77	PM1,PM7	2	5	2	.50
12	La Paz	A677	3/77	FCF1,PM1,PM7 MF	4	13	8	.42
13	La Aguja	A674	3/77	PM1,PM7,MM	3	4	5	.42
14	La Aguja	A672	3/77	PM1,PM7,MM, MF	2	7	4	.42
15	La Paz	A595	3/76	PM7	13	26	7	.56

Table 1, Continued.

Number	Weather Stations	Collection Number	Collection Date	Type of Collection[1]	Number of Karyotypes Observed +/+	+/A	A/A	Freq. 7+
16	La Aguja	A202	4/68		3	9	13	.30
17	San Pedro	A721	1/78	FCF7,PM1	5	24	43	.27
17	San Pedro	A686	3/77	FCF1,PM1,MM	0	14	32	.15
18	El Carrizal	A691	3/77	MF,MM	0	4	8	.17
19	Todos Santos	A684	3/77	FCF1,MM,MF	0	2	9	.09
20	Todos Santos	A693	3/77	MF,MM	1	2	7	.20
20	Todos Santos	A725	1/78	PM7	0	6	6	.25
21	San Bartolo Sur	A688	3/77	FCF1,PM1	0	4	41	.04
22	San Bartolo Sur	A689	3/77	FCF1,PM1	0	4	48	.04
23	Santiago	A694	3/77	FCF1,FCM	0	0	12	.00
24	Caduaño	A696	3/77	PM1,MM	1	3	17	.12
25	San José del Cabo	A723	1/78	FCF1,PM1	1	10	32	.14
26	Cabo San Lucas	A724	1/78	FCF7,PM1	1	2	9	.17

[1]All collections were found to be in Hardy-Weinberg equilibrium.
[2]Site number refers to the sites that are numbered in Figures 2 and 3.
[3]FCF7 = field caught isofemales, 7 larva squashed per female; FCF1 = field caught isofemales, 1 larva squashed per female; FCM = field caught males mated to Zaragosa females, 7 progeny squashed per male to determine his genotype; PM1 = pair matings between rot reared adults, 1 larva squashed per pair; PM7 = pair matings between rot reared adults, 7 larvae squashed per pair to determine the genotype of the parents; MM = matings between rot reared males and Zaragosa females (+/+), 7 progeny squashed per male; MF = matings between rot reared females and Zaragosa males (+/+), 7 progeny squashed per female; RL = rot larvae squashed and scored.

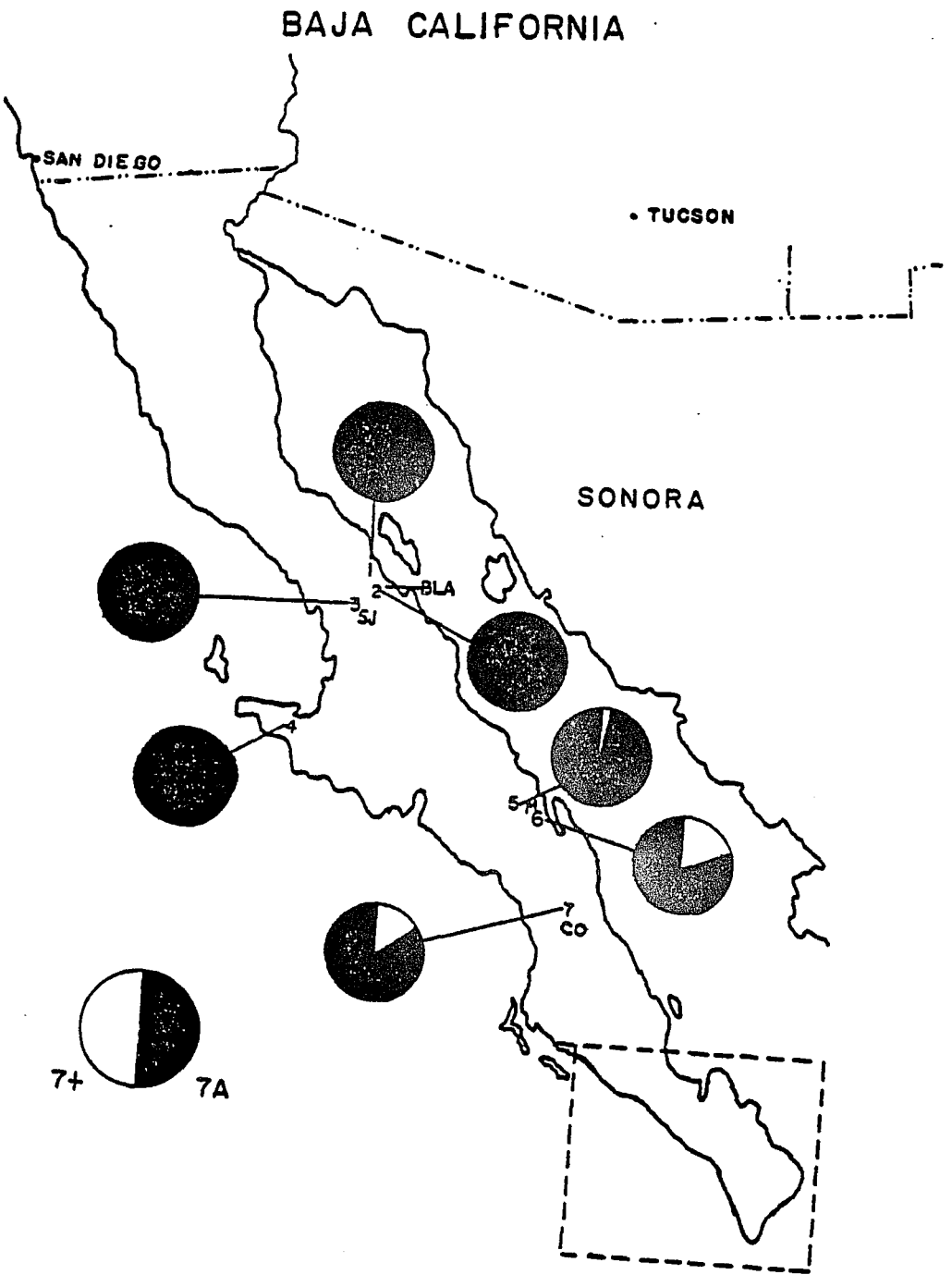

Figure 1. Frequencies of the '+' and 'A' gene arrangements in northern and central Baja California, Mexico.—BLA = Bahia de los Angeles; BT = Bahia Tortugas; CO = Comondú; M = Mulegé; SJ = San Borja.

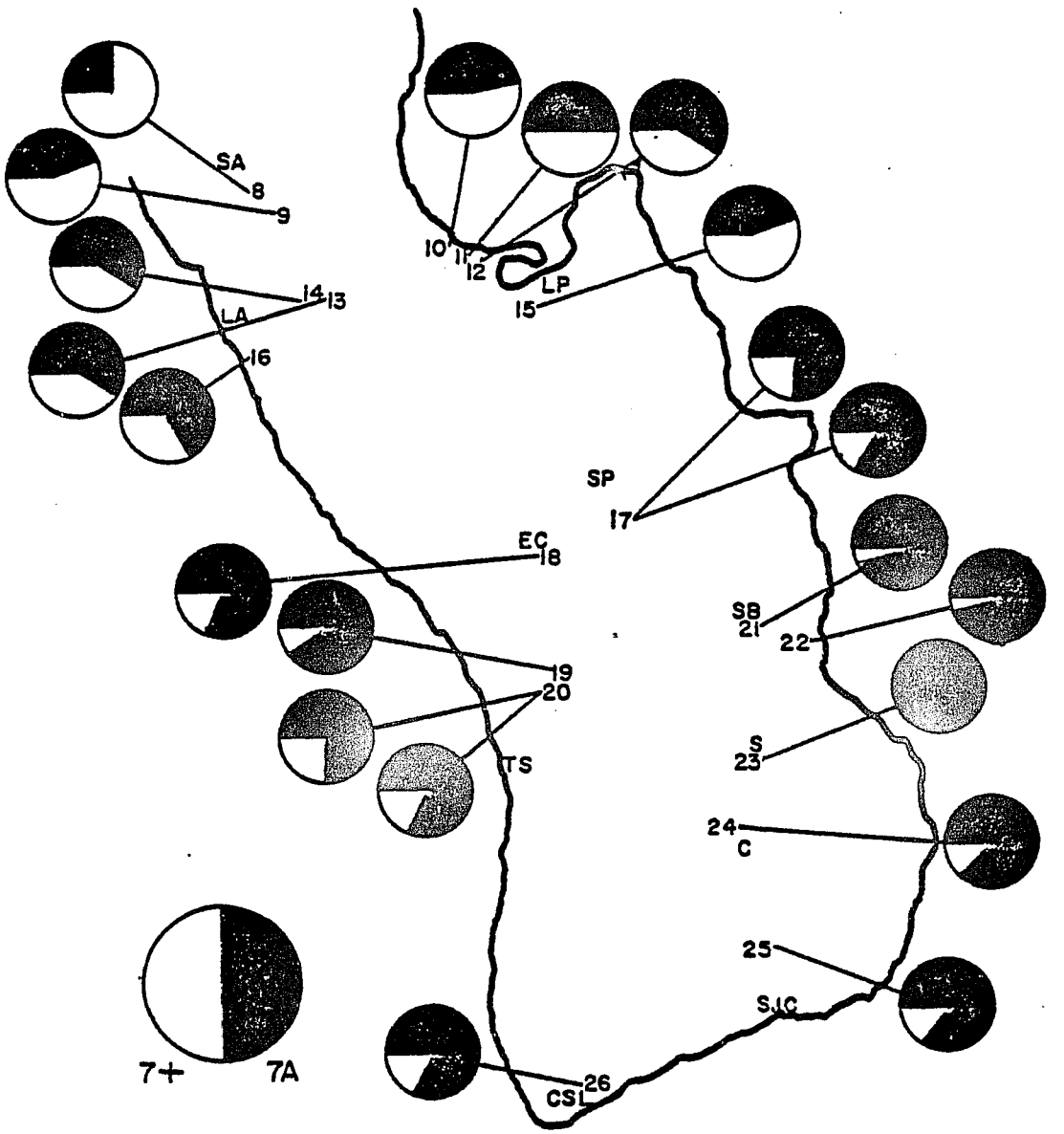

Figure 2. Frequencies of the '+' and 'A' arrangements in southern Baja California, Mexico.--C = Caduaño; CSL = Cabo San Lucas; EC = El Carrizal; LA = La Aguja; LP = La Paz; S = Santiago; SA = San Agustín; SB = San Bartolo Sur; SJC = San José del Cabo; SP = San Pedro; TS = Todos Santos.

and precipitation, surface-volume ratio of the cactus and rib number of the cactus). Similar analyses for Baja California might help determine the selective forces causing and maintaining karyotype variation in Drosophila pachea.

Materials and Methods

Collection of Flies and Determination of Karyotypes

Three collection trips were made to Baja California, Mexico, in three consecutive years (March 1976; March 1977; January 1978). The purposes of these trips were to collect adult Drosophila pachea and rotting tissue of senita cactus. Adult flies were collected with an aspirator directly the rotting substrate. Karyotypes of these adults were ascertained by one of the following procedures. (1) If isofemale lines were established in the field by placing each female in an individual vial, then the karyotypes of both parents could be deduced by examining the progeny of each isofemale using the following procedures. Over a period of several days seven larvae were individually removed from each isofemale vial and placed in 50% acetic acid. Each larva was then dissected and its salivary glands were removed and placed on a slide in a drop of acetoorcein for five to ten minutes. The salivary glands were then squashed by placing a cover glass over the drop of stain and applying pressure to the cover glass with the thumb. The karyotype of the larva was scored by observing the salivary gland polytene chromosomes under a light microscope. (2) In other cases, only one larva was similarly scored per isofemale line. This

procedure netted only half as much information per isofemale as the first procedure but took much less time. (3) When an isofemale produced no progeny, her karyotype was determined when successfully mating her to males of known karyotype and scoring at least seven of her larval progeny. (4) The karyotypes of field-caught males were also determined by this latter method, i.e., by mating them to virgin females of known karyotype and scoring progeny.

Data were also obtained from those flies emerging from the rotting tissues of senita cactus. Limbs of rotting senita, collected in the field, were carefully wrapped in paper and then brought into the laboratory where they were individually placed in covered glass containers. Drosophila pachea larvae and adults were reared from the rotting limbs in these containers. Here again, several methods were employed to obtain chromosome data. When a larva was observed within a rot, it was removed and transferred to fresh laboratory media supplemented with senita cactus in order to increase the quality of nourishment available to the larva. (Good nourishment increases the rate of successfully determining larval karyotypes by improving the quality of the salivary gland polytene chromosomes.) When a larva had reached the third instar stage, its karyotype was determined. The karyotypes of adult flies that emerged from the rots were determined by several means. (1) After segregating the adults according to sex and allowing them to reach sexual maturity, pair matings were made. If at least seven of their progeny were scored, the karyotypes of both parents were deduced. (2) Pair matings were also made in which only one larva was squashed. (3) The karyotypes of other rot reared adults were

determined by mating such flies to stock flies of known karyotype. By scoring at least seven progeny, the karyotype of each rot reared fly could be concluded.

Measurements of Cactus Rib Number

Records of rib numbers of senita cactus were made in January 1978 from six localities in southern Baja California, Mexico. The collection numbers of these localities are found in Table 2, whereas the geographic location of these collection sites can be found by finding the corresponding site number in Figure 3.

The rib number recorded for each locality was the lowest number of ribs, scored at the base of the arm, on plants within a locality (Table 2). A minimum of three plants was observed at each collection site. The lowest number of ribs on a plant was scored because ribs can be added to an arm during growth. As a result, the arms of an individual plant often have a difference of three or four ribs. That is, the tip of one arm may have six ribs while the tip of another arm on the same plant may have eight or nine ribs. In several instances, plants within a given locality had two different minimum numbers. In these instances, the numbers were simply averaged.

Statistical Methods

Simple correlation coefficients were estimated between the frequencies of the '+' gene arrangement, and vegetational and climatological variables in Baja California. These analyses required an angular transformation (= arc sin square root) of the '+' gene arrangement

Table 2. Regression analysis of rib number on the frequency of the '+' arrangement in southern Baja California, Mexico.

Site Number[a]	Collection Number	Number of Ribs (x)	Frequency of '+' (y)	Transformed '+' Frequency
8	A720	9	.74	59.34
15	A595	8	.57	49.02
17	A721	7.5[b]	.27	31.31
20	A725	7	.25	30.00
25	A723	6.5[b]	.14	21.97
26	A724	6	.17	24.35

[a]Site numbers refer to the numbers in Figure 3.

[b]When plants in a given locality had two different minimum numbers, the numbers were simply averaged.

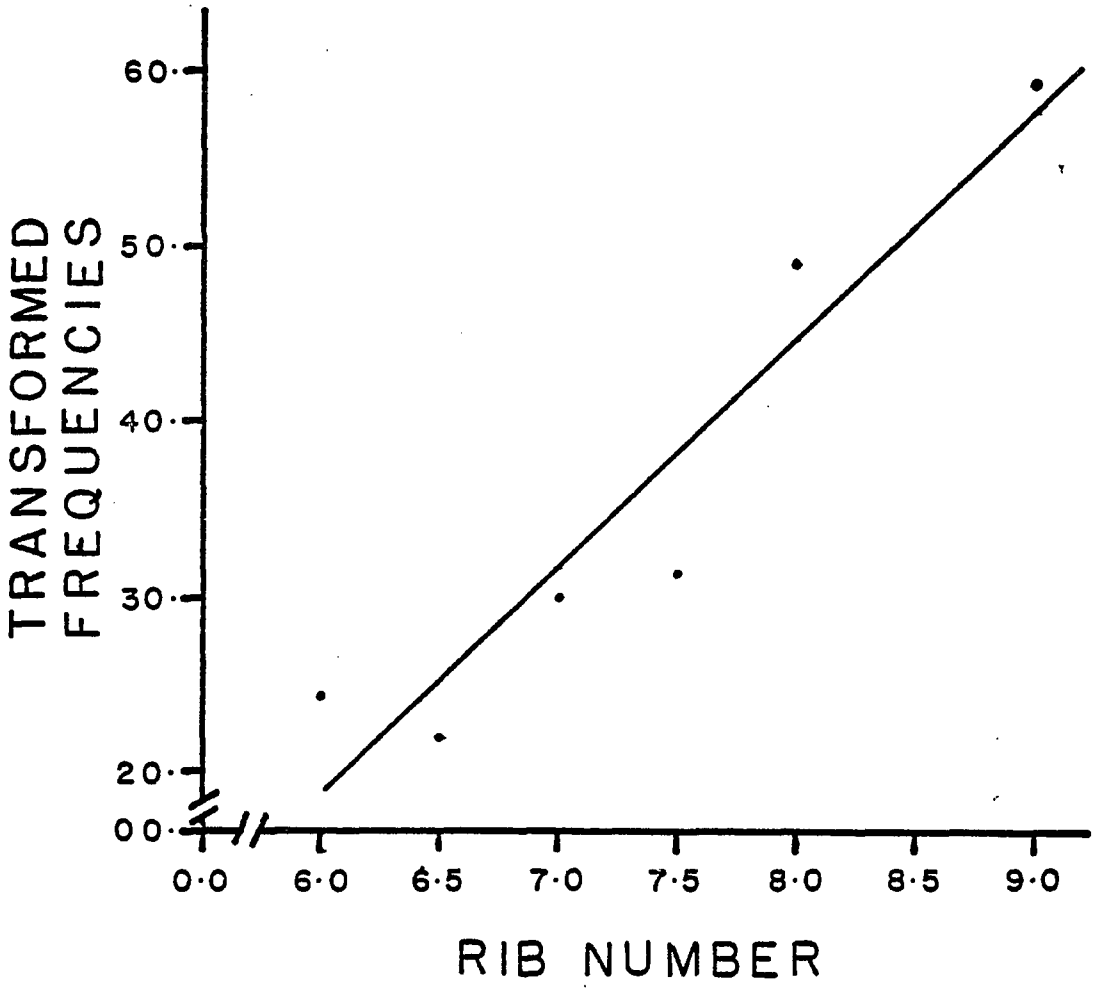

Figure 3. Relationship of transformed inversion frequency ('+' arrangement) to number of ribs of senita cactus host plants.--The plotted least squares regression line is highly significant ($r = .9469$; $P < .01$, 4df).

frequencies in order to insure independently and normally distributed experimental errors (Steel and Torrie, 1960).

Climatological data used in these analyses were obtained from Hastings and Humphrey (1969). Only mean monthly and mean seasonal temperature and precipitation data were available. Using mean monthly data, correlations were calculated not only for the month of collection but also for the two months prior to the collections. Each of the 28 collections was assigned to the nearest of 16 different weather stations for which climatological data were available in order to make the appropriate calculations. With the exception of collection number A608, all collections are believed to be within ten miles of their respective weather stations.

Results

Karyotypic Analyses

The pattern of chromosomal variation on the Baja California peninsula differs from the cline that occurs on the mainland of Mexico (Table 1, Figures 1 and 2). Collections made during the first trip only included localities in the vicinity of La Paz and to the north. The pattern of inversion frequencies for this area of Baja California is very similar to that found on mainland Sonora, Mexico; the frequency of the 'A' arrangement is fixed or nearly so in the north and gradually decreases to the south. The focus of the second trip, March 1977, was to make collections in the vicinity and south of La Paz. Results from this trip proved to be quite unexpected. Rather than continuing to decrease, as was anticipated, the 'A' arrangement increased in frequency

south of La Paz. Collections during the third trip centered around this same area, and analyses of the data confirmed the results obtained from the second trip.

In contrast to the pattern on mainland Sonora, in Baja the arrangement that is fixed in the north is also the one that is the most common in the far south. The '+' arrangement is common only near the south-central part of the peninsula.

To determine the stability of the inversion frequencies, two of the sites that were collected in March 1977 were recollected in January 1978. At both sites, 17 and 20 (Figure 2), the frequency of the '+' arrangement had increased. The frequency of the '+' arrangement at site 17 was 0.15 in 1977 (A686) and 0.27 in 1978 (A721), while at site 20 it was 0.20 in 1977 (A693) and 0.25 in 1978 (A725). These results suggest that climatological changes may have some influence on inversion frequencies, although such inversion frequency changes could also be artifacts due to sampling error.

