

IX. Genetic Characteristics of Island Populations

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INTRODUCTION

On September 17, 1835, Charles Darwin first set foot on Chatham Island of the Galapagos Archipelago. The diversity of obviously related birds which Darwin encountered laid much of the groundwork for his thoughts later expressed in *The Origin of Species*. Eighty-one years ago Alfred Russel Wallace enumerated the advantages in studying island life for understanding the distribution of plants and animals (1880). Every one of the advantages that he listed contained the one common denominator of simplicity. Ecologists have turned to the arctic, the desert and to oceanic islands to study interacting forces in a simplified environment in order to better comprehend more complex environments (for instance Fosberg, 1951). And now geneticists, interested in population structures and histories, are capturing butterflies in the Isles of Scilly in order to count the number of spots on the underside of the hind wing (E. B. Ford, 1960).

Oceanic islands serve the student of organic diversity in the same way a well-equipped laboratory is necessary to the student of DNA. The relative simplicity of interacting factors and the contrast of conditions under which island populations are maintained in comparison to continental ones enables the investigator to ferret out details often obscured on the mainland. The results of natural selection (and sampling errors) are more open to inspection in island populations and this is especially true of biparental organisms that can be cross-bred under laboratory conditions.

The present report is a continuation of the genetic studies initiated by the author (1957) and continued in conjunction with N. B. Krishnamurthy (1959) on the dumni subgroup of the cardini species group of *Drosophila* inhabiting, as far as known, all the islands of the Lesser Antilles, Puerto Rico and Jamaica (Table 1). Of the six island populations tested previously, five could be identified by their phenotype alone. The populations are: Puerto Rico (PR), St. Thomas (ST), Guadeloupe (GU), Barbados (BA), St. Vincent (SV) and Grenada (GR). Only SV and GR are phenotypically identical. All possible crosses among the stocks (30) have been made; a fertile second generation has been obtained in only five cases. Several instances of unequal sex ratios were obtained showing a Haldane effect in one series and a maternal effect in another series. The major chromosome differences between some of the populations consist of shifts in heterochromatin. The dot (IV) chromosomes of PR and ST have added heterochromatin making them short metaphase rods. This chromosome in the Jamaica population is a long rod due to the accumulation of heterochromatin. The differences in the island populations were attributable to the lack of genetic continuity between the islands and the independent adaptation (genetic change) in each island form.

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TABLE 1

Species of the cardini group and their distributions

Neotropical mainland	West Indies
1. Western hemisphere tropics <i>D. cardini</i> Sturtevant	1. Florida, Cuba, Jamaica, Hispaniola <i>D. acutilabella</i> Stalker
2. Mexico to Brazil <i>D. cardinoides</i> Dobzhansky and Pavan	2. Jamaica <i>D. belladunni</i> Heed and Krishnamurthy
3. Mexico to Trinidad <i>D. parthenogenetica</i> Stalker <i>D. neomorpha</i> Heed and Wheeler	3. Puerto Rico—St. Thomas <i>D. d. dunni</i> Townsend and Wheeler <i>D. d. thomasensis</i> n. subsp.
4. South America <i>D. polymorpha</i> * Dobzhansky and Pavan <i>D. n. neocardini</i> Streisinger <i>D. n. mourensis</i> da Cunha <i>D. n. itambacuriensis</i> da Cunha	4. St. Kitts—Guadeloupe <i>D. arawakana</i> n. sp. <i>D. a. arawakana</i> , nom. subsp. <i>D. a. kittensis</i> n. subsp.
5. Andes of Bolivia and Peru <i>D. procardinoides</i> Frydenberg	5. Martinique <i>D. caribiana</i> n. sp.
	6. St. Lucia <i>D. antillea</i> n. sp.
	7. Barbados <i>D. nigrodunni</i> Heed and Wheeler
	8. St. Vincent—Grenada <i>D. s. similis</i> Williston <i>D. s. grenadensis</i> n. subsp.

* Also present on Grenada.

The present paper attempts to give equal weight to the *similarities*, as well as the differences, between each island population. In so doing, it is believed that different types of selection pressures have been identified. The stocks recently tested are: Jamaica (JA), St. Kitts (SK), Martinique (MA) and St. Lucia (SL). On the basis of the results of these tests and of the previous ones, each island population has been given a specific or a subspecific name. Three new species and three new subspecies are described. The cardini subgroup is established to contain all members not included in the dunni subgroup. The male genitalia of all members of the cardini group are illustrated and compared. The body and wing lengths observed in each island population are recorded and compared. Salivary chromosome analysis is extended. Finally, in the discussion, the behavior of the island representatives of the dunni subgroup is compared with that of the continental representatives of the cardini subgroup. The differences are in accord with present day concepts of the different history, the isolation and the different ecologies that are bestowed upon island populations in contrast to mainland populations.

Reference will be made repeatedly to the "previous" or "first" publication which refers to Heed and Krishnamurthy (1959). Although each island population is now recognized as a taxon, they will be designated as before with the initials of the islands from which they were established.

TAXONOMY AND MORPHOLOGY

Table 1 lists the known forms in the cardini group according to their distri-

bution. Fifteen species are represented, four of which are divided into two races each. The dotted line in Table 1 separates the two subgroups: the cardini subgroup here established as consisting of the seven species on the mainland and *D. acutilabella*, and the dunni subgroup which consists of seven species distributed on 10 islands in the Lesser Antilles, Puerto Rico and Jamaica. The chief peculiarity of the dunni subgroup is a genetic one; the seven species hybridize among themselves more easily than with any member in the cardini subgroup. Three new species and three new subspecies in the dunni subgroup are described below in a brief outline form, made possible because the characteristic features such as size, color pattern, and genitalia have been analyzed in conjunction with other members of the group and are presented separately.