Correlation with Host Plant Morphology

For each of six collection localities, Table 2 lists the minimal number of ribs found on plants of senita cactus and the corresponding frequency of the '+' gene arrangement in Drosophila pachea. The six localities are listed from north to south; A720 is north of La Paz while A724 is at the cape of the peninsula. This table shows two clines, one in rib number and the other in the frequency of the '+' arrangement. In Figure 3, the data on rib number versus the transformed frequency for the '+' arrangement have been plotted, and a least-squares regression

line has been drawn. The correlation coefficient for these data is +.9469. This value is statistically significant ($P < .01$, 4 df) and indicates a high degree of correlation between these two variables. Surface-volume ratios of senita plants in Baja California were not measured.

Correlations with Climate

Transformed '+' frequencies for each collection as well as seasonal and monthly climatological data used in the following calculations are given in Appendix A, while correlations between seasonal climatological data and transformed frequencies for the '+' gene arrangement are given in Table 3. Only winter temperature is significantly correlated with inversion frequencies ($r = .4861$, $P < .01$, 26 df). Temperature was also correlated with inversion frequency for the month of collection as well as the two months prior to collection (Table 4). The correlation for the month of collection is the least significant of all. This may be because most collections were made in March, one of the three months of spring (Hastings and Humphrey, 1969), a season not shown to have a significant correlation for temperature and inversion frequency ($r = .0303$, Table 3). However, the two months prior to collection are, on the whole, winter months (December, January, and February). The correlations in Tables 3 and 4 together suggest that the frequency of the '+' arrangement is responding to winter temperatures.

There is also a highly significant negative correlation between precipitation two months prior to collection and inversion frequency (Table 4). Once again, for most collections the two month period prior

Table 3. Correlation of seasonal precipitation and temperature data with transformed frequencies of the '+' gene arrangement.

	Winter	Spring	Summer	Fall
Precipitation	-.3099	-.2343	0.0000	0.0000
Temperature	+.4861**	+.0303	-.2316	+.3136

**P < .01, 26 df

Table 4. Correlation of precipitation and temperature data during and preceding the month of collection with transformed frequencies of the '+' gene arrangement.

	Month of Collection	One Month Prior to Collection	Two Months Prior to Collection
Precipitation	+.2469	+.0572	-.5354**
Temperature	+.3222*	+.4662**	+.4533**

*P < .05, 26 df
**P < .01, 26 df

to collection was a winter month. Data in Table 3 show that winter precipitation has almost a significant negative correlation with inversion frequency. This information suggests that the '+' gene arrangement may also be responding to winter precipitation.

Discussion

Although no evidence was presented definitely linking the two gene arrangements in Drosophila pachea to climatological or host plant morphological changes, demonstrated correlations certainly suggest these relationships exist. Ward et al. (1974) have shown highly significant correlations in D. pachea between transformed inversion frequencies and seasonal temperature for all four seasons in Sonora, Mexico. Furthermore, they found highly significant correlations for inversion frequency and cactus rib number ($r = +.876$, $P < .01$, df 9), and for inversion frequency and cactus surface-volume ratio ($r = +.917$, $P < .01$, df 9). Inversion frequency also was correlated with precipitation during summer and fall ($r = +.4975$ and $+.6311$, $P < .01$) and one month prior to the collection ($r = +.2790$, $P < .05$). Ward et al. (1974) concluded that the '+' inversion is adapted for warm and possibly wet environments.

The possibility that inversions in Drosophila pachea may respond to climatic regimes is not unique. Other investigators have provided evidence that factors such as temperature and humidity may be responsible for changes in inversion frequencies. For example, Dobzhansky (1948) demonstrated fluctuations in inversion frequencies of Drosophila persimilis corresponded to seasonal and altitudinal patterns. Dubinin

and Tiniakov (1946) and Borisov (1969) observed similar seasonal changes in the inversions of D. funebris populations near Moscow.

Ward et al. (1974) were, however, reluctant to assign any direct adaptive significance to the correlations of inversion frequencies with cactus morphology because the cactus also changes along a latitudinal gradient. In Sonora, Mexico, the 'A' arrangement is in high frequency in the north and decreases southward, whereas Felger and Lowe (1967) found that senita cactus rib number is low in the north and increases southward. Lower rib number and surface-volume ratio in the north was attributed to more severe temperatures during the winter months (Felger and Lowe, 1967). The results from this investigation could perhaps alter this view, for rib number is low in northern Baja California (Richard S. Felger, personal communication, 1977) and also in the far south, just as the 'A' inversion is high in frequency in both the north and the far south. It would seem that surface-volume ratio becomes uncoupled from rib number in Baja California since the northern and southern plants have the same number of ribs but the southern form is spindly compared to the robust northern form.

Interestingly, the region of highest heterozygosity for inversion frequencies in both Sonora and Baja California correspond to subspecific changes in senita cactus as described by Lindsay (1963). In Baja California Lophocereus schottii schottii is replaced by L. s. australis whereas in Sonora the subspecific replacement is by L. s. tenuis.

The presence of so many significant correlations suggests that Drosophila pachea is responding genetically by means of inversions to

some combination of climatological forces and host plant changes simultaneously. Intuitively, climatological effects seem less likely. After all, weather conditions are extremely variable from day to day and from year to year, especially in Baja California, whereas an individual host plant provides a relatively constant environment.

It seems very plausible that the different host plant forms represent an adaptive response to climatological conditions. The existence of a long-lived host plant form in a given locality may depend either on the average climatological conditions or on climatological extremes. In other words, some weather extreme--e.g., low precipitation or low temperature--may eliminate one plant form but not another. If the inversion frequencies in Drosophila pachea are responding exclusively to the plant types, then D. pachea would be responding only indirectly to climatological conditions. This could explain why the patterns of inversion frequencies in the fly are correlated with the pattern of host plant morphology and, at the same time, weather patterns. Indeed, Kircher (1969) has found differences, although statistically nonsignificant, in the concentrations of fatty acids, non-saponifiables, and alkaloids for an appreciable portion of the senita cactus distribution in Sonora, Mexico. There could be still other differences among the gradient of senita cactus forms that have not been tested experimentally but which can be detected by the fly.

Fly-substrate tests have been attempted with little success to date. In the laboratory a portion of a limb of senita cactus was inoculated with Erwinia sp. to induce necrosis in the cactus. After 1-2 days, sexually mature adult Drosophila pachea, which had been

previously allowed to mate, were placed into the container with the rotting cactus. Difficulty was encountered due to a much more rapid rate of rot progression than under field conditions. In nature, the plant presumably has defense mechanisms for retarding rot advancement, a mechanism not available to an amputated limb in the laboratory. Perhaps some other inoculum species would produce a more ideal rate of decay but such an inoculum has not been found.

An inoculum from a naturally occurring rot was not attempted since such an inoculum could be heterogeneous and would therefore need to be characterized before and after the experiment to determine whether a differential response by the flies was due to differences in the cacti or differences in the potentially heterogeneous inoculum. At this time an experiment of this dimension is not practical.

CHAPTER 3

CLINES: LABORATORY EXPERIMENTS AND COMPUTER SIMULATIONS

Introduction

For many years a large number of evolutionists, led by Mayr (1942, 1963), argued that geographic isolation was a requisite for speciation. It was believed that a small amount of gene flow was essential for maintaining one cohesive gene pool and preventing genetic differentiation. Recently, several groups (Thoday and Gibson 1962; Maynard Smith 1966; Jain and Bradshaw 1966; Ehrlich and Raven 1969; Bush 1975; Endler 1973, 1977; and others) have presented evidence from laboratory and field studies which indicate that differentiation may proceed without geographic isolation. In these instances, individuals are able to disperse but do not appear to contribute to the gene pool of the recipient population; that is, there is dispersal without gene flow. For instance, numerous small mammal and Lepidopteran studies (for an extensive list see Endler 1977, p. 24) indicate that the aliens are less successful at producing offspring, therefore promoting little or no gene flow. Endler (1977, p. 24) provides a partial list of mechanisms that might act to reduce or restrict gene flow in these cases. This list includes, in part, social, ecological, ethological, and physiological mechanisms. These mechanisms provide a basis by which

two or more gene pools can become autonomous without being geographically isolated.

Recently, Endler (1977) reviewed and clarified the literature (Smith, 1965; White 1968, who called it stasipatric speciation; Murray, 1972) concerning a special form of speciation called parapatric speciation. In the first stage of parapatric speciation a cline is formed. Again, a cline is simply a gradient in some measurable character. Endler (1973) offers four basic conditions, one or more of which might allow for the formation of a cline: (1) random genetic drift; (2) secondary contact between formerly isolated populations; (3) spatially discontinuous changes in the environment; and (4) a continuous environmental gradient.

If parapatric speciation is to occur once the cline has been formed, the cline will begin to gradually decrease in width, even in the presence of gene flow, as reproductive barriers begin to build up. Eventually the cline will become very narrow as reproductive barriers become complete.

In support of this theory, Endler (1973, 1977) and May, Endler, and McMurtrie (1975) have shown by computer simulations and laboratory experiments that under certain conditions even high rates of gene flow may not be sufficient to stop populations from differentiating. Their experiments and simulations focus primarily on a model where a gradient of differential selection extends from one end of a distribution to the other. These investigators considered the effects of various rates of gene flow, various degrees of dominance (i.e., incomplete dominance,

complete dominance, and overdominance), asymmetrical gene flow, differential generation time, as well as combinations of the above.

Slatkin (1973), May, Endler, and McMurtrie (1975), and Endler (1977) also consider some of the above influences (i.e., gene flow, heterozygous advantage, etc.) on the ecotone model of selection. As opposed to a gradient, an ecotone is a spatially abrupt change in the environment. Under this model selection can produce conditions that result in the formation of a steep cline in some character, even with significant gene flow. Other notable contributions involving the use of computer simulations to investigate geographic variation and clines include those of Clark (1966), Jain and Bradshaw (1966), and Hastings and Rohlf (1974) (see Endler, 1977, for a more extensive list).

The following investigation on clines utilizes both Monte Carlo computer simulations and a laboratory experiment involving Drosophila pachea. The purpose of the computer simulations was two-fold. The first was to investigate the effects of various rates of gene flow on a model that was somewhat of a compromise between the gradient model of Endler (gradient extends from end to end) and the ecotone model of Slatkin. The second function of the computer simulations was to determine what combinations of conditions (e.g., gene flow and selection) might explain the inversion frequency cline observed in Drosophila pachea on mainland Sonora, Mexico.

The experimental part of this investigation was a laboratory test for the outcome of a secondary contact between two formerly isolated populations. Endler (1977) predicts four possible outcomes when two populations come into secondary contact. (1) If during

allopatry the two habitats remain identical and there is no competition among the two morphs, then the cline will disappear in less than 50 generations. (2) The habitats remain identical but competition ensues between the two morphs resulting in two possible outcomes: (a) the cline disappears due to the coexistence of the two morphs; or (b) a stepped cline will be maintained resulting from the inability of the two morphs to coexist. (3) The habitats have become selectively different, producing a cline whose shape is determined largely by the shape of the selection gradient. Lastly, (4) the habitats have become different, but the shape of the cline here is the result of the degree of competition between the two forms; that is, if competition is severe the cline will become stepped, whereas weak competition results in a smooth cline.

This experiment was designed such that the two habitats were identical, as in conditions 1 and 2 above. If no competition occurs among the two morphs (condition 1), or if competition occurs but the two morphs are able to coexist (condition 2a), how fast will the cline degrade? That is, will the experimental cline degrade at the same rate or at a different rate than that predicted by the computer simulations? If the rates are different, what force(s) might explain the difference? It was hoped that these results would help to understand further the nature of the cline for the two gene arrangements in Drosophila pachea.

Materials and Methods

Monte Carlo Computer Simulations

These computer simulation clines conform to a linear stepping-stone model. All simulations described here had the following basic ingredients. Each simulation had 50 demes and each deme had 100 individuals at the start of each generation. (The control section of the computer simulation is given in Appendix E.) In these simulations the generations were discrete and gene flow occurred before reproduction. At generation zero the frequencies of the two alternative alleles (= inversions here) were 0.50 each in all demes for all simulations. Simulations were ran for 50 generations using three different selection regimes (Tables 5, 6, and 7; Figure 4).

In simulations where there was gene flow, it occurred only between adjacent demes in a stepping-stone model. For example, if 20% gene flow was imposed on deme 25, then 10% of the individuals were dispersed to deme 24 and the other 10% to deme 26, while 80% remained in deme 25. Deme 25 was restored to 100% after receiving 10% of the individuals from deme 24 and 10% from deme 26. Thus it was possible to maintain a constant population size in all demes. Only in demes 1 and 50, the peripheral demes, was the above scheme altered. Those individuals in deme 1 which should have dispersed to the left of it (10%) and those individuals in deme 50, which should have dispersed to the right of it (10%), were placed back into the demes from which they came, that is, demes 1 and 50 respectively. Thus, this method not only maintained

Table 5. Selection gradient for a linear array of 50 demes where the heterozygote has an intermediate fitness.

Deme Number	Genotypic Fitnesses		
	A/A	A/a	a/a
1	0.00	.50	1.00
.	.	.	.
.	.	.	.
.	.	.	.
13	0.00	.50	1.00
14	.04	.50	.96
15	.08	.50	.92
16	.12	.50	.88
17	.16	.50	.84
18	.20	.50	.80
19	.24	.50	.76
20	.28	.50	.72
21	.32	.50	.68
22	.36	.50	.64
23	.40	.50	.60
24	.44	.50	.56
25	.48	.50	.52
26	.52	.50	.48
27	.56	.50	.44
28	.60	.50	.40
29	.64	.50	.36
30	.68	.50	.32
31	.72	.50	.28
32	.76	.50	.24
33	.80	.50	.20
34	.84	.50	.16
35	.88	.50	.12
36	.92	.50	.08
37	.96	.50	.04
38	1.00	.50	0.00
.	.	.	.
.	.	.	.
.	.	.	.
50	1.00	.50	0.00

Table 6. Selection gradient for a linear array of 50 demes where the heterozygote has a fitness of 1.00 in all demes.

Deme Number	Genotypic Fitnesses		
	A/A	A/a	a/a
1	0.00	1.00	1.00
.	.	.	.
.	.	.	.
.	.	.	.
13	0.00	1.00	1.00
14	.04	1.00	.96
15	.08	1.00	.92
16	.12	1.00	.88
17	.16	1.00	.84
18	.20	1.00	.80
19	.24	1.00	.76
20	.28	1.00	.72
21	.32	1.00	.68
22	.36	1.00	.64
23	.40	1.00	.60
24	.44	1.00	.56
25	.48	1.00	.52
26	.52	1.00	.48
27	.56	1.00	.44
28	.60	1.00	.40
29	.64	1.00	.36
30	.68	1.00	.32
31	.72	1.00	.28
32	.76	1.00	.24
33	.80	1.00	.20
34	.84	1.00	.16
35	.88	1.00	.12
36	.92	1.00	.08
37	.96	1.00	.04
38	1.00	1.00	0.00
.	.	.	.
.	.	.	.
.	.	.	.
50	1.00	1.00	0.00

Table 7. Selection gradient for a linear array of 50 demes where the heterozygote has a fitness of 0.90 in all demes.

Deme Number	Genotypic Fitnesses		
	A/A	A/a	a/a
1	.75	.90	1.00
.	.	.	.
.	.	.	.
.	.	.	.
13	.75	.90	1.00
14	.76	.90	.99
15	.77	.90	.98
16	.78	.90	.97
17	.79	.90	.96
18	.80	.90	.95
19	.81	.90	.94
20	.82	.90	.93
21	.83	.90	.92
22	.84	.90	.91
23	.85	.90	.90
24	.86	.90	.89
25	.87	.90	.88
26	.88	.90	.87
27	.89	.90	.86
28	.90	.90	.85
29	.91	.90	.84
30	.92	.90	.83
31	.93	.90	.82
32	.94	.90	.81
33	.95	.90	.80
34	.96	.90	.79
35	.97	.90	.78
36	.98	.90	.77
37	.99	.90	.76
38	1.00	.90	.75
.	.	.	.
.	.	.	.
.	.	.	.
50	1.00	.90	.75

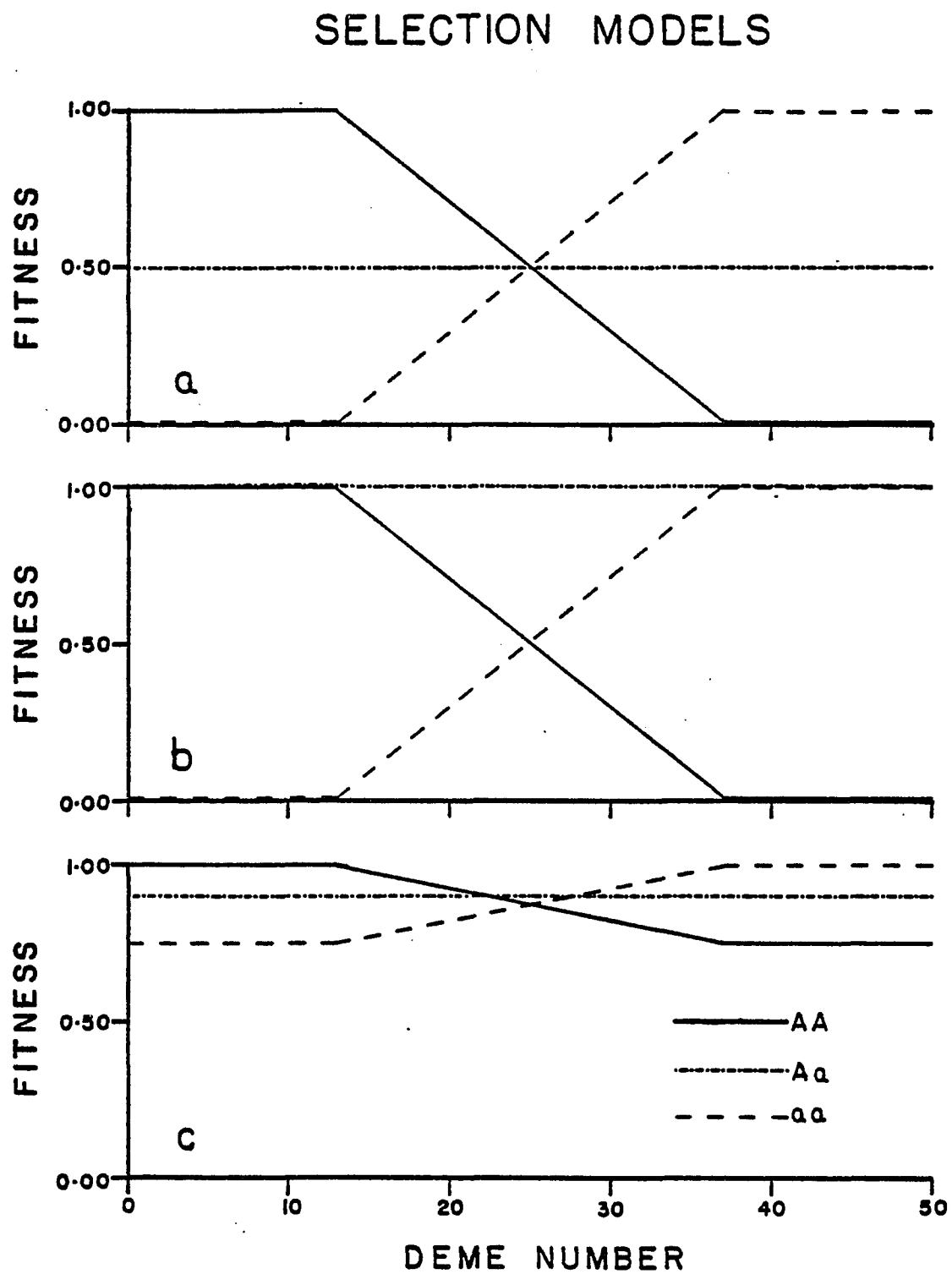

Figure 4. Three selection gradients used in Monte Carlo computer simulations, from Tables 5, 6 and 7.

a constant deme size for the central 48 demes but also for the two end demes.