Figure 1 illustrates the similarities and differences in the male apodema in the cardini group as drawn from freshly prepared slides. Variations within a species from different areas are minute. For instance, when the apodema of *D. cardini* from Florida was compared to that from Chile, no consistent differences could be found. By contrast, the differences between species (where they exist) are constant and reliable. The nigrodunni complex includes all the middle island forms in the Lesser Antilles: St. Kitts, Guadeloupe, Martinique, St. Lucia and Barbados. It is impossible to distinguish any of the five island forms by this one character. Another surprising fact is the discovery of two triads of species on the mainland. *Drosophila neocardini*, *polymorpha* and *neomorpha* are closely related to one another. *Drosophila cardinoides*, *procardinoides* and *parthenogenetica* have more characters in common with one another than with other members of the group. *Drosophila cardini* unfortunately cannot be related by this method and stands alone with a unique apodema. The dunni subgroup as a whole is quite diverse and is united in Figure 1 because of the genetic affinities within the group and the distributional pattern. *Drosophila acutilabella* is not easily placed. According to the morphology of the apodema, it could have affinities with the *neocardini-polymorpha-neomorpha* triad as well as with the dunni subgroup.

Some very obvious size differences have long been noted in the dunni subgroup strains. Figure 2 represents the results of measuring the body length (base of antenna to tip of abdomen, solid lines) and wing length (dotted lines) of 25 females and 25 males from 10 island strains reared for one complete generation at 19.5° C. in not too crowded conditions since the larvae were supplied yeasted kleenex on which to pupate. There were no controls in the sense that two strains from the same island were not tested. One might conceive that the differences between strains are those that have incidentally become fixed (homozygous) in the laboratory. This might be true to some extent but the correlations that do exist lend confidence to the data. For instance, the strains from Puerto Rico and St. Thomas belong to the same species and they differ from all other species by having very large females and small males. The St. Vincent and Grenada strains belong to the same species and they differ from all other species by having very large females and the largest males. The correlation breaks down with the third two-island species but even in this case there appears to be an explanation. The Guadeloupe and St. Kitts strains are interfertile and are regarded as belonging to the same species, although St. Kitts females have wings much shorter than the body. There is only one other strain in which the wings are shorter than the

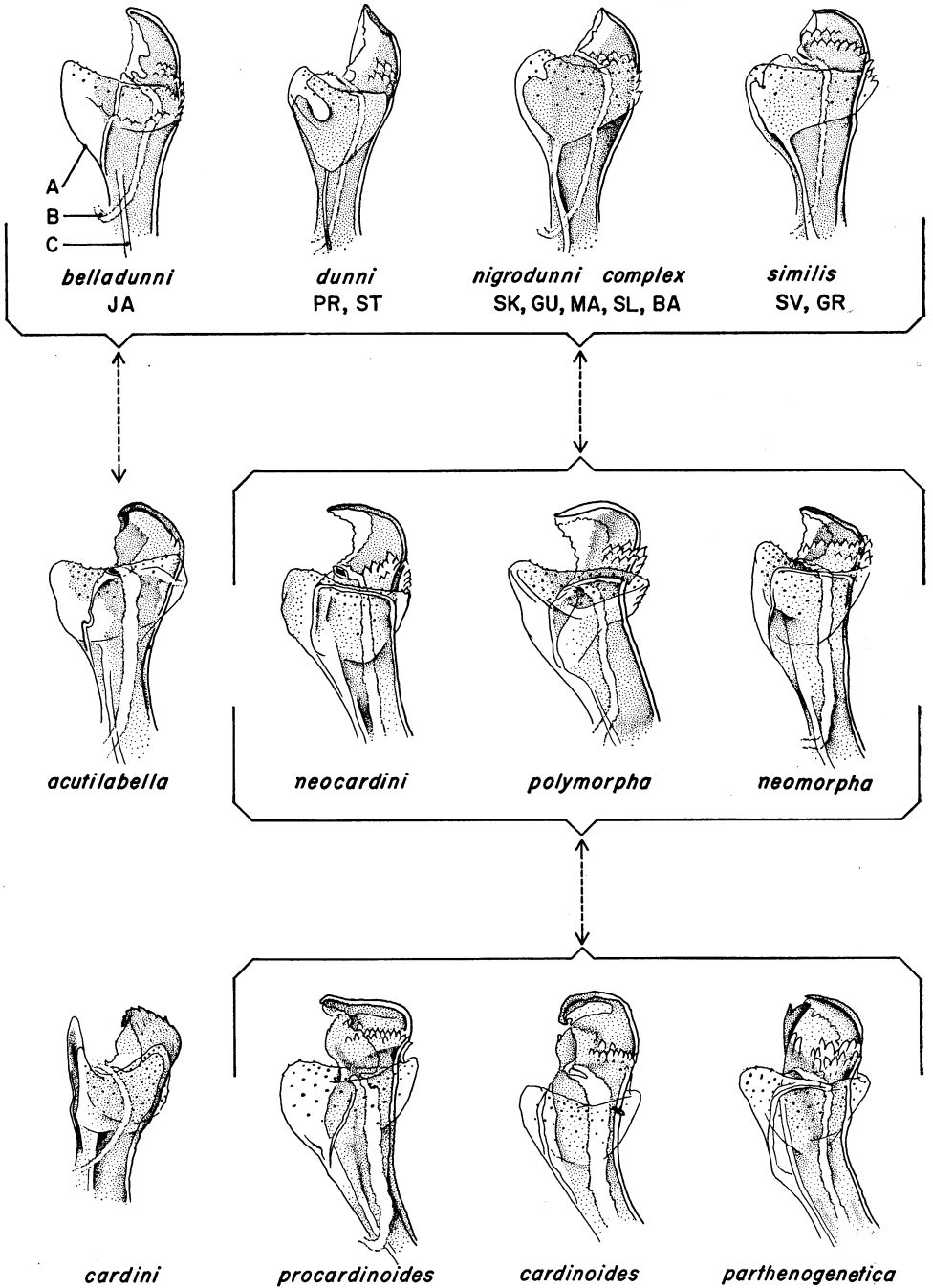


FIG. 1. Tip of apodemas (penes) of males of the cardini group species in profile. A: transparent sheath; B: sperm duct; C: apodema.

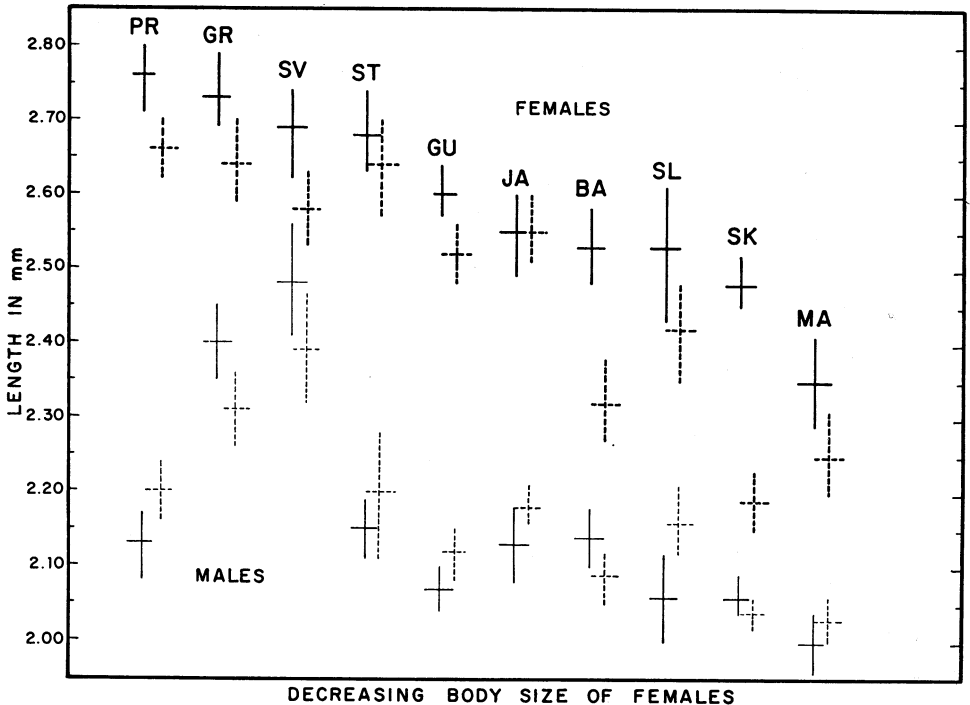


FIG. 2. Sample mean and its 95% confidence interval for body length (solid) and wing length (bars) of ten island strains reared at 19.5° C. $n=25$.

body; this is the Barbados strain. The males of St. Kitts and Barbados strains also tend to have shorter wings than body, while in all the other strains males tend to have wings longer than the body, except St. Vincent and Grenada which have exceptionally large males anyway.

The situation may conceivably be explained as follows. St. Kitts and Barbados are very open islands and planted mostly in sugar cane. Shorter wings could be of value if *Drosophila* fly in open windy country, hopping from one orchard or wood patch to the next. The other islands have comparatively large continuous areas of woodland or fincas. St. Thomas has quite broken country with scanty vegetation but the wings of its inhabitants are not exceptional.

Drosophila similis Williston.

D. similis Williston 1896. Trans. Ent. Soc. London: 415.

D. similis, Sturtevant 1921. Carn. Inst. Pub. 301: 79.

Originally described by Williston (1896) from St. Vincent. Sturtevant (1921) recorded it from Jamaica and Barbados, and stated that it was similar to *D. cardini*. Metz (1916) reported the metaphase chromosomes as five pairs of rods and a pair of dots (Cuban strain). Stalker (1953) could find no living or pinned material of *similis* and suggested that his newly described *D. acutilabella*, which certainly is a sibling species of *cardini*, could be a synonym of *similis* if it were not for the fact that *acutilabella* has two pairs of V's instead of four rods in the metaphase.

I have recently compared two cotypes (#20353, AMNH, male; #2756.1, Cornell University, female) of *D. similis* with the dunni subgroup form from St. Vincent and Grenada and have concluded that they are the same species. A third cotype (#2756.2, Cornell University, female), however, is not a cardini group form but belongs in the tripunctata group.

I have selected cotype #20353, belonging to the American Museum of Natural History, as the Lectotype of *Drosophila similis*.

Drosophila similis does not exist outside of the islands of St. Vincent and Grenada (unless it is present on the Grenadines and possibly Tobago). It does not have five pairs of rods and a pair of dots (see below). The only member of the cardini group known to have this metaphase arrangement is *D. cardini*. Additional taxonomic points of value for *D. similis* are as follows:

Abdominal pattern: As pictured in H. & K. (1959).

Apodema: Figure 1, this publication.

Size: Figure 2, this publication.

Chromosomes: Two pairs of V's, a pair of rods and a pair of dots. Figure 2, H. & K. (1959).

Drosophila similis is hereby separated into two subspecies. The form from St. Vincent is *D. similis similis* and the form from Grenada is *D. similis grenadensis*, new subspecies. The separation is based on genetic differences in crosses to other island forms. *Grenadensis* gives a more extreme sex-ratio with Martinique females, Barbados females and Guadeloupe males. The type material for the new subspecies is deposited in The University of Texas collection.