The allele (= inversion) frequency in the next generation (p'_x) after dispersal and random mating can be mathematically calculated by the equation:

$$p'_x = \frac{(1-g)\ N_x p_x + \frac{1}{2}\ g \sum_{i=1}^{2} N_i p_i}{(1-g)\ N_x + \frac{1}{2}\ g \sum_{i=1}^{2} N_i}$$

where p_x is the allele frequency in deme $\underline{x}$ before dispersal and mating, N_x is the number of individuals in deme $\underline{x}$, g is the rate of gene flow, and N_i and p_i are the numbers and allele frequencies in the adjacent demes before dispersal and mating (modified from Endler, 1977).

The selection gradient shown in Table 5 used an incomplete dominance model and can be considered very severe. In this model the heterozygote (= heterokaryotype) had an intermediate fitness of 0.50 in all demes. The a/a homozygote (or homokaryotype) had a fitness of 1.00 in the first thirteen demes while the other homozygote, A/A, had a fitness of 0.00 in these same thirteen demes (harsh selection). In the last thirteen demes (38-50) there was a reversal in the fitnesses of the two homozygotes. Six different rates of gene flow were imposed on this selection gradient: 0.00, 0.01, 0.10, 0.40, 0.80, and 1.00.

The selection gradient in Table 6 was similar to that in Table 1 except that the fitness of the heterozygote was 1.00 in all demes. In the first thirteen demes the fitness of the A/A homozygote and the heterozygote were both 1.00 while that of the a/a homozygote was 0.00.

Likewise, in the last thirteen demes (38-50) the genotypes A/a and a/a had a fitness of 1.00 while A/A was 0.00. In demes 14 through 37 the heterozygote had an advantage. Simulations utilized three different rates of gene flow (0.00, 0.10, and 0.40). Comparing the results between the selection gradients shown in Tables 5 and 6, holding gene flow constant in the comparisons, will give some information on the comparative effects that complete dominance and incomplete dominance have on clinal width and geographic variation.

Only two different rates of gene flow were imposed on the selection gradient shown in Table 7: 0.00 and 0.40. The fitness of the heterozygote in this selection gradient was intermediate between those of the two homozygotes except for the central four demes where it had a fitness greater than the two homozygotes. Compared to the previous two gradients, this selection gradient might be considered less severe, as the results will attest.

Laboratory Experiment

The karyotype and gene arrangement frequencies at generation zero are listed in Table 8. Bottles 1 through 5 were initially set up with 200 mature adult flies per bottle, 100 males and 100 females, all homozygous for the 'A' gene arrangement (obtained from collection number A187--Desemboque, Sonora, Mexico). Bottles 6 through 10 were also initiated with 200 adult flies per bottle; however, these flies were homozygous for the '+' arrangement (obtained from collection number A235--Zaragosa, Sonora, Mexico). A deme size of 200 per bottle was used in order to minimize genetic drift. Bottles were standard

half-pint milk bottles containing a yeast-agar-banana media supplemented with senita cactus. In addition a small cube of autoclaved senita cactus was placed on the surface of the media to stimulate oviposition behavior. The senita cactus used in all bottles for all generations was from the vicinity of Sonoita, Sonora, Mexico.

Each generation the following procedures were carried out. First, flies were allowed to eclose in the bottles for four to five days after the first fly eclosed, that is until a suitable number of adults had emerged. At that time the flies were removed from the bottles and approximately 150 males and 150 females were carefully segregated into separate food vials. These vials were marked as to the date, sex, and bottle number from which they came. This procedure was carried out for all 10 bottles. Thus, 1500 females and 1500 males were segregated each generation and allowed to sexually mature for 10-12 days. A transfer was made to new media 3-4 days before the end of the 10-12 day period in order to maintain optimal nutrient conditions.

Subsequent to the sexual maturation of all flies, the following steps were taken to accomplish 40% dispersal (= gene flow here) from each of the ten bottles (= demes). Twenty males from deme 5 were placed into a vial labeled deme 4, 20 males were placed into a vial labeled deme 6, and 60 males were placed into a vial labeled deme 5. Three vials containing females from deme 5 were initiated in this same manner. As a result, 40% of the flies in deme 5 were dispersed to new demes, 20% to deme 4 and 20% to deme 6. Deme 5 was restored to 100% after receiving 20 males and 20 females from deme 4, and 20 males and 20 females from deme 6. To maintain a population size of 200 in demes 1

and 10, the 20 males and 20 females that should have been placed in the adjacent, but non-existent, demes 0 and 11 were placed back into their respective demes. In other words, only 20% gene flow occurred in demes 1 and 10. The above procedures were analogous to those carried out in the computer simulations.

Results

Computer Simulations

Severe selection regimes (Table 5, Figure 4a) produced steep clines (Figure 5, Appendix B), even in the face of high rates of gene flow. In those simulations with no gene flow, only demes 25 and 26 were not fixed for one of the two alleles after 50 generations of simulation. Even with 10% gene flow only the central demes (24-28) remained variable after 50 generations. The results of the other three gene flow rates (0.40, 0.80, and 1.00) indicate, as expected, a corresponding increase in clinal width with an increase in gene flow rate. However, even with 100% gene flow the width of the cline after 50 generations is still much less than the width of the selection gradient. In fact, close scrutiny of the data in Appendix B.1 reveals that most of the change in gene frequencies occurs by generation 15. In other words, selection can dictate a rapid change in gene frequencies.

Clines were dramatically broadened (Figure 6; Appendix C) when the heterozygote had a fitness of 1.00 in all demes and the two homozygotes had the same fitness as above (Table 6). Under this selection regime the middle 22 demes remain variable after 50 generations

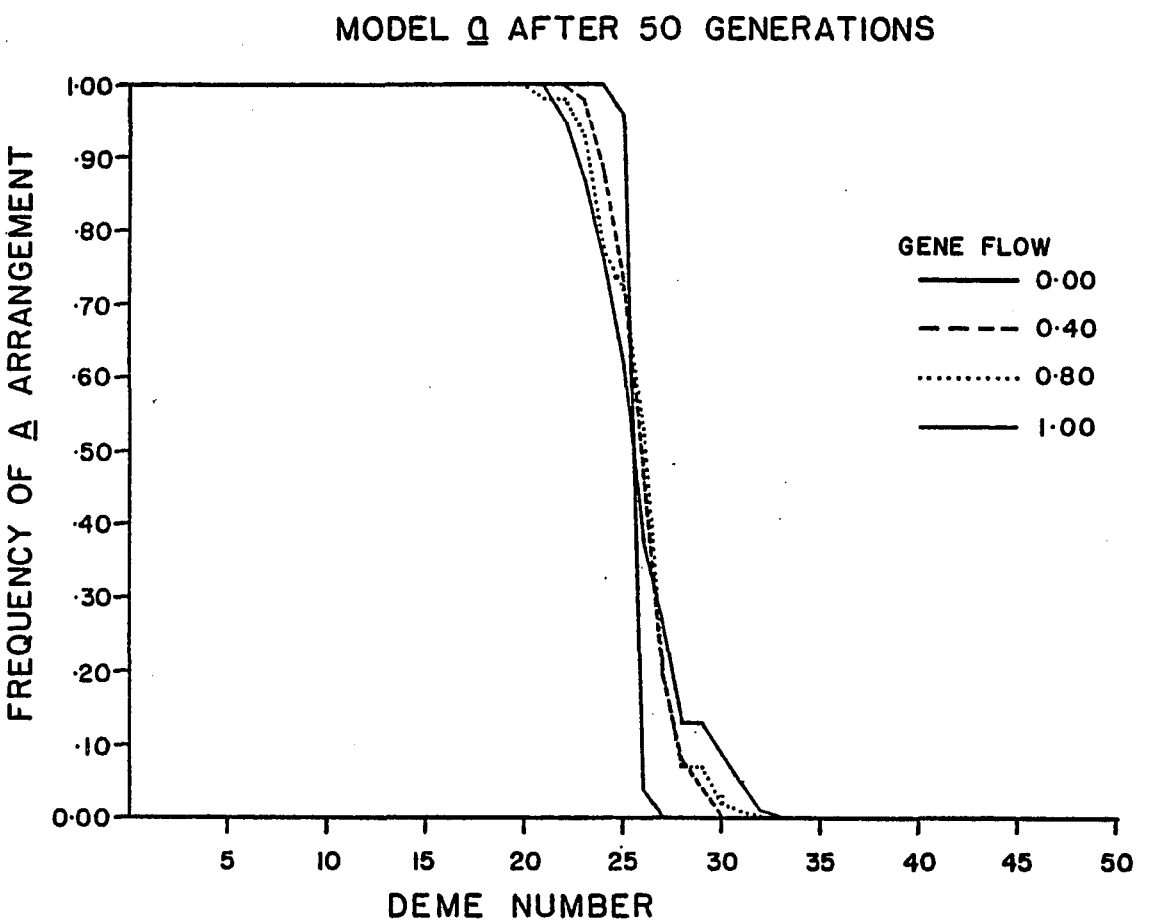

Figure 5. Results after 50 generations of computer simulation imposing the selection gradient shown in Figure 4a.

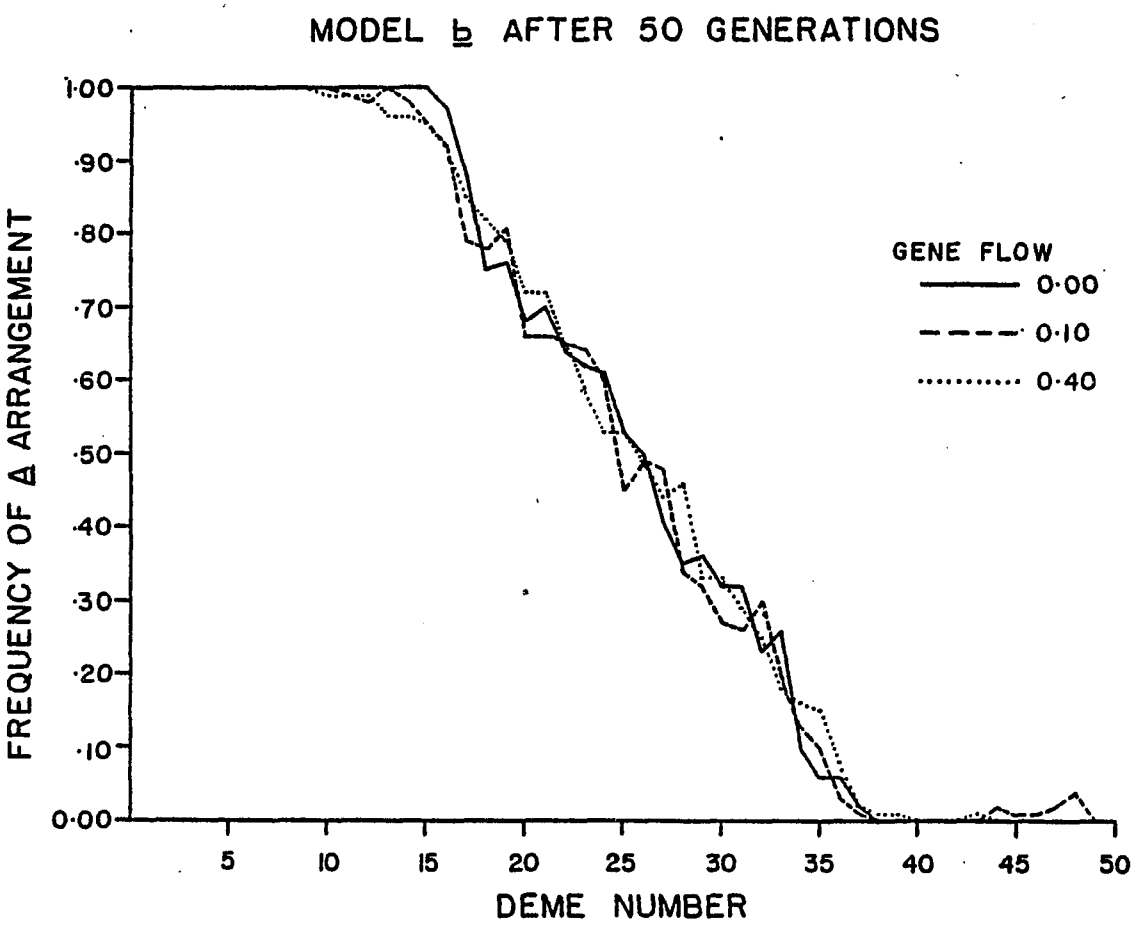

Figure 6. Results after 50 generations of computer simulation imposing the selection gradient shown in Figure 4b.

when there is no gene flow. With 10% gene flow approximately 30 demes remain variable. Unexpectedly, very similar results were obtained from those simulations with 40% gene flow; that is, the clinal widths were approximately the same. As might be predicted though, 40% gene flow produced a smoother cline than 10% and 0% gene flow. Hastings and Rohlf (1974), using computer simulations, also found that higher rates of gene flow produce smoother clines. Therefore, the greater chance element in the 10% gene flow simulations, which produces a less smooth cline, might explain the similar cline widths for the 10% and 40% gene flow simulations. Perhaps when the clines reach equilibrium in later generations, the cline with 40% gene flow will be wider.

The third selection gradient (Table 7 and Figure 4c) was comparatively the least severe since the lowest fitness of any genotype was 0.75. For those simulations with no gene flow there were 20 demes not fixed after 50 generations while for 40% gene flow there were 36 demes not fixed, although a portion of these 36 demes were only 1 and 2% from fixation (Figure 7 and Appendix D). So once again the clinal widths were about the same for the two gene flow rates, but the clinal shape was much smoother for the higher gene flow rate.

Laboratory Experiments

Table 8 and Figure 8 list and show the results of the secondary contact experiment. Unfortunately, it was impractical to sample every generation. For clarity only the results of generations 0, 5, 10, and 15 are displayed in Figure 8. In addition, the results at generation 15 from a computer simulation are also shown. The decision steps in

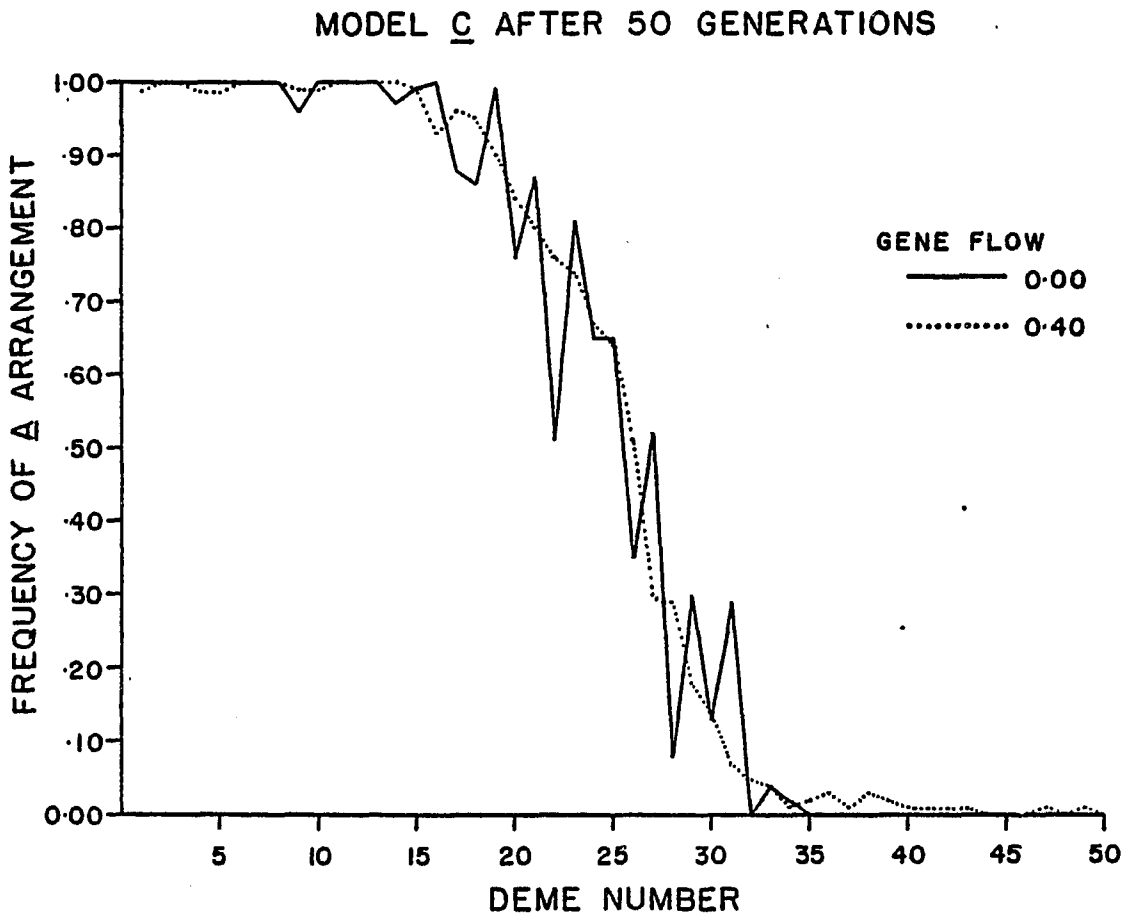

Figure 7. Results after 50 generations of computer simulation imposing the selection gradient shown in Figure 4c.

Table 8. Results of a laboratory experiment simulating secondary contact between two formerly isolated populations.--For each of the following generations, N = 50 chromosomes except where noted.

Generation Sampled[a]	Deme Number									
	1	2	3	4	5	6	7	8	9	10
0	1.00[b]	1.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00
1	1.00	1.00	1.00	1.00	.84	.20	0.00	0.00	0.00	0.00
3	1.00	1.00	1.00	.96	.78	.50	.14	0.00	0.00	0.00
5	1.00	.98	.94	.78	.72	.48	.16	.08	0.00	0.00
6	.98	.96	.82	.62	.76	.44	.22	.10	0.00	.02
10	.90	.86	.66	.68	.44	.60	.50	.31[c]	.33[d]	.06
14	.78	.64	.74	.72	.52	.60	.40	.34	.28	.12
15	.62	.63	.60	.65	.50	.43	.35	.30	.22	.23

[a] 60 chromosomes were sampled per deme at generation 15.

[b] Frequency of the 'A' gene arrangement.

[c] Only 32 chromosomes were scored.

[d] Only 20 chromosomes were scored.