***Drosophila arawakana*, new species**

This represents SK (St. Kitts) and GU (Guadeloupe) of this and previous publications. Hybrids between the two island forms are perfectly fertile.

Abdominal patterns: As illustrated in H. & K. (1959).

Apodemas: As illustrated in Figure 1, in the nigrodunni complex.

Sizes: As shown in relation to other members of the dunni subgroup, Figure 2.

Chromosomes: Two pairs of V's, a pair of rods and a pair of dots, as illustrated in H. & K. (1959).

Drosophila arawakana is divided into two subspecies: *D. arawakana arawakana* from Guadeloupe, and *D. arawakana kittensis* from St. Kitts. *D. a. kittensis* has significantly shorter wings than body whereas *arawakana* does not, nor does *kittensis* give as severe deviation from the normal sex-ratio in crosses to other island forms as does *arawakana*. Type material deposited in The University of Texas collection.

***Drosophila antillea*, new species**

Represents SL (St. Lucia) of this and earlier publications.

Abdominal pattern: Illustrated in H. & K. (1959).

Apodema: Figure 1, this publication, in the nigrodunni complex.

Size: Figure 2, this publication.

Chromosomes: Two pairs of V's, a pair of rods and a pair of dots, as illustrated in H. & K. (1959).

Distribution and types: Restricted to the island of St. Lucia, B.W.I. Type material deposited in The University of Texas collection.

***Drosophila caribiana*, new species**

Denoted as MA (Martinique) in this and earlier publications.

Abdominal pattern: Illustrated in H. & K. (1959).

Apodema: Figure 1, this publication, in the nigrodunni complex.

Size: Figure 2, this publication; the smallest member of the dunni subgroup.

Chromosomes: Two pairs of V's, a pair of rods and a pair of dots, as illustrated in H. & K. (1959).

Distribution and types: Restricted to the island of Martinique, F.W.I. Type material deposited in The University of Texas collection.

***Drosophila dunni* Townsend and Wheeler.**

D. dunni Townsend and Wheeler 1955. Jour. Agric. Univ. Puerto Rico 39: 60.

D. dunni is hereby separated into two subspecies: *D. dunni dunni*, typical subspecies, from Puerto Rico; and *D. dunni thomasensis*, new subspecies, from St. Thomas.

The distinguishing characters are that *thomasensis* has a darker grayish abdomen than the nominate race and its metaphase differs in that it has a J-shaped X chromosome instead of a rod-shaped X as in *dunni*, and one of the autosomes is J-shaped instead of V-shaped as in *dunni*. Type material of the subspecies deposited in The University of Texas collection.

HYBRIDIZATION TESTS AND CYTOLOGY

St. Kitts. Fertile with Guadeloupe and gives a normal sex-ratio in the progeny (Table 2). The sex-ratios among the hybrids from BA × SK and SV × SK are abnormal, but not as sharply so as those among the hybrids from BA × GU and SV × GU. Hybrids of SK with PR, ST and JA are completely sterile, but gene exchange is possible through backcrosses with BA and SV.

Martinique. The most genetically isolated species in the dunni subgroup (Table 3). All hybrid males and females are sterile among themselves and are sterile when backcrossed to the parents (Figure 3). Dissections, where made, showed the presence of aborted ovaries and testes in the majority of cases. Martinique males show extremely abnormal sex-ratios with other island females located south of Martinique in that the majority of the hybrid male zygotes are lethal. The Y chromosome from MA is lethal or near lethal in combination with southern island X's. Martinique females show a maternal cross-lethal effect in that many of the hybrid females do not survive in tests with SV and GR males. The cross-lethal gene or gene complex in the X chromosome of Grenada acts as a dominant, and that of St. Vincent as a semi-dominant, in Martinique cytoplasm. In Grenada cytoplasm with hybrid genotype, the females are viable.

St. Lucia. Quite unambiguously isolated from PR and ST to the north and SV and GR to the south (Table 4). In most of these tests no hybrids were produced although dissections showed that the majority of the females in each cross were

TABLE 2
Hybridization Tests with St. Kitts

No.	F×M	Total F ₁	Per cent males	Remarks
1.	14 SK × 11 PR	0	...	Females fertilized
2.	11 PR × 14 SK	33	33.3	Males sterile
3.	10 PR/SK × 35 SK	0
4.	7 SK × 7 ST	0
5.	13 SK × 12 GU	53	43.4	Fertile
6.	24 SK × 20 GU	142	43.0	Fertile
7.	22 GU × 28 SK	many	...	Fertile
8.	16 BA × 6 SK	477	28.3	Males sterile; 95% males deformed wings
9.	27 BA/SK × 26 BA	767	34.9	Fertile
10.	17 BA/SK × 20 SK	421	40.0	Males sterile
11.	19 BA/SK/SK × 26 SK	170	44.7	Fertile
12.	14 SV × 15 SK	323	33.1	Males sterile; 44% males abnormal abdomen and deformed wings
13.	10 SV × 7 SK	150	26.0	Few males fertile
14.	F ₁ of No. 13	8	50.0	Males sterile
15.	14 SV/SK × 9 SV	78	43.5	Males sterile
16.	6 SV/SK/SV × 14 SV	33	30.3	Males sterile
17.	20 SV/SK/SV/SV × 14 SV	54	40.0	Fertile
18.	21 SV/SK × 24 SK	360	31.4	Males sterile
19.	30 SV/SK/SK × 26 SK	40	57.5	Males sterile
20.	15 SK × 12 SV	49	47.0	Males sterile
21.	6 SK/SV × 18 SK	24	50.0	Males sterile; 75% males deformed wings
22.	6 SK/SV × 10 SV	11	27.3	Males sterile
23.	12 SK × 10 GR	31	64.5	Males sterile; 35% males and females abnormal abdomen
24.	9 SK/GR × 20 SK	4	0
25.	15 SK × 16 JA	0	...	Females fertilized
26.	8 JA × 10 SK	14	0
27.	14 JA/SK × 21 SK	1	0	Most females aborted ovaries

inseminated but the sperm were dead. In the series of crosses listed in Table 4 the hybrid males were sterile but the females were not tested for fertility in backcrosses. Comparison of Table 4 with Table 7 shows that while sperm from SL will not live in SV females, they can survive and function in SV/GU hybrid females.