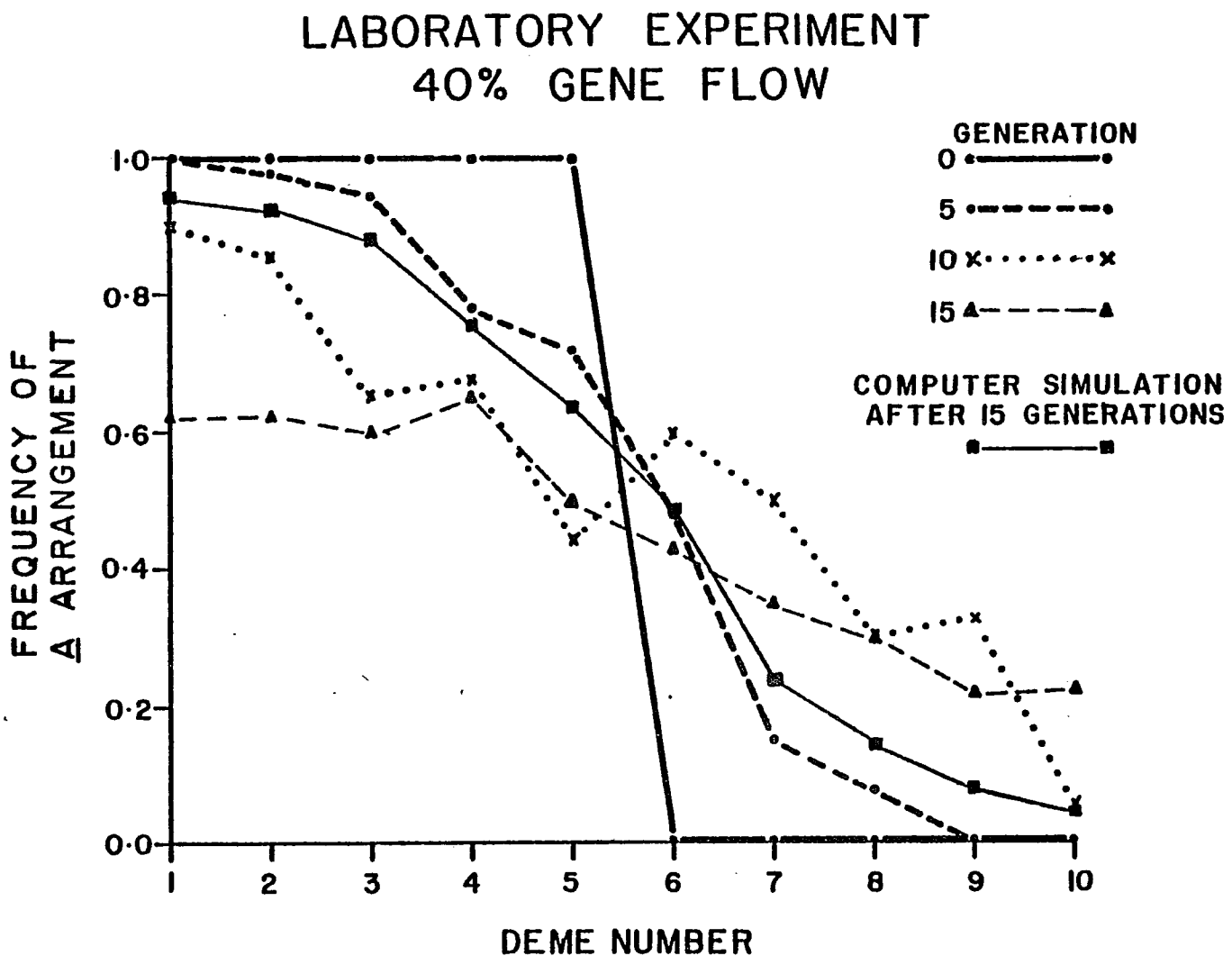

Figure 8. Comparison of results between a computer simulation and a laboratory experiment for secondary contact with 40% gene flow each generation.

this computer simulation were the same as those discussed above except that no differential selection was invoked; i.e., all three genotypes (= karyotypes here) had the same fitness.

As can be readily seen in Figure 8 there was a progressive decay in the cline through time after the secondary contact (i.e., after generation 0). At generation 15 the shape of the cline produced by the laboratory experiment was much different than that produced by the computer simulations. That is, the cline produced in the laboratory experiment decayed much faster than that produced by the computer simulations.

Discussion

These simulations (Figures 5, 6, 7 and Appendices D-E in particular), as well as those of Endler (1973, 1977), demonstrate that stepped clines do not require stepped environments. Therefore, when an abrupt change is observed in the frequency of some morph, genotype, or allele, there may not be a correspondingly abrupt change in the environment. On the other hand when the selection gradient is weak or the heterozygote has a high fitness, a broad cline will be produced. Under these conditions a cline may be made smooth by a moderate rate of gene flow. This is shown most dramatically in Figure 7 where gene flow smooths out the cline, but does not, however, significantly broaden it. Therefore, under certain conditions, as Endler (1973, 1977) has previously pointed out, gene flow appears not to be as strong a dedifferentiation influence as was once thought.

Stepped clines can evolve even when gene flow is continuous and the selection gradient is smooth provided that the gene flow distance (ℓ) is not large. However, if gene flow takes place over longer distances (i.e., ℓ is larger) the amount of differentiation between areas can be greatly reduced (Endler, 1977). Thus, the effect of gene flow will be the same (i.e., same ℓ) when a few individuals disperse long distances (and reproduce) as when a lot of individuals disperse short distances (and reproduce).

Other factors must be accounted for in determining gene flow distance besides the percentage of individuals dispersing and the distance traveled. Endler (1978) has investigated some life history parameters--including generation time, egg laying pattern, and mortality pattern--that can influence gene flow distance. For example, a female may disperse a long distance and may even mate after arriving at some destination, but if she is near the end of her reproductive period, then she will contribute very little to the recipient gene pool. If most of the females in a species behave in this manner then the dispersal distance will be long but the gene flow distance will be short.

Endler (1977) has also investigated the effect of assortative matings on clines with computer simulations. Using O'Donald's (1960) assortative mating model, he found, as O'Donald had predicted, that there was no significant effect on the gene frequency cline although the genotype frequency cline became steeper. Endler (1977) argues that a combination of assortative mating and small deme size might steepen a gene frequency cline because of an increased rate of drift

due to the low likelihood of an individual of a rare genotype finding a mate with the right genotype. One would infer from this description that Endler has only considered positive assortative matings. It seems intuitive, however, that negative assortative matings would influence gene frequency clines by increasing clinal width, much the same as a heterozygous advantage. This type of mating preference needs further investigation.

The laboratory experiment (Table 8 and Figure 8) produced some interesting results. First, the rapid decay in the cline strongly indicates that either there was no competition between the two morphs or if there was competition they were able to coexist. This is further supported by their sympatry in natural populations. Second, the overall shape of the cline suggests that the 'A' arrangement may be slightly favored under these laboratory conditions since the cline is somewhat displaced in its favor. If given enough time, perhaps the 'A' arrangement would have completely displaced the '+' arrangement. Third, and perhaps most important, the general pattern of results indicates that the laboratory cline decayed at a faster rate than the one produced by the computer simulations. A deme size of 200 argues against drift as an explanation for the faster decay rate in the laboratory experiment. However, at least two suitable explanations do exist: (1) there is a heterokaryotype advantage; and (2) there is some degree of negative assortative mating. This latter effect should be most evident in the peripheral demes, as indeed it appears to be in this experiment. That is, the rate of change in the peripheral demes is much more

dramatic than in the central demes. Evidence favoring the above two explanations will be discussed in subsequent chapters.

CHAPTER 4

DEVELOPMENTAL ADVANTAGE

Introduction

Since the pioneering work of Wright and Dobzhansky (1946) on Drosophila pseudoobscura numerous published examples indicate that chromosomal polymorphism in natural populations can be maintained by a heterokaryotypic advantage. Species of Drosophila among this list include D. persimilis (Dobzhansky and Levene, 1948; Spiess, 1957), D. willistoni and D. paulistorum (Pavan, Dobzhansky, and da Cunha, 1957), and D. pavani (Brncic and del Solar, 1961; Koref-Santibanez and Brncic, 1965; Brncic et al., 1969). Superiority of the heterokaryotype has been demonstrated for such fitness components as viability, longevity, sexual activity, hatchability, and rate of development.

In Drosophila pachea there are at least two indications of a heterokaryotype advantage for one or more fitness components. Firstly, of the twelve collections from the Guaymas-Empalme area of Sonora, Mexico, nine produced an excess of heterokaryotypes ($P > .05$). Secondly, it is the impression of several individuals who have worked with this species that an excess of heterokaryotypes occurs during the first few days of pupation, suggesting a developmental rate advantage in favor of heterokaryotypic individuals.

The purpose of this investigation was to test the hypothesis that there is a heterokaryotypic advantage in Drosophila pachea for

rate of development from the egg to the pupa. As Lewontin (1974) points out, developmental rate is an important component in the overall fitness of a species that has continuous generations. This is intuitive since the shorter the generation time of a particular genotype, the greater its contribution to future generations. The importance of developmental rate is compounded in such a species as Drosophila pachea since development must be completed before the rotting host tissue loses its nutritive value.

Two experiments were designed to test this hypothesis. The first experiment was an interdemic cross between two laboratory stocks of known genotypes, +/+ and A/A. The interest here is in the karyotypic ratio of the F_2 progeny. The second experiment was designed to test the hypothesis that heterokaryotypic individuals have an advantage in all parts of the species distribution. There were, however, two alternative hypotheses. (a) The heterokaryotype has an advantage in only some areas. (b) The heterokaryotype has no advantage in any part of the species distribution. This experiment involved intrademic crosses of recently collected flies from several localities in Baja California, Mexico. These intrademic crosses all involved pair matings between homokaryotypes (+/+ and A/A). As above, the interest was in the karyotypic ratios of the F_2 progeny.

There are two important reasons for designing experiments in which the parents of the progeny to be tested are both heterokaryotypes (or heterozygotes). (1) The design eliminates the possibility of mating preferences between flies of different karyotypes. (2) An expected ratio of progeny can be predicted when the karyotypes of the

parents are known. Here, a deviation from the expected frequencies of .25 +/+ : .50 +/A : .25 A/A would indicate an advantage or disadvantage to one or two of the karyotypes.

Materials and Methods

Interdemic Crosses

By crossing males homokaryotypic for the standard arrangement (collection number A235--Zaragosa, Sonora, Mexico) to females homokaryotypic for the 'A' arrangement (collection number A187--Desemboque, Sonora, Mexico), F_1 progeny were produced that were heterokaryotypic (+/A). Upon eclosion, these F_1 adults were sexually segregated for twelve days. This isolation period allowed for sexual maturation of both sexes and prevented uncontrolled copulations. Following this period of abstinence, males and females were placed together in four standard 8 oz. milk bottles containing an agar-yeast-banana media supplemented with senita cactus. In addition, a cube of autoclaved senita cactus was placed on the surface of the media to stimulate oviposition behavior. Two bottles were placed in a 24°C incubator and two in a 32°C incubator, both with an alternating dark and light cycle of twelve hours. The senita cactus used in all bottles was from the vicinity of Sonoita, Sonora, Mexico.

After a period of 48 hours, during which numerous matings were observed, the flies were transferred to new media bottles. They were allowed to mate and oviposit for an additional 24 hour period after which the females were removed. The males were allowed to remain since

feeding by adult flies appears to help control bacterial and fungal growth.

The bottles were kept at their respective temperatures until late third instar larvae were observed. Larvae at this stage of development were removed from the bottles and placed in 50% acetic acid. The salivary glands were dissected out of the larvae and placed in acetoorcein stain. After approximately 10 minutes, the salivary glands were squashed in the stain and then scored for karyotype under a light microscope. Larvae were sampled from each of the four bottles for at least five days.

Intrademic Crosses

The design of this experiment was very similar to that discussed immediately above, with the following differences. (1) The parents were from the same deme, rather than from different demes. (2) Single pair matings, rather than mass matings, were performed for each of four localities in southern Baja California, Mexico--A719 (San Agustín), A720 (San Agustín), A721 (San Pedro), and A723 (San José del Cabo) (see Figure 2 and Table 1).

The P_1 generation for each locality was reared from rotting senita cactus collected from Baja California Sur, Mexico, in January 1978. These adults were sexually segregated upon eclosion from the rots. After achieving sexual maturation, the adults were pair-mated and their genotypes determined by examining the karyotypes of their F_1 progeny (preparation for karyotype examination as described above). One pair-mating from each of four localities was of the type +/+ X

A/A. Again, this meant that all of the F_1 progeny of these matings were heterokaryotypes.

The F_1 adults were segregated according to sex and allowed to mature. Following maturation, adults from the same parents (i.e., same locality) were placed together in a large vial containing the same media preparation as discussed above, including the cube of autoclaved senita cactus. As above, the senita cactus used in all bottles was from the vicinity of Sonoita, Sonora, Mexico, and the media for the four bottles representing the four localities was from the same batch. The vials were placed in the same environmental chamber with a constant temperature of 28°C and a lighting pattern changing from dark to light every 12 hours. After 48 hours these adults were transferred to new food vials for a period of 24 hours. This routine was repeated several times to obtain additional samples from the same adults. Those vials containing eggs were left in the environmental chamber until pupation began. At that time, vials were taken out of the chamber and those larvae about to pupate (late third instar) were removed from their respective vials and dissected in 50% acetic acid. The salivary glands were then transferred to acetoorcein stain for approximately ten minutes, after which they were squashed and scored. The vials were placed back into the environmental chamber until the next day. Due to circumstances beyond experimental control, only two days of emergence data were collected.

Results

Interdemic Crosses

Since the F_1 progeny were all heterokaryotypes, the F_2 progeny were expected in the frequencies .25 +/+ : .50 +/A : .25 A/A if all three genotypes develop at the same rate. Table 9 and Figure 9 list and show the F_2 results of this experiment. The general trend in the results for the first four days is that of a heterokaryotype advantage; i.e., there was a greater proportion of heterokaryotypes than expected. These excesses, however, were not statistically significant. Sample 2 at 24°C proved to be exceptional, never showing an excess of heterokaryotypes.

Following the fourth consecutive day of scoring, a switch in the trend occurred. At this time there were fewer heterokaryotypes observed than expected.

Intrademic Crosses

Table 10 lists the F_2 karyotype frequencies and inversion frequencies for the four crosses. Once again, the F_1 parents were +/A for all four crosses; thus, the expected frequencies in the F_2 for all crosses was .25 +/+ : .50 +/A : .25 A/A, assuming each karyotype had the same developmental rate. Based on these expected karyotype frequencies, the expected inversion frequencies would be .5 for each.

Only collection number A719 shows an apparent excess of heterokaryotypes although the X^2 value in Table 11 indicates that this excess is non-significant (P = .20-.10). The two inversion frequencies for this cross approach the expected of 0.50. The other three crosses

Table 9. Frequency of heterokaryotypes for four samples at two temperatures through the first six days of pupation.

Temperature	Sample Number	Day Number 1	2	3	4	5	6
24°C	1	.73	.50	.73	.67	.25	.33
24°C	2	.45	.41	.44	.37	.47	.37
32°C	1	.55	.52	.41	.59	.67	
32°C	2	.56	.67	.62	.60	.36	.41

Table 10. F_2 karyotype frequencies and gene arrangement (inversion) frequencies for four intrademic crosses.[a]

Collection Number	Karyotype Frequencies +/+	+/A	A/A	n	Inversion Frequencies +	A
A720	.46	.36	.18	33	.64	.36
A719	.18	.71	.13	24	.52	.48
A721	.09	.39	.52	33	.29	.71
A723	.00	.43	.57	30	.22	.78

[a]In all four sites the P_1 pair-mated, rot-reared adults were of the karyotypes A/A and +/+. One such mating from each locality was isolated. The F_1 heterokaryotypes were then selfed to produce the F_2. For each collection number a 1 : 2 : 1 karyotypic ratio would be expected and a frequency of 0.5 for each of the two gene arrangements.

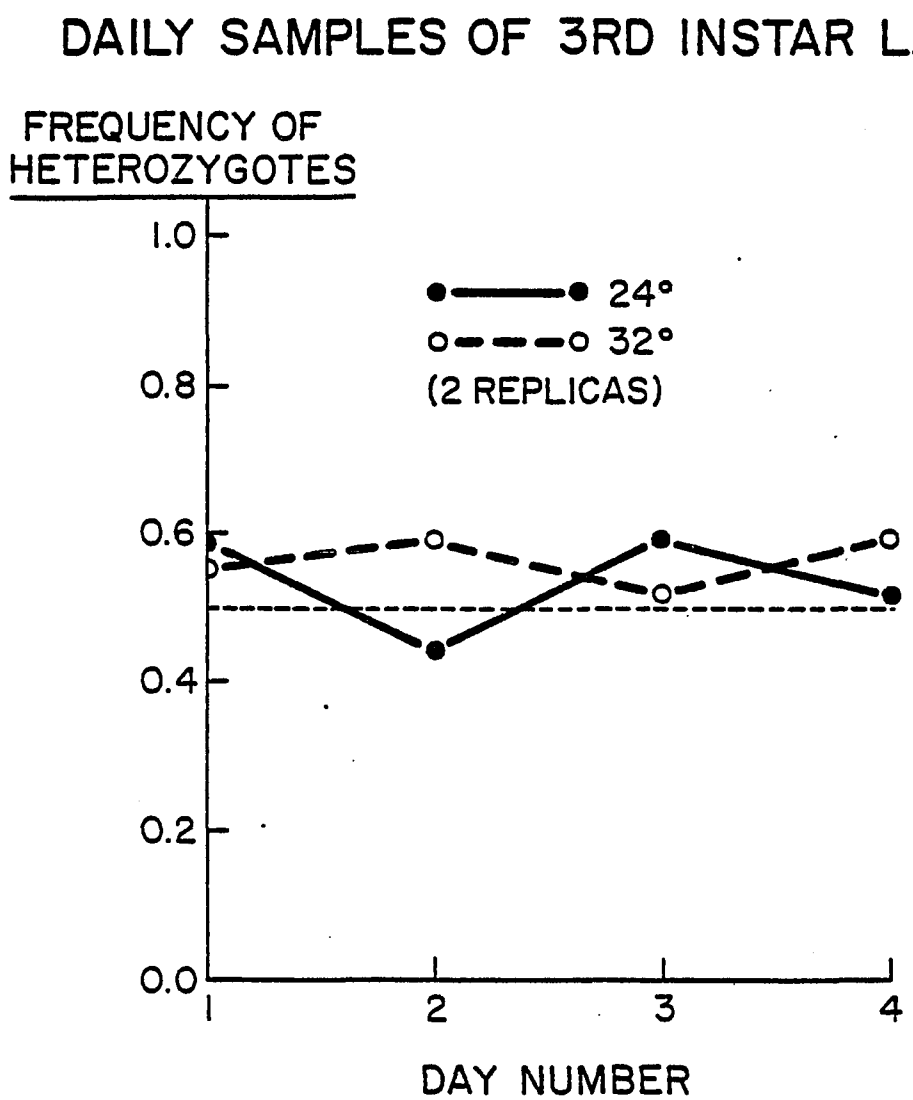

Figure 9. Heterokaryotype frequencies for the first four days of eclosion at 24° C and 32° C, two replicas at each temperature.

Table 11. Chi-square values based on an expected genotypic ratio of 1 : 2 : 1.

	+/+	+/A	A/A	n
Collection No. A720				
Observed	15	12	6	33
Expected	8.25	16.50	8.25	
$X^2 = 7.36$ $P < .05$				
Collection No. A719				
Observed	4	17	3	24
Expected	6	12	6	
$X^2 = 4.25$ $P = .20-.10$				
Collection No. A721				
Observed	3	13	17	33
Expected	8.25	16.5	8.25	
$X^2 = 13.36$ $P < .01$				
Collection No. A723				
Observed	0	13	17	30
Expected	7.5	15	7.5	
$X^2 = 20.32$ $P < .001$				

(collections A720, A721, and A723) show a deficiency of heterokaryotypes and an excess of one or the other of the homokaryotypes but not both. Interestingly, the X^2 values for all three of these crosses (Table 11) are either significant or highly significant ($P < .05$, $P < .01$, and $P < .001$, respectively). Not surprisingly then, the inversion frequencies do not approach 0.50. Collection number A720 (north of La Paz) is biased in favor of the '+' gene arrangement, while collection numbers A721 and A723 (both south of La Paz) are in favor of the 'A' arrangement.

Discussion

Several explanations might be proposed, with regard to the results of the interdemic cross, to account for the decreased frequency of the heterokaryotypes after four days of pupation. One explanation is that the heterokaryotypes lost whatever advantage they had due to changes in such factors as nutritive and competitive conditions. However, the experiment was designed such that the nutritive conditions were very likely optimal, and the competitive conditions minimal, throughout the duration of the experiment. Considering these conditions, a more probable interpretation is that by the end of the fourth day most of the heterokaryotypes had already completed larval development. At the same time, however, a larger proportion of homokaryotypes had yet to conclude development.

The favored hypothesis would suggest that, had all of the progeny been scored and summed for all days, the expected Mendelian ratio would have been observed since all progeny would have been able to

complete development. Unfortunately, this can only be conjecture since the last several days of stragglers were not scored.

The advantage given to the heterozygote in rate of development might be accounted for by one of two theories, both of which are commonly proposed to explain any heterozygous advantage. The first theory suggests that a heterozygote can produce a superior metabolic gene product(s) because of the benefit of two different alleles from a given locus, rather than just one allele in homozygous condition. For example, the heterozygote may be able to produce a dimeric protein that can associate into one of three possible combinations: AA, AA', or A'A'. One combination may be more efficient during one stage of development or in one environment, whereas one of the other combinations may be more efficient during a different stage of development or in a different environment. In other words, the heterozygote has the best of all worlds. Another combination that fits this theory would be when two alleles direct the formation of two polypeptides with slightly different enzymatic functions, each producing a different metabolic substance. The heterozygote, then, would be able to produce both substances, reaping whatever advantage that might be gained by the presence of both substances. Still other conditions might be proposed to fit this theory.