Table 7 also establishes that hybrid females with $\frac{1}{2}$ SL genes and $\frac{1}{4}$ GU and $\frac{1}{4}$ SV genes are at least partially fertile even to BA males and this is indicated in Figure 3 as GU × SL.

Jamaica. A total of 38 tests were made with JA crossed to other members of the dumni subgroup in large and small mass matings, Table 5. JA males will mate with all other members but do not produce hybrids. JA males will, however, produce progeny with JA/GR hybrids, but by the third backcross to JA males no offspring at all are produced (Nos. 24, 25 and 26). The situation is all the more unusual since the original cross involved JA egg cytoplasm. Theoretically

TABLE 3

Hybridization tests with Martinique (20 males and 20 females each)

No.	F × M	Total F ₁	Per cent Males	Remarks
1.	PR × MA	242	40.1
2.	ST × MA	380	41.8	1% females and males abnormal abdomen.
3.	GU × MA	540	31.7	5% females and males abnormal abdomen.
4.	MA × MA	208	53.4
5.	SL × MA	66	9.1	50% males rough eyes; ovaries aborted.
6.	BA × MA	178	2.8	4% females abnormal abdomen.
7.	SV × MA	331	0.3	9% females abnormal abdomen; ovaries aborted in all.
8.	SV × MA	474	0.6
9.	GR × MA	289	0.4	3% females abnormal abdomen; ovaries aborted in all.
10.	GR × MA	271	1.1
11.	*JA × MA	0
12.	MA × PR	62	32.3	50% males and females abnormal abdomen.
13.	MA × ST	67	34.3	All males rough eyes; 50% both sexes abnormal abdomen.
14.	MA × GU	514	48.4
15.	MA × MA	208	53.4
16.	MA × SL	736	52.3	Ovaries aborted.
17.	MA × SL	127	44.1	Testes aborted.
18.	MA × BA	662	54.2	Ovaries and testes aborted.
19.	MA × BA	563	53.3
20.	MA × SV	98	62.2	All males rough eyes; testes aborted; 20% both sexes abnormal abdomen.
21.	MA × SV	141	70.2	Same as above.
22.	MA × GR	12	91.7	All males rough eyes; 30% males abnormal abdomen.
23.	MA × GR	113	100.0	All males rough eyes; 3% abnormal abdomen, testes aborted.
24.	MA × JA	0

* Two mass matings.

by the third backcross the hybrid female should contain about 17% GR genes. Apparently this dosage is more critical than higher dosages of the foreign genes. This interesting cross is being repeated.

JA females crossed to males from all other islands, except Grenada and Barbados, produce sterile progenies. JA females were not tested to SV males. Fertile progeny of both sexes are produced in the first backcross to GR males and in the second backcross to BA males. Unequal sex-ratios are evident when GU and SK are used as males. This was not totally unexpected since the Y chromosomes from these islands are known to be lethal or near lethal with other island X chromosomes. However, in Table 5, test No. 8, 18 of the total of 19 males emerged in the last three days of a 15-day emergence period as though nullo-Y sperm were produced in quantities by one of the GU males. It is also possible that the GU population has several types of Y chromosomes, some of which are not lethal in the hybrid males. To check this, 49 pair matings of JA females × GU males were prepared (Table 6). Out of the 21 pairs that were fertile, only one pair

♂ ♀	PR	ST	SK	GU	MA	SL	BA	SV	GR	JA
PR			S		S	O	PF	N	N	O
ST				S	S	O	S	S		O
SK	O	O						PF	S	O
GU	PF	S			S	PF	PF	PF	S	O
MA	N	N		N		S	S	S	S	O
SL	O	O		N	S		N	N	O	
BA	N	N	PF	N	S	N		PF	PF	O
SV	PF	PF	PF	PF	S	O	N			O
GR	N	PF		PF	S	O	PF			O
JA	O	O	S	S	O	N	PF		PF	

FIG. 3. Fertility relations in the dunni subgroup. Shaded squares: both sexes of hybrids fertile. Open squares: not tested. PF: hybrid females partially fertile in backcrosses. S: both sexes of hybrids sterile. N: hybrid females not tested for fertility in backcrosses. O: no hybrids (or very few) produced.

TABLE 4

Hybridization tests with St. Lucia (20 males and 20 females each)

No.	F×M	Total F ₁	Per cent males	No.	F×M	Total F ₁	Per cent males
1.	PR × SL	0	...	13.	†SL × PR	2	0
2.	†ST × SL	0	...	14.	†SL × ST	6	0
3.	GU × SL	361	42.4	15.	SL × GU	0	...
4.	*GU × SL	123	39.0	16.	*SL × GU	62	19.4
5.	MA × SL	127	44.1	17.	SL × MA	1	0
6.	SL × SL	298	47.3	18.	SL × SL	298	47.3
7.	*SL × SL	168	44.0	19.	*SL × SL	168	44.0
8.	BA × SL	145	36.6	20.	SL × BA	163	54.0
9.	*BA × SL	204	48.5	21.	*SL × BA	520	50.2
10.	‡SV × SL	0	...	22.	†SL × SV	4	25.0
11.	†GR × SL	0	...	23.	*SL × SV	58	17.2
12.	JA × SL	82	46.4	24.	SL × GR	0	...
				25.	SL × JA	not made	...

* Incomplete mass mating.
 † Two mass matings.
 ‡ Three mass matings.

TABLE 5
Hybridization tests with Jamaica (*D. belladunni*)

No.	F × M	Total F ₁	Per cent males	Fertility	Phenotype
1.	24 JA × 26 PR	2	50.0	Sterile	Equals JA
2.	20 JA × 20 PR	6	83.0	Sterile	Almost JA
3.	19 PR × 6 JA/PR	0	...	Testes aborted
4.	2 JA/PR × 16 PR	0	...	Ovaries aborted
5.	20 JA × 20 ST	2	50.0	Sterile	Males JA; females almost JA
6.	8 JA × 10 SK	14	0	} {Most females aborted ovaries
7.	14 JA/SK × 21 SK	1	0	
8.	19 JA × 23 GU	105	18.1		Sterile
9.	14 JA/GU × 14 JA	0	...	Females sterile
10.	16 JA/GU × 30 GU	0	...	Females sterile
11.	20 JA/GU × 30 SK	0	...	Females sterile
12.	20 JA × 20 SV/GU*	24	0
13.	22 JA/SV/GU × 23 GU	0	...	Females sterile
14.	25 JA × 18 MA	0
15.	20 JA × 20 MA	3 pupae
16.	22 JA × 21 SL	82	46.3	Males sterile	Intermediate
17.	20 JA × 20 BA	126	47.6	Males sterile	Intermediate
18.	14 JA × 25 BA	133	54.1	Males sterile	Intermediate
19.	27 JA/BA × 30 BA	171	30.0	Males sterile	BA to intermediate
20.	11 JA/BA/BA × 25 BA	104	41.1	Fertile	BA to dilute BA
21.	F ₁ of No. 20	many	...	Fertile	All equal BA
22.	19 JA × 19 GR	36	41.1	Males sterile	Males JA; females almost JA
23.	10 GR × 8 JA/GR	0
24.	10 JA/GR × 9 JA	79	36.7	Males sterile	All equal JA
25.	20 JA/GR/JA × 18 JA	21	33.3	Males sterile
26.	14 JA/GR/JA/JA × 16 JA	0
27.	11 JA/GR × 17 GR	48	43.7	Fertile	Variable to almost JA and GR
28.	F ₁ of No. 27	25	68.0	Fertile	Males vary; females almost GR
29.	F ₂ of No. 27	196	38.7	Fertile	All equal GR
30.	20 JA × 20 JA	432	46.8	Fertile
31.	Females of all islands × JA males	0	...	All females inseminated

* SV/GU is F₁₂ hybrid.

TABLE 6
D. belladunni (JA) retests with GU

F × M	No. pairs	Fertile	Females	Males	Aborted ovaries	Eggs present but sterile
JA (356.3f) × GU	22	11	109	0	83	10
JA (356.3d) × GU	15	7	136	0	..	23
JA (356.3d) × GU	12	3	101	1
Total	49	21	346	1

produced a male. The total sex ratio was 346 females to one male or 0.28% males. This is believed to be a truer ratio than that seen in the mass mating and places Jamaica as the extreme "southern" island in the sex-ratio cline with GU males crossed to southern island females (Table 13).

Four-way island crosses. The list of crosses in Table 7 illustrates the theoretical possibility that genes from one island could be transmitted to the populations of other islands in the right combinations although the backcrosses were only carried for four generations. The fourth generation females in the majority of cases laid eggs and were no doubt at least partially fertile. It is also true that certain combinations which ought to work do not. For instance in test No. 6, it is surprising that MA males produced no progeny with the triple hybrid females, because MA males produce offspring with SV, GU and BA separately. It is also surprising that SL males in test No. 7 produced very few progeny with the triple hybrid since it worked with BA and GU alone but not with SV (even after three attempts in mass matings, Table 4), but did work with SV/GU (test No. 9). Thus, the general combining ability among the island forms is fair to poor and predictability is not always possible.

Tests with the cardini subgroup. All members of the dumni subgroup, except SK, were tested both ways in mass matings to *D. acutilabella* from Jamaica (stock no. H355.3 iso female). The only island forms that produced hybrids were SV and GR. GR \times *acutilabella* gave 18 females and 12 males; *acutilabella* \times GR gave one male; SV \times *acutilabella* gave four females and five males. All the hybrids were sterile. Another stock of *acutilabella* from the Everglades, Florida (No. H415.7c) produced a few hybrids with GU and SV (the only strains tested) and the hybrids were sterile.

Drosophila cardini (No. H415.9 cardini) from the Everglades, Florida was tested with BA, PR, GU, SL and JA in small mass matings. No hybrids were produced except GU \times *cardini* produced two pupae. Many of the females were inseminated in each cross but the sperm were usually dead. In the test BA \times *cardini*, four of the eight BA females dissected had a typical insemination reaction, the first case encountered in the dumni subgroup.