An alternate hypothesis has been given by some animal and plant breeders. Basically, they find that the F_1 progeny of crosses between two separate inbred lines are superior to both of the inbred parent lines. To explain these results, they propose that inbreeding results in the accumulation of recessive deleterious alleles at

different loci in different inbred lines. Consequently, the heterozygous F_1 progeny are superior to the parents because of the masking of recessive, deleterious alleles at several loci by dominant, non-deleterious alleles.

The experimental design and the results from the interdemic crosses using Drosophila pachea cannot distinguish between these two hypotheses. Experiments at the molecular level are needed. Such experiments would require the knowledge of the different loci within the inversion and the area adjacent to the inversion. At this time, such information is not available.

The results of the four intrademic crosses indicate that the heterokaryotype may have an advantage in certain parts of the species distribution, but not throughout the entire distribution. The significance of these results, however, are more clearly understood only after one has compared the inversion frequencies from the four crosses (Table 10) with those frequencies at the sites from which they were collected (Table 1). For example, the cross involving collection number A720 produced an excess frequency of the '+' arrangement (0.64), a frequency similar to that of the field site from which it was collected (0.74). When one compares the frequencies produced by the other three crosses with the respective frequencies found in the field, one finds that each of these is also comparable to its respective counterpart.

From the results in Table 10 it is noteworthy that the inversion frequencies in the crosses involving A719, A721, and A723 are accounted for almost entirely by two of the three karyotypes. That is, in these three cases there is a large deficiency of one of the

homokaryotypes. These results suggest that when the most common inversion is present, it allows the fly carrying that inversion, whether it is a homokaryotype or a heterokaryotype, to develop at a faster rate. In other words, it seems that the most common gene arrangement has become "coadapted" to the genetic constitution of the deme from which it came. This indicates the effectiveness of selection and suggests a very high form of genetic organization of the gene pool, a form one might call "genomic coadaptation".

Endler (1977), expanding on the previous work of Clark (1966), provides a more concrete explanation that may account for these results. He proposes that there are two types of fitness-modifier genes in natural populations. Those which he calls TYPE I modifiers have an advantageous or neutral effect on all major genotypes. Those which he calls TYPE II modifiers, however, have an advantageous or neutral effect on some genotypes while a deleterious effect on others. By these descriptions then, TYPE I modifiers can be expected to be found throughout a cline, whereas TYPE II modifiers would be found only in regions where they confer an additional advantage to the favored genotype(s). "Therefore, if one were to sample a large number of demes with a variety of gene frequencies, and TYPE II modifiers were present, one would expect a positive relationship between gene frequency and the observed fitness of the most common genotypes, other fitnesses being equal" (Endler, 1977, p. 101). As applied to Drosophila pachea, fitness was measured in terms of rate of development.

Although the pattern of results from this experiment is convincing, the number of collections and the number of progeny assayed

is not overwhelmingly large. If such an experiment is to be extended, several modifications should be implemented, in addition to increased sample size, increased number of samples, and increased number of collection sites. For example, similar collections and tests could be made from sites in mainland Sonora, Mexico, to determine if similar patterns occur there. Also, if one is able to obtain a reasonably large sample size of F_1 adults (+/A), then transfers of these F_1 adults could be made every 24 hours in order to obtain replicated samples from the same adults. By using the same F_1 adults to produce additional samples, some experimental error is eliminated due to chance differences in the background chromosomes of the flies.

As a concluding thought, one might pose the question: Why does it take approximately 10 days to develop from the egg stage to the late third instar larva and 15 days from the egg to the first emerging adults (at 25°C) in Drosophila pachea, while it only takes D. melanogaster 6 and 10 days to go through the same respective stages of development at 25°C? In other words, if developmental rate is so important to the fitness of D. pachea, why does it not develop from egg to third instar at a faster rate than 10 days? One solution may be that there is some form of trade-off resulting in an optimum rate of development. For instance, if a certain genotype in D. pachea developed any faster than it actually does, perhaps its ovariole number would be lowered, and thus its fitness. On the other hand, if it develops too slowly it may not be able to complete its development before the rot terminates. (The duration of the rot itself could depend on a number of things, such as the size of the cactus, temperature, wind

(Rockwood-Sluss et al., 1973), the type of bacteria and yeast in the rotting tissue, the defense ability of the individual plant--old plants seem to have a decreased resistance to a spreading infection--among other things.) Normalizing selection may, therefore, be operating to determine the optimum fitness of the fly.

CHAPTER 5

MATING BEHAVIOR

Introduction

Spieth (1952) has presented the most extensive survey of mating behavior in the genus Drosophila by organizing and analyzing data on some 101 species and subspecies. He found that mating behaviors are quite diverse. For example, premating behaviors range from a series of elaborate courtship displays to rape. Copulation times are also quite diverse; some species copulate for less than a minute, such as D. polychaeta, while a few exceptional species, such as D. ancanthoptera, copulate for over 1-½ hours.

The element of mating behavior that most influences the genetic structure of populations is the system of mate acceptance where individuals may show preferences for mates. Preferences can range from high negative assortative (= heterogamic) matings to high positive assortative (= homogamic) mating. A random mating system would be one in which individuals mate without mate preference. Negative assortative mating, on the other hand, is when individuals prefer to mate with individuals different from themselves, while positive assortitive mating is when there is a mating preference between similar individuals. The question here is: How does mating preference influence geographic variation, particularly that in the form of a cline? The answer is intuitively straightforward. Negative assortative matings

should increase clinal width, compared with that produced by completely random mating, because this type of mating system will tend to increase similarity between demes. That is, dispersing individuals will be very effective in producing gene flow since they are likely to be different from those individuals in the recipient population. On the other hand, a positive assortative mating system will tend to decrease clinal width since dispersal will be ineffective in producing gene flow.

This experiment attempted to determine if there was a mating preference in a natural population of Drosophila pachea. Matings were scored according to karyotype, as determined by salivary gland polytene chromosome analysis.

Materials and Methods

Female Drosophila pachea were collected in the field at site A721. This site is south of La Paz, Baja California, Mexico, (see Table 1 and Figure 2) and is polymorphic for the two gene arrangements. Each female was placed into an individual vial containing an agar-yeast-banana media supplemented with senita cactus and kept isolated throughout the experiment. The salivary gland polytene chromosomes of at least seven late third instar larvae were scored for each isofemale. From these results the karyotypes of both parents were ascertained with reasonable confidence. To prevent assigning the wrong karyotypes to the parents, the seven larval progeny scored from a single female were collected over a period of three or four days. This precaution eliminates the effect of differential larval development due to karyotype.

Results

Mating combinations according to karyotype and their observed and expected frequencies are listed in Table 12. The X^2 value of 9.11 is marginally significant ($P \simeq .10$, df 5). As shown in Table 13, this X^2 value cannot be attributed to a deviation of one or more of the individual karyotypes ($X^2 = 0.06$, $P < .05$, df 1). A close inspection of Table 12 reveals that a tendency toward negative assortative mating can account for most of the deviations from the expected frequencies. That is, negative assortative matings (primarily +/+ X +/A and +/A X A/A) are in excess while positive assortative matings (+/A X +/A and A/A X A/A) are deficient. These results, although not statistically overwhelming, are consistent with those obtained by Jefferson (1977) in the laboratory.

Discussion

Knowledge of the type of mating system that a species uses, whether plant or animal, not only promotes a more comprehensive understanding of how variation in that species is patterned geographically, but can also help to minimize erroneous conclusions about the selection, adaptation, and evolution of that species. Furthermore, knowledge of the mating system employed can suggest whether that species is in the dynamic or static process of speciating. For example, if there is evidence that a system of positive assortative mating is evolving in a species, such evidence would suggest that this species is in the dynamic process of forming two or more species. On the other hand,

Table 12. X^2 table listing types of matings.

Type of Mating	o	e*	$\frac{(o-e)^2}{e}$
(1) +/+ X +/+	0	.04	.04
(2) +/+ X A/A	0	1.20	1.20
(2) +/+ X +/A	2	.72	2.28
(2) +/A X A/A	15	10.08	2.40
(1) +/A X +/A	0	2.88	2.88
(1) A/A X A/A	7	8.64	.31
			X^2 = 9.11
			P ≈ .10, df 5

*The expected mating frequencies are based upon the following karyotype frequencies which were demonstrated to be in Hardy-Weinberg Equilibrium in Table 13: +/+ = .04; +/A = .35; A/A = .60

Table 13. X^2 table to determine if the three karyotypes are in Hardy-Weinberg Equilibrium.

Class	o	e*	$\frac{(o-e)^2}{e}$
+/+	2	2.32	.04
+/A	17	16.47	.02
A/A	29	29.20	.00
			X^2 = .06
			P = .90-.70, df 1

*Expected numbers are calculated based on a frequency of 0.22 for the '+' arrangement and 0.78 for the 'A' arrangement.

evidence of negative assortative mating would imply that the speciation process is being retarded.

Since Drosophila pachea appears to employ a negative assortative mating system, it follows that the observed clinal variation is adaptive because it is maintained in the face of a breeding system that tends to retard genetic differentiation and parapatric speciation (see Endler, 1977, for a discussion on clines and parapatric speciation). Because of the ability and need for dispersal in D. pachea (i.e., a flying insect utilizing an ephemeral substrate), a negative assortative mating system probably tends to increase clinal width relative to the width that would have occurred under random mating.

Evidence of assortative mating in an organism, whether positive or negative, suggests the presence of a mechanism whereby individuals are able to discriminate among one another. That is, they must have some means of discerning who is the same and who is different. In a number of species of insects, including some species of Drosophila, a group of chemical compounds called pheromones have been implicated in this discriminating process (Shorey and Bartell, 1970; Ehrman, 1972; Averhoff and Richardson, 1974 and 1976). Perhaps pheromones are the communicating device in D. pachea whereby individuals, probably females, discriminate against genetically similar individuals during the mate acceptance process. Experiments using an olfactometer could conceivably answer this question.

Available evidence suggests that a negative assortative mating system is an essential component of the genetic structure of natural

populations of Drosophila pachea. In the laboratory, Jefferson (1977) has shown that several generations of inbreeding causes an excessive degree of inbreeding depression, as reflected by decreases in such reproductive components as egg number and ovariole number. Besides a negative assortative mating system, an additional mechanism for overcoming inbreeding depression in D. pachea is differential sexual maturation. It takes a female approximately five days to reach sexual maturity after eclosion, while it takes a male at least ten days (Jefferson, 1977). Thus in nature where there is an overlapping of generations, differential sexual maturation decreases the probability that a female will mate with one of her male siblings. For these reasons, a female who successfully disperses to a new substrate has the advantage of: (1) further decreasing the probability of mating with one of her male siblings, and (2) increasing the probability of mating with a male different from herself. The presence of a negative assortative mating preference insures the likelihood of this latter advantage.

If this type of field experiment is to be repeated in the future, the following modifications are suggested to improve on the experimental design. First, the most conclusive information is going to be gained by aspirating mating pairs directly off the rotting substrate in the field. Each pair should immediately be placed into an individual food vial that is carefully marked. As soon as possible the male should be transferred to a new food vial and marked appropriately for subsequent identification. The female, which requires

repeated mating in order to keep up her fertility (Jefferson, 1977), will effectively become de-spermed after several days. At this time, each male and female pair, as collected in the field, should be placed together again in a new food vial and allowed to mate for several days. By squashing and scoring at least seven of their third instar larval progeny, the karyotypes of the parents can be assigned. To determine which karyotype belongs to which parent, the male can be transferred to a new food vial containing several virgin females of known karyotype. If the male successfully mates with these females, his karyotype can be ascertained. By deduction, the karyotype of the original female can be assigned. To determine if there are any mating preferences, the karyotypes of all flies at a rot must be determined. Based on the overall frequencies of the three karyotypes, a statistical analysis will reveal any mating preferences.

CHAPTER 6

SUMMARY AND CONCLUSIONS

Drosophila pachea, a member of the nannoptera species group, is one of four Drosophila species living in the "stress area" of the Sonoran Desert. Due to the requirement of several unique sterols, D. pachea is restricted to the decaying tissues of senita cactus, Lophocereus schottii. In addition, D. pachea is essentially removed from competition with other desert drosophilids due to the presence of certain toxic alkaloids in senita cactus. Thus D. pachea and senita cactus are nearly coincident in their distributions.

On mainland Mexico Ward et al. (1974) have described a cline in the frequencies of two gene arrangements, as determined by larval salivary gland polytene chromosome analysis. The 'A' arrangement, which differs from the '+' arrangement by a single paracentric inversion, was found to be near fixation in the north while the '+' was fixed in the south with a gradient in frequencies between the two areas. This cline in inversion frequencies was correlated with several parameters of potential importance to the flies: temperature, precipitation, latitude, and two characters of the host plant, surface-volume ratio and rib number.

The present investigation examined the frequencies of the same two gene arrangements in Baja California, Mexico. Here the 'A' arrangement was found to be fixed in the north and decreased in frequency

southwardly until north of La Paz. But instead of continuing to decrease in frequency south of this area, as was expected, the 'A' arrangement rapidly increased. In other words, the 'A' arrangement was found to be the predominant form in both the north and the far south. The '+' arrangement was high in frequency only in a limited area north of La Paz. Temperature and host plant rib number were correlated with this pattern of inversion frequencies. To explain these correlations it was argued that perhaps the cactus was responding to temperature while the inversions in D. pachea were responding to the cactus and only secondarily to temperature. For instance, the fly might be sensitive to differences in alkaloid concentrations in the cactus. Kircher (1969) has shown that the alkaloid concentrations in senita plants from northern Sonora, Mexico, are greater than those from southern Sonora, Mexico. That is, perhaps individuals carrying the '+' arrangement might be more sensitive to the higher alkaloid concentrations found in the northern plants.

Computer simulations, laboratory experiments, and field experiments were employed to investigate factors that might influence clinal structure, both the width and the smoothness of the cline. Computer simulations demonstrated that the fitness of the heterozygote (= heterokaryotype here) was, for those selective regimes examined, the major influence on clinal width. The influence of gene flow was primarily that of smoothing clines while broadening them only slightly, if at all.

Experiments simulating secondary contact between two populations were performed in the laboratory and by use of the computer. The

cline formed between the two populations decayed more rapidly in the laboratory experiment than in the computer analog. Heterozygous advantage and/or negative assortative mating preference were offered as hypotheses to explain the differences in rates of clinal decay.

Two experiments were designed to test for the fitness of the heterokaryotype in D. pachea. Developmental rate was used as a measure of fitness since it is considered to be a major component of the overall fitness of an organism living on an ephemeral substrate and having continuous generations. The first experiment was an interdemic cross between the same two strains used in the above laboratory experiment simulating secondary contact. The F_2 results demonstrated a slight excess of heterokaryotypes for the first four days of pupation. The question was then asked: Does the heterokaryotype have a developmental advantage in all parts of the species distribution? The second experiment, again measuring developmental rate, involved intrademic pair matings of flies reared from four rots, each rot collected from a different locality in southern Baja California, Mexico. The evidence from this experiment indicates that individuals which develop the fastest carry the inversion that is the most common in the area from which the rot was originally collected. The presence of modifier genes was given as a hypothesis to explain these results.

A field experiment examining mating preference was also conducted. Adult flies were aspirated directly off a senita rot in Baja California and isofemale lines were established. The progeny were subsequently analyzed in order to determine the karyotypes of the parents. Although the sample size was not large and the data were

marginally statistically significant, the results suggested a preference for negative assortative mating. This pattern is consistent with the results obtained by Jefferson (1977) in the laboratory.

In conclusion, it is increasingly apparent that the patterns of chromosomal variation in Drosophila pachea on both mainland Mexico and the Baja California peninsula are adaptive. The mechanisms maintaining this pattern are not ones classically thought to promote parapatric speciation. The smooth clines in chromosomal variation in D. pachea on both land masses are likely due, at least in part, to the smoothing effects of gene flow. The requirement for gene flow is dictated by the ephemeral nature of the substrate.

APPENDIX A

TRANSFORMED INVERSION FREQUENCIES AND CLIMATOLOGICAL DATA USED IN CALCULATING CORRELATION COEFFICIENTS

Table A.1. Collection numbers and their respective frequencies for each of 16 weather stations in Baja California, Mexico.

Weather Stations[a]	Collection Number	Transformed Frequency[b]	Collection Number	Transformed Frequency
Bahia de los Angeles	A191[m]	0.00	A606[m]	0.00
San Borja	A605[m]	0.00		
Bahia Tortugas	A608[m]	0.00		
Mulegé	A603[m]	8.13	A607[m]	26.56
Comondú	A62.2[m]	24.35		
San Agustín	A720[j]	59.34	A719[j]	47.87
La Aguja	A674[m]	40.40	A672[m]	40.40
	A202[ap]	33.21		
La Paz	A596[m]	47.29	A679[m]	45.00
	A677[m]	40.40	A595[m]	48.45
San Pedro	A721[j]	31.31	A686[m]	22.79
El Carrizal	A691[m]	24.35		
Todos Santos	A684[m]	17.46	A693[m]	26.56
	A725[j]	30.00		
San Bartolo Sur	A688[m]	11.54	A689[m]	11.54
Santiago	A694[m]	0.00		
Caduaño	A696[m]	20.27		
San José del Cabo	A723[j]	21.97		
Cabo San Lucas	A724[j]	24.35		

[a]16 weather stations (i.e., sites where climatological data were available); 26 collection localities; 28 collections.

[b]Table of angular (= arc sin) transformations was found in Bliss (1970).

[ap]Collection was made in the month of April.

[j]Collection was made in the month of January.

[m]Collection was made in the month of March.

Table A.2. Season statistics for precipitation at 16 weather stations in Baja California, Mexico.[a]

Weather Stations	Winter	Spring	Summer	Fall
Bahia de los Angeles	32.4[b]	.9	3.9	34.1
San Borja	73.9	14.0	14.1	32.9
Bahia Tortugas	65.9	4.7	5.9	16.0
Mulegé	22.5	2.5	33.1	49.3
Comondú	45.8	3.3	45.5	48.5
San Agustín	33.1	2.4	48.2	50.3
La Aguja	10.2	0.0	22.1	15.9
La Paz	37.8	2.0	58.1	82.8
San Pedro	34.2	10.9	158.0	129.0
El Carrizal	34.1	.9	128.8	122.1
Todos Santos	40.7	3.0	47.0	78.9
San Bartolo Sur	26.9	1.7	116.3	169.5
Santiago	30.2	2.5	93.3	186.0
Caduaño	33.7	4.0	157.2	225.7
San José del Cabo	39.0	1.8	52.2	169.5
Cabo San Lucas	35.0	3.9	61.6	139.3

[a]Data are from Hastings and Humphrey (1969).

[b]Precipitation was measured in millimeters.

Table A.3. Season statistics for temperature at 16 weather stations in Baja California, Mexico.[a]

Weather Station	Winter	Spring	Summer	Fall
Bahia de los Angeles	16.5[b]	21.2	29.7	25.3
San Borja	15.4	18.0	24.3	22.0
Bahia Tortugas	17.2	18.4	23.2	22.3
Mulegé	15.7	20.7	29.7	25.0
Comondú	18.0	20.2	27.4	24.9
San Agustín	17.9	18.6	23.5	23.1
La Aguja	18.3	19.5	25.5	26.1
La Paz	18.5	22.3	28.5	26.1
San Pedro	18.1	21.3	27.7	25.4
El Carrizal	17.3	20.3	26.5	25.3
Todos Santos	19.4	18.8	24.6	25.2
San Bartolo Sur	16.7	20.8	27.3	23.1
Santiago	17.6	22.0	29.4	25.5
Caduaño	17.4	22.2	29.2	25.5
San José del Cabo	20.0	22.2	27.6	26.0
Cabo San Lucas	20.3	22.5	27.6	26.6

[a]Date are from Hastings and Humphrey (1969).

[b]Temperature is in degrees centigrade.

Table A.4. Statistics for mean monthly precipitation at 16 weather stations in Baja California, Mexico.[a]

Weather Stations	Nov.	Dec.	Jan.	Feb.	Mar.	n[b]
Bahia de los Angeles	3.8[c]	14.1	10.5	6.9	1.5	14
San Borja	5.7	43.0	19.4	16.5	10.6	10
Bahia Tortugas	3.9	14.9	46.4	8.5	4.5	12
Mulegé	3.7	11.1	6.0	5.1	2.1	44
Comondú	2.9	20.6	19.5	5.7	2.5	29
San Agustín	.4	12.1	20.1	.9	2.4	8
La Aguja	0.0	8.2	2.4	2.2	0.0[d]	5
La Paz	8.1	22.5	19.6	4.4	1.2	52
San Pedro	3.6	19.3	14.1	.8	9.3	21
El Carrizal	.5	27.2	7.6	1.9	.9	7
Todos Santos	4.4	22.8	17.0	.9	1.5	30
San Bartolo Sur	3.4	17.4	8.9	.6	.7	27
Santiago	11.3	19.1	18.3	.6	.6	30
Caduaño	9.8	13.3	19.7	.8	1.0	25
San José del Cabo	12.1	17.5	15.6	2.6	.4	32
Cabo San Lucas	4.7	15.1	17.7	1.5	1.6	26

[a]Data were obtained from Hastings and Humphrey (1969)

[b]Mean sample size was 23.25

[c]Precipitation was measured in millimeters.

[d]Collection A202 was collected in April; the mean monthly precipitation was 0.00 for April.

Table A.5. Statistics for mean monthly temperature at 16 weather stations in Baja California, Mexico.[a]

Weather Stations	Nov.	Dec.	Jan.	Feb.	Mar.	n[b]
Bahia de los Angeles	20.5[c]	17.1	15.7	16.7	18.0	14
San Borja	19.2	16.0	15.0	15.3	16.5	10
Bahia Tortugas	19.3	17.9	16.8	16.9	17.9	10
Mulegé	20.2	16.3	14.8	16.1	17.8	44
Comondú	21.5	19.0	17.4	17.6	18.5	29
San Agustín	21.4	18.7	17.5	17.4	17.0	8
La Aguja	25.3	19.2	18.1	17.6	17.8[d]	5
La Paz	22.8	19.4	17.8	18.4	20.0	42
San Pedro	22.5	18.8	17.8	17.7	19.0	16
El Carrizal	21.7	18.4	16.4	17.0	18.5	7
Todos Santos	22.7	20.6	18.9	18.6	18.3	30
San Bartolo Sur	20.1	17.4	16.2	16.5	18.0	27
Santiago	21.8	18.5	16.8	17.5	19.3	28
Caduaño	22.3	18.6	16.7	16.9	18.9	17
San José del Cabo	23.6	20.9	19.3	19.7	20.1	30
Cabo San Lucas	24.3	21.8	19.8	19.3	20.6	23

[a]Data are from Hastings and Humphrey (1969).

[b]Mean sample size was 21.25.

[d]Collection A202 was collected in April; the mean monthly temperature was 20.0 for April.

[c]Temperature was measured in degrees centigrade.

APPENDIX B

TABLES OF COMPUTER SIMULATION DATA FOR VARIOUS RATES OF GENE FLOW IMPOSED ON THE SELECTION GRADIENT SHOWN IN TABLE 5

Table B.1. Heterozygote has an intermediate fitness of 0.50 in all demes; gene flow = 0.00.--Data are frequencies of the 'a' allele.[a]

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
1	.50	.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
2	.50	.98	.	.	.	.	.	.	.	.	.
3	.50	.98	.	.	.	.	.	.	.	.	.
4	.50	1.00	.	.	.	.	.	.	.	.	.
5	.50	.99	.	.	.	.	.	.	.	.	.
6	.50	.99	.	.	.	.	.	.	.	.	.
7	.50	.99	.	.	.	.	.	.	.	.	.
8	.50	.99	.	.	.	.	.	.	.	.	.
9	.50	.99	.	.	.	.	.	.	.	.	.
10	.50	.98	.	.	.	.	.	.	.	.	.
11	.50	.99	.	.	.	.	.	.	.	.	.
12	.50	.98	1.00	.	.	.	.	.	.	.	.
13	.50	.98	.99	.	.	.	.	.	.	.	.
14	.50	.96	1.00	.	.	.	.	.	.	.	.
15	.50	.97	.	.	.	.	.	.	.	.	.
16	.50	.97	.	.	.	.	.	.	.	.	.
17	.50	.97	.	.	.	.	.	.	.	.	.
18	.50	.94	1.00	.	.	.	.	.	.	.	.
19	.50	.94	.99	.	.	.	.	.	.	.	.
20	.50	.89	.99	1.00	.	.	.	.	.	.	.
21	.50	.85	.97	.99	.	.	.	.	.	.	.
22	.50	.76	.93	1.00	1.00	1.00	.	.	.	.	.
23	.50	.76	.87	.95	.98	.99	1.00	1.00	1.00	1.00	.
24	.50	.72	.85	.91	.89	.89	.94	.93	.98	.98	1.00
25	.50	.63	.63	.68	.67	.76	.84	.86	.89	.92	.96

Table B.1, Continued.

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
26	.50	.39	.35	.24	.17	.11	.12	.09	.10	.05	.04
27	.50	.41	.29	.19	.09	.06	.07	.01	0.00	0.00	0.00
28	.50	.27	.14	.09	0.00	0.00	0.00	0.00	.	.	.
29	.50	.20	.04	.01	0.00	0.00	.	.	.	.	.
30	.50	.15	.06	.02	.02	.02	.	.	.	.	.
31	.50	.08	.02	.01	0.00	0.00	.	.	.	.	.
32	.50	.10	.02	0.00	.	.	.	.	.	.	.
33	.50	.08	.01	.	.	.	.	.	.	.	.
34	.50	.01	0.00	.	.	.	.	.	.	.	.
35	.50	.04	.	.	.	.	.	.	.	.	.
36	.50	.04	.	.	.	.	.	.	.	.	.
37	.50	.04	.	.	.	.	.	.	.	.	.
38	.50	.02	.	.	.	.	.	.	.	.	.
39	.50	.03	.	.	.	.	.	.	.	.	.
40	.50	.01	.	.	.	.	.	.	.	.	.
41	.50	.04	.	.	.	.	.	.	.	.	.
42	.50	.01	.	.	.	.	.	.	.	.	.
43	.50	.01	.	.	.	.	.	.	.	.	.
44	.50	.01	.	.	.	.	.	.	.	.	.
45	.50	.01	0.00	.	.	.	.	.	.	.	.
46	.50	.01	.01	.	.	.	.	.	.	.	.
47	.50	.03	0.00	.	.	.	.	.	.	.	.
48	.50	.03	.	.	.	.	.	.	.	.	.
49	.50	.02	.	.	.	.	.	.	.	.	.
50	.50	.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

[a]The above values are the averages of three simulations.

Table B.2. Heterozygote has an intermediate fitness of 0.50 in all demes; gene flow = 0.01.--Data are frequencies of the 'a' allele.[a]

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
1	.50	.94	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
2	.50	1.00	.	.	.	.	.	.	.	.	.
3	.50	.99	.	.	.	.	.	.	.	.	.
4	.50	1.00	.	.	.	.	.	.	.	.	.
5	.50	1.00	.	.	.	.	.	.	.	.	.
6	.50	.97	.	.	.	.	.	.	.	.	.
7	.50	.96	.	.	.	.	.	.	.	.	.
8	.50	1.00	.	.	.	.	.	.	.	.	.
9	.50	.99	.	.	.	.	.	.	.	.	.
10	.50	.99	.	.	.	.	.	.	.	.	.
11	.50	.98	.	.	.	.	.	.	.	.	.
12	.50	.99	.	.	.	.	.	.	.	.	.
13	.50	1.00	.	.	.	.	.	.	.	.	.
14	.50	1.00	.	.	.	.	.	.	.	.	.
15	.50	.97	.	.	.	.	.	.	.	.	.
16	.50	.95	.	.	.	.	.	.	.	.	.
17	.50	.97	.	.	.	.	.	.	.	.	.
18	.50	.93	1.00	.	.	.	.	.	.	.	.
19	.50	.88	.96	.	.	.	.	.	.	.	.
20	.50	.93	.96	.	.	.	.	.	.	.	.
21	.50	.94	.99	1.00	1.00	.	.	.	.	.	.
22	.50	.76	.88	.96	.96	.	.	.	.	.	.
23	.50	.85	.94	1.00	1.00	1.00	1.00	1.00	.	.	.
24	.50	.89	.92	.99	.94	.97	.96	.98	1.00	1.00	1.00
25	.50	.73	.87	.80	.69	.84	.81	.74	.82	.88	.85

Table B.2, Continued.

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
26	.50	.47	.41	.34	.32	.34	.28	.15	.08	0.00	.01
27	.50	.42	.32	.28	.11	.02	.01	0.00	0.00	.	0.00
28	.50	.25	.13	.08	.02	.02	0.00	.	.	.	.
29	.50	.26	.13	.10	0.00	0.00	.	.	.	.	.
30	.50	.21	.06	0.00	.	.	.	.	.	.	.
31	.50	.13	.02	.	.	.	.	.	.	.	.
32	.50	.08	.01	.	.	.	.	.	.	.	.
33	.50	.05	0.00	.	.	.	.	.	.	.	.
34	.50	.08	.	.	.	.	.	.	.	.	.
35	.50	.07	.	.	.	.	.	.	.	.	.
36	.50	.03	.	.	.	.	.	.	.	.	.
37	.50	.02	.	.	.	.	.	.	.	.	.
38	.50	0.00	.	.	.	.	.	.	.	.	.
39	.50	.01	.	.	.	.	.	.	.	.	.
40	.50	.01	.	.	.	.	.	.	.	.	.
41	.50	.03	.	.	.	.	.	.	.	.	.
42	.50	0.00	.	.	.	.	.	.	.	.	.
43	.50	.01	.	.	.	.	.	.	.	.	.
44	.50	.01	.	.	.	.	.	.	.	.	.
45	.50	0.00	.	.	.	.	.	.	.	.	.
46	.50	.06	.	.	.	.	.	.	.	.	.
47	.50	.01	.	.	.	.	.	.	.	.	.
48	.50	0.00	.	.	.	.	.	.	.	.	.
49	.50	.02	.	.	.	.	.	.	.	.	.
50	.50	.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

[a]The above values are from one simulation.

Table B.3. Heterozygote has an intermediate fitness of 0.50 in all demes; gene flow = 0.10.— Data are frequencies of the 'a' allele.[a]

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
1	.50	.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
2	.50	.99	.	.	.	.	.	.	.	.	.
3	.50	.98	.	.	.	.	.	.	.	.	.
4	.50	.98	.	.	.	.	.	.	.	.	.
5	.50	.99	.	.	.	.	.	.	.	.	.
6	.50	.99	.	.	.	.	.	.	.	.	.
7	.50	.99	.	.	.	.	.	.	.	.	.
8	.50	.99	.	.	.	.	.	.	.	.	.
9	.50	.97	.	.	.	.	.	.	.	.	.
10	.50	.98	.	.	.	.	.	.	.	.	.
11	.50	.99	.	.	.	.	.	.	.	.	.
12	.50	.98	.	.	.	.	.	.	.	.	.
13	.50	.98	1.00	.	.	.	.	.	.	.	.
14	.50	.98	.99	.	.	.	.	.	.	.	.
15	.50	.99	1.00	.	.	.	.	.	.	.	.
16	.50	.98	.	.	.	.	.	.	.	.	.
17	.50	.95	.	.	.	.	.	.	.	.	.
18	.50	.91	.	.	.	.	.	.	.	.	.
19	.50	.95	1.00	1.00	.	.	.	.	.	.	.
20	.50	.88	.97	.99	.	.	.	.	.	.	.
21	.50	.87	.96	.99	.	.	.	1.00	.	.	.
22	.50	.83	.94	.98	1.00	1.00	1.00	.99	1.00	1.00	.
23	.50	.73	.93	.94	.97	.97	.97	.93	.99	.99	1.00
24	.50	.76	.76	.90	.95	.91	.92	.87	.87	.95	.93
25	.50	.46	.47	.46	.56	.55	.57	.56	.63	.60	.64

Table B.3, Continued.

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
26	.50	.45	.40	.25	.12	.18	.20	.17	.17	.21	.25
27	.50	.42	.26	.08	.05	.07	.10	.07	.06	.10	.08
28	.50	.27	.12	.04	.02	.04	.01	.01	0.00	.03	.02
29	.50	.22	.09	.02	.03	0.00	0.00	0.00	.	0.00	0.00
30	.50	.16	.08	.02	0.00	.	.	.	.	.	.
31	.50	.12	.07	.02	.	.	.	.	.	.	.
32	.50	.12	.02	.01	.	.	.	.	.	.	.
33	.50	.07	.01	0.00	.	.	.	.	.	.	.
34	.50	.06	0.00	.	.	.	.	.	.	.	.
35	.50	.03	0.00	.	.	.	.	.	.	.	.
36	.50	.04	.01	.	.	.	.	.	.	.	.
37	.50	.01	0.00	.	.	.	.	.	.	.	.
38	.50	.03	.	.	.	.	.	.	.	.	.
39	.50	.03	.	.	.	.	.	.	.	.	.
40	.50	.03	.	.	.	.	.	.	.	.	.
41	.50	.02	.	.	.	.	.	.	.	.	.
42	.50	.02	.	.	.	.	.	.	.	.	.
43	.50	.03	.	.	.	.	.	.	.	.	.
44	.50	.02	.	.	.	.	.	.	.	.	.
45	.50	.01	.	.	.	.	.	.	.	.	.
46	.50	.02	.	.	.	.	.	.	.	.	.
47	.50	0.00	.	.	.	.	.	.	.	.	.
48	.50	.02	.	.	.	.	.	.	.	.	.
49	.50	.02	.	.	.	.	.	.	.	.	.
50	.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

[a]The above values are the averages of three simulations.

Table B.4. Heterozygote has an intermediate fitness of 0.50 in all demes; gene flow = 0.40.-- Data are frequencies of the 'a' allele.[a]

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
1	.50	.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
2	.50	.98	.	.	.	.	.	.	.	.	.
3	.50	.99	.	.	.	.	.	.	.	.	.
4	.50	.99	.	.	.	.	.	.	.	.	.
5	.50	1.00	.	.	.	.	.	.	.	.	.
6	.50	.98	.	.	.	.	.	.	.	.	.
7	.50	.99	.	.	.	.	.	.	.	.	.
8	.50	1.00	.	.	.	.	.	.	.	.	.
9	.50	.99	.	.	.	.	.	.	.	.	.
10	.50	.99	.	.	.	.	.	.	.	.	.
11	.50	.99	.	.	.	.	.	.	.	.	.
12	.50	1.00	.	.	.	.	.	.	.	.	.
13	.50	.98	.	.	.	.	.	.	.	.	.
14	.50	.98	.	.	.	.	.	.	.	.	.
15	.50	.98	.	.	.	.	.	.	.	.	.
16	.50	.95	.	.	.	.	.	.	.	.	.
17	.50	.97	1.00	.	.	.	.	.	.	.	.
18	.50	.95	.99	.	.	.	.	.	.	.	.
19	.50	.91	1.00	1.00	.	.	.	.	.	.	.
20	.50	.89	.99	.99	1.00	1.00	1.00	1.00	.	.	.
21	.50	.87	.95	.99	.99	.99	.99	.99	1.00	1.00	.
22	.50	.85	.92	.98	.99	.98	.98	1.00	.97	.98	1.00
23	.50	.77	.83	.91	.94	.93	.94	.95	.90	.96	.98
24	.50	.60	.71	.82	.83	.84	.77	.87	.75	.86	.88
25	.50	.53	.62	.71	.83	.60	.59	.62	.61	.68	.74

Table B.4, Continued.

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
26	.50	.48	.47	.48	.39	.35	.38	.31	.38	.38	.48
27	.50	.43	.30	.36	.23	.15	.20	.18	.21	.22	.20
28	.50	.33	.19	.20	.07	.07	.09	.06	.07	.10	.08
29	.50	.20	.10	.06	.03	.03	.04	.01	.02	.02	.04
30	.50	.13	.04	.01	0.00	.01	.01	0.00	0.00	0.00	0.00
31	.50	.15	.01	0.00	.	0.00	0.00	.	.	.	.
32	.50	.07	0.00	.	.	.	.	.	.	.	.
33	.50	.02	.	.	.	.	.	.	.	.	.
34	.50	.04	.	.	.	.	.	.	.	.	.
35	.50	.03	0.00	.	.	.	.	.	.	.	.
36	.50	.04	.01	.	.	.	.	.	.	.	.
37	.50	.02	0.00	.	.	.	.	.	.	.	.
38	.50	.01	.	.	.	.	.	.	.	.	.
39	.50	.02	.	.	.	.	.	.	.	.	.
40	.50	.01	.	.	.	.	.	.	.	.	.
41	.50	.02	.	.	.	.	.	.	.	.	.
42	.50	.02	.	.	.	.	.	.	.	.	.
43	.50	0.00	.	.	.	.	.	.	.	.	.
44	.50	.01	.	.	.	.	.	.	.	.	.
45	.50	.01	.	.	.	.	.	.	.	.	.
46	.50	.01	.	.	.	.	.	.	.	.	.
47	.50	.02	.	.	.	.	.	.	.	.	.
48	.50	.02	.	.	.	.	.	.	.	.	.
49	.50	.01	.	.	.	.	.	.	.	.	.
50	.50	.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

[a]The above values are the averages of three simulations.

Table B.5. Heterozygote has an intermediate fitness of 0.50 in all demes; gene flow = 0.80.-- Data are frequencies of the 'a' allele.[a]

Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
1	.50	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
2	.50	.95	.	.	.	.	.	.	.	.	.
3	.50	1.00	.	.	.	.	.	.	.	.	.
4	.50	.99	.	.	.	.	.	.	.	.	.
5	.50	1.00	.	.	.	.	.	.	.	.	.
6	.50	1.00	.	.	.	.	.	.	.	.	.
7	.50	1.00	.	.	.	.	.	.	.	.	.
8	.50	.98	.	.	.	.	.	.	.	.	.
9	.50	1.00	.	.	.	.	.	.	.	.	.
10	.50	.99	.	.	.	.	.	.	.	.	.
11	.50	.98	.	.	.	.	.	.	.	.	.
12	.50	.99	.	.	.	.	.	.	.	.	.
13	.50	.95	.	.	.	.	.	.	.	.	.
14	.50	.97	1.00	.	.	.	.	.	.	.	.
15	.50	.99	.99	.	.	.	.	.	.	.	.
16	.50	.96	1.00	.	.	.	.	.	.	.	1.00
17	.50	.91	1.00	.	.	.	.	.	.	.	.98
18	.50	.95	1.00	.	.	.	.	.	.	.	.99
19	.50	.90	.99	.	1.00	.	.	.	.	.	1.00
20	.50	.78	.98	1.00	.99	1.00	1.00	1.00	.	1.00	1.00
21	.50	.86	.98	.95	.90	.98	.99	.98	1.00	.97	.98
22	.50	.77	.88	.88	.93	.95	.97	.87	.92	.94	.98
23	.50	.80	.80	.85	.85	.94	.79	.81	.90	.86	.93
24	.50	.70	.60	.77	.73	.76	.65	.69	.77	.82	.78
25	.50	.67	.53	.62	.64	.48	.49	.61	.62	.74	.72

Table B.5, Continued.