TABLE 7

Results of continued backcrosses to other islands

No.	F \times M	Total F ₁	Per cent males	Fertility
1.	19 SV \times 23 GU	342	23.4	Males sterile
2.	20 SV/GU \times 41 BA	601	27.1	Males sterile
3.	31 SV/GU/BA \times 45 PR	10	60.0	Males sterile
4.	48 SV/GU/BA \times 43 ST	5	40.0
5.	55 SV/GU/BA \times 54 GU	214	13.1	Males sterile
6.	14 SV/GU/BA \times 20 MA	0
7.	30 SV/GU/BA \times 30 SL	2	50.0
8.	40 SV/GU/BA \times 40 SV	228	42.5	Males sterile
9.	20 SV/GU \times 31 SL	26	23.1	Males sterile
10.	20 SV/GU/SL \times 50 BA	89	40.4	Males sterile
11.	30 SV/GU \times 43 PR	48	25.0	Males sterile
12.	26 SV/GU/PR \times 50 BA	23	17.4	Males sterile

TABLE 8

Mass matings and reciprocals of BA, SV and GR to other members of the cardini group

<i>D. cardini</i>	<i>D. polymorpha</i>
Florida × BA and GR	Trinidad × BA and SV
Chile × BA and GR	Brazil × BA and SV
<i>D. acutilabella</i>	<i>D. procardinoides</i>
Miami, Fla. × BA and SV*	Bolivia × BA and SV
Everglades, Fla. × BA* and SV*	
<i>D. neomorpha</i>	<i>D. neocardini</i>
Nicaragua × BA and SV	Colombia × BA and SV
Panama × BA	Brazil × SV
<i>D. parthenogenetica</i>	
Mexico × BA and GR	
Colombia × BA and GR	

* No hybrids produced except where marked. Hybrids with SV and *acutilabella* sterile. Hybrids with BA and *acutilabella* fertile when backcrossed to BA males.

Table 8 shows the remainder of the crosses with members of the cardini subgroup. In this set of crosses BA and SV or GR only were chosen for testing. The only tests that produced hybrids were again with *acutilabella*. An average of four females was dissected for each cross that did not go. Fertilization had occurred in most cases but the sperm were usually dead. The stock of *acutilabella* (No. H415.9 acuti) from the Everglades, Florida is an exceptionally fertile one to many cardini group species and this stock threw fertile hybrid females with BA: *acutilabella* females × BA males gave 27 females and 16 males and the hybrid females were fertile to BA males.

Cytology. There are several corrections and additions to be made to the cytological picture in the dumni subgroup as presented in the first publication. Figure 8 in H. & K. (1959) is not correct in the sense that there are no inversion differences between PR, ST and SV, GR. Also the inversion difference between SV, GR and the central islands (SK, GU, MA, SL and BA) is not 2LB but rather 3RB. In other words 2LB does not exist and the only main inversion difference in the dumni subgroup is 3RB which is fixed in all the central islands.

These errors were found when JA was being tested to all other island strains. There are no inversion differences between JA and PR, ST or SV, GR. When JA is tested with the central islands, 3RB shows up in heterozygous condition in every case. As a result of this PR, ST and SV, GR were tested with one another and found to be homozygous.

Also the inversion difference between *D. acutilabella*, from Jamaica, and St. Vincent was previously reported as a small mid-inversion in the X chromosome. The strains of *acutilabella* from Jamaica, Cuba, St. Petersburg and Floral City, Florida, are identical in the gene arrangement in all chromosomes. The strain of *acutilabella* used recently is from the Everglades (H415.9 acuti). This strain shows overlapping inversions with very little pairing in the basal half of the X chromosome in hybrids with SV. This one fact illustrates that *acutilabella* cannot be related by a simple interpretation to the dumni subgroup. The new strain has not yet been tested with other *acutilabella* strains.

There is one inversion that has recently been found heterozygous in St. Kitts.

It is a short basal inversion (about 1/7 total length of arm) in the left arm of chromosome II. The inversion attracted attention for study because the homozygous standard arrangement (that common to all the islands) was picked up only in very low frequencies at first. A more thorough analysis showed that the SK homozygote and heterozygote were almost three times more frequent in the SK stock than the standard homozygote: SK/SK 75, SK/ST 74, ST/ST 28 larvae. In order to test whether ST homozygous is not as viable as the other arrangements, two types of matings were prepared. In the first test the ST gene arrangement from Guadeloupe was tested with the SK arrangement from St. Kitts in the hybrids of the mating SK \times GU and the reciprocal in one small mass mating each. From seven sample vials of the F₄ generation, the total count of the three arrangements fits the expectation on the Hardy-Weinberg equilibrium basis:

	SK/SK	SK/ST	ST/ST*	
Obs.	41	87	55	
Exp.	45.75	91.5	45.75	P = .10

* From Guadeloupe.

Of the seven vials, three gave results fitting the Hardy-Weinberg expectation, three gave deviations at the 1 to 5% level of significance, and one showed extreme heterosis.

In the second test the two gene arrangements in St. Kitts, previously made homozygous, were tested in small mass matings of SK/SK \times ST/ST and the reciprocal. The data below represent the total larvae dissected of the F₃ generation from four sample vials:

	SK/SK	SK/ST	ST/ST*	
Obs.	46	77	20	
Exp.	35.75	71.5	35.75	P < .01

* From St. Kitts.

Of the four vials, two were very unbalanced against ST/ST and two were balanced.

The data indicate that the standard arrangement in St. Kitts is indeed less viable in competition with the inversion (SK). It is tempting to speculate that the value, and thus high incidence, of the new inversion (for it is apparently restricted to St. Kitts) is to shield a semi-vital gene complex. However, the strains have not been independently tested for fertility, fecundity and viability.

It is interesting to compare the frequency of inversions in the dumni subgroup and in the cardini subgroup. Of the seven species in the former, two species are heterozygous for one inversion each. Da Cunha *et al.* (1953) found 6 inversions in *polymorpha* from three localities and 3 inversions in *cardinoides* from three localities. A recent survey in this laboratory showed the following interstrain inversions from two localities each of the following species: *polymorpha* 3, *neomorpha* 3, *parthenogenetica* 2 and *cardini* 1. The cardini subgroup has a higher frequency of inversions than the dumni subgroup even though the number of inversions is low. More information on inversions is reported in the discussion.