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
26	.50	.38	.31	.41	.42	.25	.30	.35	.48	.45	.53
27	.50	.39	.17	.22	.19	.17	.12	.23	.12	.25	.21
28	.50	.19	.17	.14	.08	.10	.04	.10	.10	.08	.07
29	.50	.11	.06	.05	.03	.03	.04	.04	.04	.03	.07
30	.50	.11	.04	.03	0.00	.01	.01	.02	.02	.01	.02
31	.50	.14	.02	.01	.	0.00	.01	0.00	.02	0.00	.01
32	.50	.10	.01	0.00	.	.	.01	.	0.00	.	0.00
33	.50	.06	.01	.	.	.	0.00	.	.	.	.
34	.50	.02	.02	.	.	.	.	.	.	.	.
35	.50	.06	0.00	.	.	.	.	.	.	.	.
36	.50	.07	.	.	.	.	.	.	.	.	.
37	.50	0.00	.	.	.	.	.	.	.	.	.
38	.50	.02	.	.	.	.	.	.	.	.	.
39	.50	.01	.	.	.	.	.	.	.	.	.
40	.50	.05	.	.	.	.	.	.	.	.	.
41	.50	0.00	.	.	.	.	.	.	.	.	.
42	.50	.01	.	.	.	.	.	.	.	.	.
43	.50	.01	0.00	.	.	.	.	.	.	.	.
44	.50	.02	.01	.	.	.	.	.	.	.	.
45	.50	.01	.01	.	.	.	.	.	.	.	.
46	.50	.01	.01	.	.	.	.	.	.	.	.
47	.50	.01	0.00	.	.	.	.	.	.	.	.
48	.50	.01	.	.	.	.	.	.	.	.	.
49	.50	.01	.	.	.	.	.	.	.	.	.
50	.50	.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

[a]The above values are from one simulation.

Table B.6. Heterozygote has an intermediate fitness of 0.50 in all demes; gene flow = 1.00.— Data are frequencies of the 'a' allele.[a]

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
1	.50	.97	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
2	.50	.98	.	.	.	.	.	.	.	.	.
3	.50	.99	.	.	.	.	.	.	.	.	.
4	.50	1.00	.	.	.	.	.	.	.	.	.
5	.50	1.00	.	.	.	.	.	.	.	.	.
6	.50	1.00	.	.	.	.	.	.	.	.	.
7	.50	.99	.	.	.	.	.	.	.	.	.
8	.50	1.00	.	.	.	.	.	.	.	.	.
9	.50	1.00	.	.	.	.	.	.	.	.	.
10	.50	.94	.	.	.	.	.	.	.	.	.
11	.50	.99	.	.	.	.	.	.	.	.	.
12	.50	.98	.	.	.	.	.	.	.	.	.
13	.50	.99	.	.	.	.	.	.	.	.	.
14	.50	.99	.	.	.	.	.	.	.	.	.
15	.50	.95	.	.	.	.	.	.	.	.	.
16	.50	.97	.	.	.	.	.	.	.	.	.
17	.50	.97	1.00	.	.	.	.	.	.	.	.
18	.50	.95	.99	.	.	1.00	.	.	.	.99	.
19	.50	.87	.99	.	1.00	.99	.	.	1.00	1.00	.
20	.50	.92	.99	1.00	.99	.99	.	1.00	.97	.95	.
21	.50	.85	.97	.97	.94	.93	1.00	.98	.96	.98	1.00
22	.50	.88	.97	.89	.89	.98	.89	.97	.83	.91	.95
23	.50	.78	.79	.80	.85	.76	.88	.87	.88	.82	.87
24	.50	.64	.70	.77	.69	.92	.66	.75	.58	.76	.76
25	.50	.49	.59	.56	.68	.48	.65	.46	.48	.53	.62

Table B.6, Continued.

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
26	.50	.54	.46	.43	.45	.36	.48	.35	.33	.38	.38
27	.50	.43	.35	.33	.42	.13	.29	.17	.21	.18	.27
28	.50	.46	.22	.15	.10	.19	.07	.10	.09	.15	.13
29	.50	.33	.17	.12	.05	.02	.09	.01	.04	.02	.13
30	.50	.19	.13	.06	.01	.08	.04	.01	.03	.05	.03
31	.50	.21	.02	.01	.02	.04	.03	0.00	0.00	0.00	.05
32	.50	.13	.07	.02	0.00	.01	.01	.01	.	.01	.01
33	.50	.09	.02	0.00	.	0.00	0.00	0.00	.	0.00	0.00
34	.50	.08	.02	.	.	.	.	.	.	.	.
35	.50	.03	.01	.	.	.	.	.	.	.	.
36	.50	.02	0.00	.	.	.	.	.	.	.	.
37	.50	.01	0.00	.	.	.	.	.	.	.	.
38	.50	.01	.01	.	.	.	.	.	.	.	.
39	.50	.02	0.00	.	.	.	.	.	.	.	.
40	.50	.02	.	.	.	.	.	.	.	.	.
41	.50	.01	.	.	.	.	.	.	.	.	.
42	.50	0.00	.	.	.	.	.	.	.	.	.
43	.50	.01	0.00	.	.	.	.	.	.	.	.
44	.50	.01	.01	.	.	.	.	.	.	.	.
45	.50	.02	0.00	.	.	.	.	.	.	.	.
46	.50	.01	.	.	.	.	.	.	.	.	.
47	.50	.01	.	.	.	.	.	.	.	.	.
48	.50	.02	.	.	.	.	.	.	.	.	.
49	.50	.03	.	.	.	.	.	.	.	.	.
50	.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

[a]The above values are from one simulation.

APPENDIX C

TABLES OF COMPUTER SIMULATION DATA FOR VARIOUS RATES OF GENE FLOW IMPOSED ON THE SELECTION GRADIENT SHOWN IN TABLE 6

Table C.1. Heterozygote has a fitness of 1.00 in all demes; gene flow = 0.00; deme size = 100.-- Data are frequencies of the 'a' allele.[a]

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
1	.50	.86	.93	.92	.93	.96	.98	.98	.99	.99	1.00
2	.50	.81	.92	.93	.94	.97	1.00	1.00	1.00	1.00	.
3	.50	.86	.97	.98	1.00	1.00	1.00	1.00	.	.	.
4	.50	.90	.93	.94	.95	.98	.98	1.00	.	.	.
5	.50	.88	.89	.93	.95	.97	.97	.99	.	.	.
6	.50	.79	.87	.93	.92	.94	.98	1.00	.	.	.
7	.50	.87	.94	.99	.99	.97	.96	.97	.	.	.
8	.50	.90	.93	.97	.98	.98	1.00	1.00	.	.	.
9	.50	.88	.90	.94	.98	.98	.98	1.00	1.00	1.00	.
10	.50	.89	.90	.95	.97	.99	1.00	.97	.99	.99	.
11	.50	.88	.92	.96	.99	.94	.98	.99	1.00	1.00	.
12	.50	.86	.92	.95	.98	.96	.99	.99	1.00	1.00	.
13	.50	.91	.97	.94	.94	.96	.96	.99	.97	.96	.
14	.50	.89	.92	.96	.99	.97	.99	.99	.99	.99	.
15	.50	.85	.91	.95	.92	.92	.93	.91	.94	.95	1.00
16	.50	.77	.84	.81	.88	.88	.90	.89	.96	.96	.97
17	.50	.78	.82	.80	.79	.82	.83	.81	.86	.81	.88
18	.50	.76	.77	.79	.74	.79	.80	.82	.76	.75	.75
19	.50	.73	.75	.82	.75	.75	.74	.69	.73	.76	.76
20	.50	.64	.70	.71	.78	.74	.75	.76	.70	.73	.68
21	.50	.65	.67	.71	.66	.68	.68	.67	.70	.71	.70
22	.50	.60	.62	.66	.66	.70	.56	.60	.62	.77	.64
23	.50	.58	.55	.61	.62	.59	.57	.61	.59	.60	.62
24	.50	.56	.56	.57	.59	.62	.57	.51	.52	.56	.61
25	.50	.52	.48	.47	.49	.54	.49	.50	.49	.54	.53

Table C.1, Continued.

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
26	.50	.52	.45	.51	.48	.49	.47	.54	.45	.50	.50
27	.50	.51	.47	.40	.42	.46	.45	.40	.45	.43	.41
28	.50	.39	.45	.37	.39	.40	.39	.41	.37	.43	.35
29	.50	.31	.29	.38	.43	.40	.36	.40	.38	.37	.36
30	.50	.30	.35	.33	.33	.31	.34	.25	.37	.36	.32
31	.50	.28	.24	.27	.25	.25	.27	.28	.24	.30	.32
32	.50	.29	.24	.22	.18	.23	.18	.21	.23	.24	.23
33	.50	.25	.19	.23	.21	.17	.18	.18	.24	.25	.26
34	.50	.20	.17	.12	.12	.14	.16	.11	.11	.09	.10
35	.50	.19	.12	.18	.11	.10	.12	.11	.09	.07	.06
36	.50	.20	.09	.06	.11	.10	.08	.10	.07	.07	.06
37	.50	.18	.10	.07	.06	.02	.02	.03	.03	.02	.02
38	.50	.16	.08	.09	.03	.02	.01	0.00	0.00	0.00	0.00
39	.50	.17	.06	.01	0.00	0.00	0.00	.	.	.	.
40	.50	.11	.06	.03	.02	0.00	0.00	.	.	.	.
41	.50	.12	.07	.05	.03	.01	.02	.	.	.	.
42	.50	.10	.07	.03	0.00	0.00	0.00	.	.	.	.
43	.50	.10	.02	.02	.01	0.00	.	.	.	.	.
44	.50	.16	.12	.02	0.00	0.00	0.00	0.00	0.00	.	.
45	.50	.13	.07	.05	.05	.03	.01	.01	.01	.	.
46	.50	.16	.08	.03	.04	.01	0.00	0.00	0.00	.	.
47	.50	.13	.03	.02	.01	.01	0.00	.	.	.	.
48	.50	.16	.07	.03	.02	.03	.01	.	.	.	.
49	.50	.16	.10	.08	.07	0.00	0.00	.	.	.	.
50	.50	.11	.05	.03	.02	0.00	0.00	0.00	0.00	0.00	0.00

[a]The above values are the averages of three simulations.

Table C.2. Heterozygote has a fitness of 1.00 in all demes; gene flow = 0.10; deme size = 100.--Data are frequencies of the 'a' allele.[a]

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
1	.50	.88	.95	.99	.97	.97	.98	1.00	1.00	1.00	1.00
2	.50	.89	.96	.99	.99	1.00	.98	1.00	.	1.00	.
3	.50	.83	.87	.96	.95	.96	.97	.99	1.00	.98	.
4	.50	.89	.92	.97	.96	.94	.98	.97	.97	1.00	.
5	.50	.90	.94	.95	.98	.97	.99	1.00	.99	.	.
6	.50	.83	.89	.96	.96	.97	1.00	1.00	1.00	.	.
7	.50	.83	.92	.98	.99	.97	1.00	1.00	.	.	.
8	.50	.87	.92	.97	.98	.99	1.00	.99	.	.	.
9	.50	.86	.92	.96	.97	.98	.99	.99	1.00	1.00	.
10	.50	.85	.94	.93	.96	.99	.98	.98	.98	.99	1.00
11	.50	.86	.95	.94	.95	.96	.98	.99	1.00	1.00	.99
12	.50	.83	.94	.96	.98	.98	.97	.99	.98	.96	.98
13	.50	.88	.97	.95	.97	.96	.97	.99	1.00	1.00	1.00
14	.50	.86	.94	.95	.96	.98	.93	.97	.99	1.00	.98
15	.50	.82	.84	.87	.88	.88	.95	.95	.95	.94	.89
16	.50	.79	.78	.84	.87	.85	.87	.90	.88	.86	.92
17	.50	.78	.78	.85	.83	.80	.78	.87	.87	.85	.79
18	.50	.72	.78	.85	.79	.72	.77	.78	.84	.84	.78
19	.50	.71	.76	.82	.75	.75	.75	.73	.72	.80	.81
20	.50	.67	.69	.71	.73	.69	.76	.70	.73	.72	.66
21	.50	.70	.66	.69	.64	.65	.65	.64	.66	.68	.66
22	.50	.66	.69	.64	.62	.66	.60	.64	.65	.67	.65
23	.50	.59	.60	.57	.58	.60	.59	.60	.63	.57	.64
24	.50	.50	.59	.52	.64	.54	.54	.53	.60	.61	.60
25	.50	.52	.52	.52	.48	.51	.51	.51	.50	.50	.45

Table C.2, Continued.

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
26	.50	.47	.46	.47	.52	.49	.48	.46	.52	.50	.49
27	.50	.45	.48	.41	.44	.46	.45	.49	.46	.40	.48
28	.50	.41	.40	.39	.40	.40	.33	.38	.40	.35	.34
29	.50	.36	.35	.35	.37	.37	.38	.40	.33	.32	.32
30	.50	.33	.31	.34	.33	.33	.29	.32	.29	.29	.27
31	.50	.37	.21	.24	.28	.28	.32	.28	.29	.32	.26
32	.50	.28	.27	.29	.21	.27	.23	.25	.23	.24	.30
33	.50	.25	.15	.21	.15	.19	.23	.12	.16	.18	.20
34	.50	.23	.18	.18	.13	.09	.09	.14	.13	.12	.13
35	.50	.19	.21	.18	.08	.09	.09	.07	.04	.09	.10
36	.50	.19	.16	.14	.06	.04	.04	.02	.07	.04	.03
37	.50	.19	.10	.09	.10	.05	.05	.02	.01	.01	.01
38	.50	.16	.11	.03	.02	0.00	0.00	0.00	0.00	.01	0.00
39	.50	.16	.06	.02	.01	0.00	0.00	.	0.00	0.00	.
40	.50	.14	.04	.07	.04	.02	.01	.	.	.	.
41	.50	.13	.08	.04	.02	.03	.01	.	0.00	0.00	.
42	.50	.14	.13	.07	.03	.03	.02	0.00	.01	.01	.
43	.50	.12	.09	.05	.03	.01	0.00	.01	0.00	0.00	0.00
44	.50	.14	.05	.06	.04	.01	0.00	.02	.01	.01	.02
45	.50	.14	.08	.03	.05	.05	.01	.01	.01	.02	.01
46	.50	.08	.07	.03	.02	.03	.01	.01	.01	.02	.01
47	.50	.13	.09	.07	.02	.01	.01	.04	.02	.06	.02
48	.50	.16	.08	.06	.02	.02	.04	.01	.03	.02	.04
49	.50	.16	.09	.06	.06	.06	.02	.01	.02	.01	0.00
50	.50	.16	.03	.08	.08	.04	.03	.01	.01	0.00	0.00

[a]The above values are the averages of three simulations.

Table C.3. Heterozygote has a fitness of 1.00 in all demes; gene flow = 0.40; deme size = 1.00.— Data are frequencies of the 'a' allele.[a]

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
1	.50	.84	.91	.92	.97	.99	1.00	1.00	1.00	1.00	1.00
2	.50	.82	.88	.92	.96	.99	1.00	1.00	1.00	.	.
3	.50	.85	.90	.91	.96	.98	.99	.98	.99	.	.
4	.50	.87	.92	.94	.94	.98	1.00	.97	.99	.	.
5	.50	.84	.92	.96	.94	.99	.97	.98	.98	.	.
6	.50	.89	.93	.97	.95	.98	1.00	.99	.99	.	.
7	.50	.88	.92	.93	.96	.96	.98	1.00	1.00	.	.
8	.50	.85	.89	.95	.96	.97	.99	1.00	.	.	.
9	.50	.85	.93	.94	.97	.99	.99	.99	1.00	.	1.00
10	.50	.85	.95	.91	.96	.95	.96	.98	.99	.	.99
11	.50	.90	.92	.95	.96	.94	.95	.99	.99	1.00	.99
12	.50	.89	.95	.90	.96	.93	.95	.96	.97	.99	.99
13	.50	.84	.91	.95	.91	.91	.92	.95	.97	.97	.96
14	.50	.85	.91	.93	.90	.94	.95	.90	.95	.97	.96
15	.50	.82	.87	.90	.87	.91	.87	.89	.93	.92	.95
16	.50	.83	.86	.88	.88	.85	.86	.88	.88	.89	.92
17	.50	.78	.81	.87	.82	.82	.83	.84	.87	.87	.85
18	.50	.75	.79	.75	.85	.80	.81	.84	.79	.80	.82
19	.50	.69	.70	.73	.73	.72	.79	.79	.76	.76	.79
20	.50	.70	.75	.73	.80	.70	.71	.69	.75	.68	.72
21	.50	.67	.68	.68	.70	.70	.65	.69	.65	.66	.72
22	.50	.60	.65	.63	.64	.67	.62	.67	.60	.63	.65
23	.50	.58	.60	.56	.63	.61	.59	.61	.64	.62	.59
24	.50	.52	.60	.55	.55	.57	.57	.58	.58	.59	.53
25	.50	.48	.50	.55	.55	.50	.50	.50	.51	.52	.53

Table C.3, Continued.

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
26	.50	.40	.52	.48	.46	.45	.43	.51	.47	.48	.49
27	.50	.47	.39	.40	.45	.46	.43	.43	.45	.45	.44
28	.50	.44	.44	.37	.42	.39	.41	.41	.39	.38	.46
29	.50	.37	.39	.37	.35	.36	.39	.32	.34	.32	.33
30	.50	.32	.32	.34	.32	.30	.31	.31	.28	.30	.33
31	.50	.27	.22	.27	.27	.24	.26	.26	.26	.29	.29
32	.50	.27	.24	.25	.22	.24	.25	.25	.19	.25	.25
33	.50	.28	.20	.17	.11	.15	.22	.20	.18	.20	.18
34	.50	.23	.21	.13	.10	.14	.19	.12	.18	.13	.16
35	.50	.17	.18	.11	.12	.12	.11	.12	.10	.11	.15
36	.50	.17	.14	.08	.10	.08	.04	.10	.09	.06	.08
37	.50	.16	.13	.08	.06	.06	.05	.07	.05	.03	.02
38	.50	.18	.07	.06	.06	.02	.02	.03	.02	.01	.01
39	.50	.13	.09	.08	.05	.04	.01	.01	.01	0.00	.01
40	.50	.15	.08	.05	.03	.03	.01	.03	0.00	.	0.00
41	.50	.11	.05	.07	.03	.04	.01	.03	.	.	.
42	.50	.14	.10	.09	.04	.02	.02	.03	0.00	0.00	0.00
43	.50	.15	.10	.05	.05	.02	.03	0.00	.03	.01	.01
44	.50	.16	.09	.09	.04	.05	.05	.02	.02	.01	0.00
45	.50	.12	.08	.06	.03	.04	.04	.02	.02	.01	.
46	.50	.15	.09	.05	.03	.04	.03	.04	.03	.01	.
47	.50	.18	.10	.03	.04	.02	.04	.02	.03	.01	.
48	.50	.14	.11	.04	.03	.03	.05	.01	.01	0.00	.
49	.50	.17	.06	.05	.04	.01	.02	.02	0.00	.	.
50	.50	.14	.07	.02	.01	.04	.02	.01	0.00	0.00	0.00

[a]The above values are the averages of three simulations.

APPENDIX D

TABLES OF COMPUTER SIMULATION DATA FOR VARIOUS RATES OF GENE FLOW IMPOSED ON THE SELECTION GRADIENT SHOWN IN TABLE 7

Table D.1. Heterozygote has an intermediate fitness of 0.90 in all demes; gene flow = 0.00; deme size = 100.--Data are frequencies of the 'a' allele.[a]

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
1	.50	.74	.83	.89	.96	.98	1.00	1.00	1.00	1.00	1.00
2	.50	.62	.81	.90	.97	.98	1.00	.	.	.	.
3	.50	.65	.71	.87	.94	.98	1.00	.	.	.	.
4	.50	.79	.85	.95	.98	.99	.99	1.00	.	.	.
5	.50	.70	.78	.78	.88	.94	.93	.97	1.00	1.00	.
6	.50	.66	.74	.75	.84	.90	.97	.96	.98	.99	.
7	.50	.67	.85	.81	.91	.90	.98	.97	1.00	1.00	.
8	.50	.70	.83	.80	.97	.98	1.00	1.00	1.00	1.00	1.00
9	.50	.68	.78	.85	.92	.97	.95	.98	.91	.96	.96
10	.50	.70	.84	.85	.95	.94	.99	1.00	1.00	1.00	1.00
11	.50	.66	.82	.91	.94	.98	.96	.96	1.00	.	.
12	.50	.60	.74	.85	.83	.91	1.00	.97	.98	.	.
13	.50	.69	.89	.95	1.00	1.00	1.00	1.00	1.00	1.00	1.00
14	.50	.59	.77	.82	.93	.93	.93	.93	.95	.98	.97
15	.50	.58	.71	.84	.82	.83	.89	.95	.95	.93	.99
16	.50	.68	.73	.88	.91	.91	.99	1.00	1.00	1.00	1.00
17	.50	.69	.80	.88	.85	.81	.85	.92	.89	.89	.88
18	.50	.68	.74	.70	.81	.88	.89	.87	.88	.87	.86
19	.50	.46	.59	.74	.74	.75	.80	.86	.91	.88	.99
20	.50	.57	.47	.63	.70	.73	.72	.70	.74	.79	.76
21	.50	.60	.66	.64	.71	.73	.77	.64	.76	.87	.87
22	.50	.53	.64	.57	.54	.53	.49	.48	.53	.54	.51
23	.50	.59	.69	.72	.88	.89	.92	.89	.87	.87	.81
24	.50	.41	.34	.41	.46	.52	.52	.52	.47	.65	.65
25	.50	.59	.57	.57	.46	.50	.53	.59	.61	.66	.65

Table D.1, Continued.

Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
26	.50	.52	.53	.58	.54	.39	.31	.31	.44	.41	.35
27	.50	.54	.57	.49	.51	.49	.44	.46	.44	.49	.52
28	.50	.37	.27	.29	.26	.21	.19	.11	.17	.12	.08
29	.50	.39	.19	.24	.24	.20	.24	.27	.19	.17	.30
30	.50	.47	.33	.33	.23	.24	.13	.11	.15	.15	.13
31	.50	.58	.45	.37	.31	.34	.26	.26	.29	.33	.29
32	.50	.43	.38	.36	.33	.24	.12	.06	.02	0.00	0.00
33	.50	.49	.45	.36	.29	.27	.17	.19	.13	.14	.04
34	.50	.53	.46	.37	.29	.16	.08	.02	.05	.06	.02
35	.50	.41	.29	.13	.08	.06	.02	.01	.03	0.00	0.00
36	.50	.47	.37	.20	.17	.09	.09	.07	.03	.01	.
37	.50	.33	.17	.10	.08	.04	.01	.01	.01	0.00	.
38	.50	.23	.17	.14	.10	.07	.02	.02	.01	.01	.
39	.50	.44	.27	.17	.13	.06	0.00	0.00	0.00	0.00	.
40	.50	.27	.16	.13	.08	.07	.04	.01	.01	.02	.
41	.50	.47	.30	.21	.13	.06	.08	.06	.04	.01	.
42	.50	.47	.41	.27	.11	.05	.02	.01	0.00	0.00	.
43	.50	.32	.20	.15	.11	.05	.04	.01	.	.	.
44	.50	.39	.28	.12	.04	.01	0.00	0.00	0.00	0.00	.
45	.50	.32	.34	.20	.11	.06	.06	.05	.04	.01	.
46	.50	.39	.19	.07	.04	.07	.05	.02	.04	0.00	.
47	.50	.30	.17	.06	.03	.02	.01	.02	.03	.01	.
48	.50	.32	.22	.06	0.00	0.00	0.00	0.00	0.00	0.00	.
49	.50	.30	.24	.09	.01	0.00	0.00	.	.	.	.
50	.50	.24	.12	.07	.05	.03	.01	0.00	0.00	0.00	0.00

[a]The above values are the averages of three simulations.

Table D.2. Heterozygote has an intermediate fitness of 0.90 in all demes; gene flow = 0.40; deme size = 100.--Data are frequencies of the 'a' allele.[a]

Deme Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
1	.50	.62	.70	.79	.84	.91	.97	.99	.99	.99	.99
2	.50	.63	.74	.85	.84	.90	.94	.98	.96	.98	1.00
3	.50	.64	.69	.82	.85	.93	.98	.98	1.00	1.00	1.00
4	.50	.60	.79	.87	.85	.89	.95	.99	.99	.	.99
5	.50	.62	.81	.84	.84	.81	.95	.97	1.00	1.00	.99
6	.50	.65	.83	.86	.88	.78	.94	.99	1.00	.99	1.00
7	.50	.74	.75	.86	.95	.92	.96	.95	.97	.99	1.00
8	.50	.72	.87	.90	.92	.91	.97	.95	.99	.97	1.00
9	.50	.64	.79	.87	.92	.98	.99	.98	.98	.99	.99
10	.50	.70	.81	.91	.96	.94	.98	.98	.99	1.00	.99
11	.50	.65	.81	.87	.93	.96	.99	.99	1.00	.	1.00
12	.50	.65	.77	.88	.91	.95	.95	.98	1.00	.	.
13	.50	.69	.73	.84	.93	.97	.96	.98	.99	.	1.00
14	.50	.65	.76	.84	.94	.94	.93	.95	.97	1.00	1.00
15	.50	.54	.74	.89	.92	.93	.92	.93	.96	.99	.99
16	.50	.69	.68	.86	.88	.92	.92	.94	.95	.99	.93
17	.50	.62	.71	.76	.82	.85	.91	.89	.92	.92	.96
18	.50	.68	.63	.75	.82	.84	.85	.84	.92	.91	.95
19	.50	.61	.61	.68	.77	.76	.79	.82	.92	.87	.90
20	.50	.54	.65	.68	.71	.72	.78	.83	.82	.84	.84
21	.50	.51	.57	.61	.65	.72	.69	.77	.83	.85	.80
22	.50	.51	.57	.55	.71	.69	.71	.75	.76	.81	.76
23	.50	.51	.47	.54	.61	.63	.60	.55	.66	.70	.74
24	.50	.54	.49	.47	.51	.55	.54	.51	.60	.64	.67
25	.50	.59	.55	.54	.50	.52	.44	.44	.51	.51	.64

Table D.2, Continued.

Number	Generation Number										
	0	5	10	15	20	25	30	35	40	45	50
26	.50	.53	.52	.49	.49	.42	.37	.39	.48	.40	.51
27	.50	.58	.54	.43	.44	.37	.34	.42	.35	.38	.30
28	.50	.49	.50	.45	.36	.32	.31	.35	.26	.23	.29
29	.50	.42	.43	.32	.32	.27	.25	.23	.21	.20	.18
30	.50	.46	.38	.27	.24	.31	.17	.21	.17	.10	.14
31	.50	.41	.34	.26	.14	.14	.13	.13	.14	.07	.07
32	.50	.38	.27	.21	.18	.10	.13	.10	.08	.10	.05
33	.50	.32	.21	.16	.14	.09	.11	.09	.07	.03	.04
34	.50	.32	.27	.18	.12	.08	.08	.09	.07	.05	.01
35	.50	.35	.28	.19	.12	.15	.09	.08	.08	.04	.02
36	.50	.42	.23	.21	.10	.11	.10	.06	.03	.03	.03
37	.50	.40	.23	.13	.05	.06	.02	.02	.05	0.00	.01
38	.50	.38	.22	.18	.07	.05	.03	.04	.02	0.00	.03
39	.50	.31	.21	.14	.06	.05	.02	.02	.01	.01	.02
40	.50	.29	.16	.12	.09	.07	.03	.01	.01	.02	.01
41	.50	.31	.23	.13	.09	.06	.04	.02	.04	.01	.01
42	.50	.37	.22	.17	.11	.08	.03	.05	.02	.02	.01
43	.50	.31	.27	.14	.12	.08	.05	.04	.03	.01	.01
44	.50	.33	.21	.10	.07	.09	.06	.02	.01	0.00	0.00
45	.50	.34	.19	.10	.06	.09	.01	.02	.02	.	.
46	.50	.33	.15	.13	.09	.03	.02	.01	.01	0.00	0.00
47	.50	.32	.19	.14	.06	.02	.02	.02	0.00	.01	.01
48	.50	.35	.29	.14	.09	.03	.01	0.00	.	0.00	0.00
49	.50	.36	.22	.14	.07	.03	0.00	.	.	.	.01
50	.50	.35	.28	.18	.09	.06	.02	0.00	0.00	0.00	0.00

[a]The above values are the averages of three simulations.

APPENDIX E

CONTROL SECTION OF COMPUTER PROGRAM

```
      PROGRAM MIGRATE(INPUT,OUTPUT,TAPE1=INPUT,TAPE2=OUTPUT)
C
C---THIS PROGRAM DETERMINES NEW GENOTYPIC FREQUENCIES AND GENE FREQUENCIES EACH
C----GENERATION FOR A LINEAR SERIES OF SUBPOPULATIONS.  THE TWO GENES ARE
C----SYMBOLIZED A AND B, WHILE THE THREE GENOTYPES ARE SYMBOLIED AA,AB,AND BB.
C----THE NUMBER OF GENERATIONS(IT),THE NUMBER OF SUBPOPULATIONS(K), THE NUMBER OF
C----INDIVIDUALS IN EACH SUBPOPULATION(NN), THE INITIAL FREQUENCY OF THE ,A, GENE
C----IN EACH SUBPOPULATION(P), THE FITNESS OF EACH OF THE GENOTYPES IN EACH
C----SUBPOPULATION, AND THE AMOUNT OF GENE FLOW BETWEEN SUBPOPULATIONS (PM) ARE
C----READ IN.  GENE FLOW CONSISTS OF A MIGRATION EVENT FOLLOWED BY A MATING
C----EVENT.  ONCE THE MIGRATION EVENT HAS OCCURRED, PAIR MATINGS ARE RANDOMLY
C----FORMED BETWEEN INDIVIDUALS OF A SUBPOPULATIONS UNTIL 100 SURVIVING PROGENY
C----ARE PRODUCED.  MATINGS OCCUR WITH REPLACEMENT AND SELECTION OCCURS AT THE
C----PROGENY LEVEL.
C
      DIMENSION NN(50),P(50),AA(50),AB(50),BB(50),AAN(50),ABN(50),
     1BBN(50),AANN(50),ABNN(50),BBNN(50),AAF(50),ABF(50),BBF(50),
     2AF(50),BF(50),W11(50),W12(50),W22(50)
      CALL RANSET(1)
      READ(1,1) IT,K,PM,NOSUB
    1 FORMAT(I10,I10,F10.2,I10)
      WRITE(2,501) IT,K,PM,NOSUB
  501 FORMAT(1H1,/////,1X,*NO. GENERATIONS = *,I2,//,1X,*NO. SUBPOPULATI
     1ONS = *,I2,//,1X,*GENE FLOW = *,F4.2,//,1X,*INITIAL NO. OF INDIVID
     2UALS IN EACH SUBPOPULATION = *,I4)
      READ(1,2) (NN(I),P(I),W11(I),W12(I),W22(I),I=1,K)
    2 FORMAT(I10,F10.2,F10.2,F10.2,F10.2)
      WRITE(2,492)
  492 FORMAT(1X,10(/),29X,*GENOTYPIC FITNESSES*,12X,*NUMBER OF*,/,14X,
     1*SUBPOPULATION*,32X,*INDIVIDUALS*,/,17X,*NUMBER*,6X,*AA*,7X,*AB*,
     27X,*BB*,9X,*IN EACH SUBPOP*,//)
      DO 617 JI=1,K
      WRITE(2,493) JI,W11(JI),W12(JI),W22(JI),NN(JI)
  493 FORMAT (19X,I2,F11.2,F9.2,F9.2,13X,I3)
  617 CONTINUE
      IGEN=0
      WRITE(2,10)
      DO 5 I=1,K
      AA(I)=(P(I)**2)*NN(I)
      AB(I)=(P(I)*(1.-P(I))*2.*NN(I))
      BB(I)=NN(I)-(AA(I)+AB(I))
      AAF(I)=AA(I)/NN(I)
      ABF(I)=AB(I)/NN(I)
      BBF(I)=1.-(AAF(I)+ABF(I))
      AF(I)=AAF(I)+.5*(ABF(I))
      BF(I)=1.-AF(I)
    5 CONTINUE
      DO 30 J=1,K
      IF(J.GT.1) GOTO 31
      WRITE(2,12) IGEN,J, AAF(J),ABF(J),BBF(J),AF(J),BF(J)
      GOTO 30
   31 WRITE(2,13)J,AAF(J),ABF(J),BBF(J),AF(J),BF(J)
   30 CONTINUE
   10 FORMAT(1H1,29X,*GENOTYPIC FREQUENCIES     GENE FREQUENCIES*,/,14X,
     1*SUBPOPULATION*,/,17X,*NUMBER*,7X,*AA*,7X,*AB*,7X,*BB*,9X,*A*,9X,
     2*B*,///)
   12 FORMAT(//,1X,*GENERATION*,I3,I7,8X,F4.2,2(5X,F4.2),2(6X,F4.2))
   13 FORMAT(19X,I2,8X,F4.2,2(5X,F4.2),2(6X,F4.2))
      DO 100 I=1,IT
      IGEN=IGEN+1
      DO 724 IX=1,K
      AAN(IX)=0
      ABN(IX)=0
      BBN(IX)=0
```

```
  724 CONTINUE
      DO 106 J=1,K
      NJ=AA(J)+AB(J)+BB(J)
      P1=AA(J)/NJ
      P2=1.-BB(J)/NJ
      DO 106 JJ=1,NJ
      RF=RANF(0)
      IF(RF.LE.P1) GOTO 102
      IF(RF.GE.P2) GOTO 103
C--IF THE HETEROZYGOTE IS CONSIDERED-
      CALL MOVE (ABN,PM,J,K)
      GOTO 106
  102 CALL MOVE (AAN,PM,J,K)
      GOTO 106
  103 CALL MOVE (BBN,PM,J,K)
  106 CONTINUE
C
C
      DO 299 N=1,K
      AANN(N)=0
      ABNN(N)=0
  299 BBNN(N)=0
C
C--RANDOM MATINGS NOW OCCUR WITHIN EACH SUBPOPULATION
C
      DO 300 M=1,K
      SUM=0
C--THE NUMBER OF INDIVIDUALS IN THE SUBPOPULATION IS--
      SUM=AAN(M)+ABN(M)+BBN(M)
C--SAMPLING OCCURS WITH REPLACEMENT.
      SCH=0
  301 IF(SCH.GE.100) GOTO 300
      HAA=AAN(M)/SUM
      HAB=(AAN(M)+ABN(M))/SUM
C--THE FIRST INDIVIDUAL OF THE MATING PAIR IS NOW RANDOMLY CHOSEN.
      RF=RANF(0)
      IF(RF.LE.HAA) GOTO 302
      IF(RF.LE.HAB) GOTO 303
C--THE SECOND INDIVIDUAL OF THE MATING PAIR IS NOW RANDOMLY CHOSEN.
      CALL MATE2 (IM,HAA,HAB)
C--THE GENOTYPE OF THE SECOND INDIVIDUAL IS NOW DETERMINED.
      IF(IM.EQ.1) GOTO 306
      IF(IM.EQ.2) GOTO 310
C--THE MATING PAIR CAN NOW POTENTIALLY PRODUCE TWO PROGENY (SELECTION DETERMINES
C---IF A PROGENY WILL SURVIVE BASED UPON THE FITNESS OF THE GENOTYPE OF THE
C---RESPECTIVE PROGENY FOR THAT DEME).
  309 CALL SELECT (BBNN,M,W22,SCH)
      CALL SELECT (BBNN,M,W22,SCH)
      GOTO 301
C--THE SECOND INDIVIDUAL OF THE MATING PAIR IS NOW RANDOMLY CHOSEN.
  302 CALL MATE2 (IM,HAA,HAB)
      IF(IM.EQ.1) GOTO 304
      IF(IM.EQ.2) GOTO 305
  306 CALL SELECT (ABNN,M,W12,SCH)
      CALL SELECT (ABNN,M,W12,SCH)
      GOTO 301
  304 CALL SELECT (AANN,M,W11,SCH)
      CALL SELECT (AANN,M,W11,SCH)
      GOTO 301
  305 RF=RANF(0)
      IF(RF.LE..25) GOTO 304
      IF(RF.GE..75) GOTO 306
  312 CALL SELECT (AANN,M,W11,SCH)
      CALL SELECT (ABNN,M,W12,SCH)
      GOTO 301
C--THE SECOND INDIVIDUAL OF THE MATING PAIR IS NOW RANDOMLY CHOSEN.
```

```
  303 CALL MATE2 (IM,HAA,HAB)
      IF(IM.EQ.1) GOTO305
      IF(IM.EQ.2) GOTO 309
  310 RF=RANF(0)
      IF(RF.LE..25) GOTO 309
      IF(RF.GE..75) GOTO 306
  313 CALL SELECT (ABNN,M,W12,SCH)
      CALL SELECT (BBNN,M,W22,SCH)
      GOTO301
  308 RF=RANF(0)
      IF(RF.LE..0625) GOTO 304
      IF(RF.LE..3125) GOTO 312
      IF(RF.LE..4375) GOTO 314
      IF(RF.LE..6875) GOTO 306
      IF(RF.LE..9375) GOTO 313
      GOTO 309
  314 CALL SELECT (AANN,M,W11,SCH)
      CALL SELECT (BBNN,M,W22,SCH)
      GOTO 301
C
  300 CONTINUE
C
      DO 40 L=1,K
      NN(L)=AANN(L)+ABNN(L)+BBNN(L)
      AAF(L)=AANN(L)/NN(L)
      ABF(L)=ABNN(L)/NN(L)
      BBF(L)=1.-(AAF(L)+ABF(L))
      AF(L)=AAF(L)+.5*(ABF(L))
      BF(L)=1.-AF(L)
   40 CONTINUE
      DO 50 J=1,K
      IF(J.GT.1) GOTO 71
      WRITE(2,12) IGEN,J,AAF(J),ABF(J),BBF(J),AF(J),BF(J)
      GOTO 50
   71 WRITE(2,13) J,AAF(J),ABF(J),BBF(J),AF(J),BF(J)
   50 CONTINUE
      DO 600 IS=1,K
      AA(IS)=AANN(IS)
      AB(IS)=ABNN(IS)
  600 BB(IS)=BBNN(IS)
  100 CONTINUE
      STOP
      END
      SUBROUTINE MOVE(X,P,J,K)
C-- THIS SUBROUTINE DETERMINES WHETHER THE INDIVIDUAL MIGRATES OR NOT.IF IT DOES
C  MIGRATE, THEN THE DIRECTION OF MIGRATION IS DETERMINED (I.E.,THE INDIVIDUAL
C---CAN EITHER MIGRATE TO THE SUBPOPULATION ON THE LEFT OR TO THE ONE ON THE
C---RIGHT).
C
      DIMENSION X(50)
      RF=RANF(0)
      IF(RF.LE.P) GOTO 1
C--IF THE INDIVIDUAL DOES NOT MIGRATE, THEN THE SUBPOPULATION WHICH IT IS FROM
C---IS INCREMENTED
      X(J)=X(J)+1
      RETURN
C--INDIVIDUALS FROM EXTREME SUBPOPULATIONS CAN ONLY MIGRATE IN ONE DIRECTION.
    1 IF(J.EQ.1) GOTO 2
      IF(J.EQ.K) GOTO 3
C--OTHERWISE, THEY CAN MIGRATE IN ONE OF TWO DIRECTIONS.
      RF=RANF(0)
      IF(RF.LE..5) GOTO 5
      GOTO 4
    2 RF=RANF(0)
      IF(RF.LE..5) GOTO4
      X(J)=X(J)+1
```

```
      RETURN
    3 RF=RANF(0)
      IF(RF.LE..5) GOTO 5
      X(J)=X(J)+1
      RETURN
    4 JK=J+1
      X(JK)=X(JK)+1
      RETURN
    5 JK=J-1
      X(JK)=X(JK)+1
      RETURN
      END
      SUBROUTINE MATE2(IM,HAA,HAB)
C--THE SECOND INDIVIDUAL OF THE MATING PAIR IS NOW RANDOMLY CHOSEN.
      RF=RANF(0)
      IF(RF.LE.HAA) GOTO 1
      IF(RF.LE.HAB) GOTO 2
      IM=3
      RETURN
    1 IM=1
      RETURN
    2 IM=2
      RETURN
      END
      SUBROUTINE SELECT (X,M,W,S)
      DIMENSION X(50),W(50)
      B=W(M)
      RF=RANF(0)
      IF(RF.GT.B) GOTO 1
      X(M)=X(M)+1
      S=S+1
    1 RETURN
      END
```

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