PHENOTYPES

In many of the tests with the dumni subgroup the abdominal patterns of the hybrid females were scored as being intermediate or closer to one or the other parent. The data are too extensive and complex to analyze but a few generalizations may be made. It should be recalled that all island stocks are quite uniform in phenotype within themselves.

There are in general three classes of hybrid phenotypes. Some of the hybrids are "intermediate and uniform"; hybrids in other crosses are "variable", ranging from one parental type (or almost) to the other parental type (or almost); in still other crosses the hybrids show dominance in varying degrees of one parental type. Table 9 shows that when Barbados is one of the parents the hybrids are usually of the first type and when Guadeloupe is one of the parents the hybrids are of the second class. However single individuals of Guadeloupe can apparently be fixed homozygous for color genes since in one case with Grenada all hybrids (48 females) were close to GU and in another pair mating all hybrids (12 females) with Grenada were intermediate and uniform. Also, BA females throw variable hybrids, in mass matings, with ST and SK, and BA males are variable with SL females. Other hybrids that are variable in mass matings are: GR \times ST, SL \times MA, MA \times SL, SL \times SV and SV \times ST.

In general, the populations ST, SK, GU, MA and SL produce variable hybrid offspring when crossed to each other or to the populations of other islands. The island populations that generally give intermediate hybrids with other islands are: PR, BA, SV and GR. There is no relation of the above two classes to the third category: partial dominance.

A "variable" island may be partially dominant to another "variable" island or to an "intermediate" island. However an "intermediate" island is partially dominant only to "variable" islands. Also a light phenotype may be dominant to a darker phenotype or vice-versa, and one cross may show dominance but the reciprocal may fall in one of the other two categories. One sequence of partial dominance is interesting: GR > ST > GU > SL > BA > MA in one or both of the

TABLE 9
Phenotypes from pair matings

No.	F \times M	No. pairs	Phenotypes of females
1.	ST \times BA	6	Mostly intermediate and uniform
2.	GU \times BA	11	Mostly intermediate and uniform
3.	BA \times SV	4	Mostly intermediate and uniform
4.	BA \times GR	1	Mostly intermediate and uniform
5.	SV \times BA	6	Mostly intermediate and uniform
6.	GR \times BA	6	Mostly intermediate and uniform
7.	GU \times SV	4	Variable
8.	GU \times GR	3	Variable and GR present in low frequency
9.	BA \times GU	10	Variable but closer to BA
10.	SV \times GU	9	Variable, SV and GU in low frequency
11.	GR \times GU	7	Variable and GR present in low frequency
12.	GR \times GU	1	All 48 females close to GU
13.	GR \times GU	1	All 12 females intermediate and uniform

reciprocal crosses. St. Vincent females are partially dominant in the cross to SK males. There are a few examples in which the hybrids were either lighter or darker than either parental type. For instance GU \times ST produced two females that were darker than either parent.

The hybrid phenotypes of Jamaica (strain H356.3d) with other island males illustrate all three classes (Table 5). JA shows almost complete dominance to PR and ST in the north and GR in the south. Hybrids with GU are variable but intermediate with SL and BA. Table 10 shows the scoring of phenotypes from the 21

TABLE 10
Variability in F₁ hybrid color patterns from pair matings of JA \times GU

	Close to GU	(Int.)	Intermediate	(Int.)	Close to JA	JA
With JA (356.3d)						
Pair 1	8	12	24	10	4	0
Pair 2	8	10	6	4	0	0
Pair 3	24	22	11	7	0	0
7 pairs	17	31	23	2	14	1
	—	—	—	—	—	—
Total	57	75	64	23	18	1
With JA (356.3f)						
11 pairs	0	2	0	3	63	33

pair matings made up to test for non-disjunction as mentioned previously. Two strains established from single females of JA were used in crossing to GU males (from a multiple stock). The difference between the two strains is striking. Strain "d" shows high variability and strain "f" shows 33% complete dominance in the hybrid females. This is good evidence that the abdominal patterns are under rather strict genetic control.

The tests that gave an F₂ are recorded in Table 11. There appears to be strong selection for the male parental phenotype in three of the four tests. There is good indication that only one or very few F₁ males were fertile in each test. The data from many of the early backcrosses is given in Table 12. Each test is from a mass mating and many of the total numbers of offspring are well below the original parental crosses indicating that selection is strongly operating on the recombinations, and in favor of the phenotype to which the hybrids are crossed.

TABLE 11
Frequency of extreme phenotypes in F₂

No.	F \times M	F ₁ phenotype	F ₂ females	F ₂ phenotypes
1.	GU \times BA	Mostly intermediate	34	50% BA 50% BA to intermediate
2.	BA \times GU	Variable	9	All intermediate
3.	BA \times SV	Mostly intermediate	217	20% SV 5% close to BA 6% lighter than either
4.	SV \times GU	Variable	222	45% GU 4% SV

TABLE 12
Frequency of extreme phenotypes from backcrosses

No.	F×M	No. females scored	Phenotype of females
1.	ST/BA × ST	86	30.3% ST
2.	ST/SV × ST	90	11.1% ST
3.	SV/ST × ST	217	3.3% close to SV
			25.3% ST
			1.3% close to SV
			6.0% lighter than either (whitish)
4.	GU/BA × GU	220	21.8% GU
5.	GU/SV × GU	186	39.0% GU
6.	GR/GU × GU	223	39.1% GU
7.	ST/BA × BA	70	22.8% BA
8.	GU/BA × BA	178	21.9% BA
9.	BA/SV × BA	276	3.4% close to GU
			37.8% BA
			1.1% darker than either parent
			1.1% lighter than either parent
10.	BA/GR × BA	183	8.9% BA
			1.1% close to GR
			1 female lighter than either parent
11.	GR/BA × BA	175	25.7% BA
			3.4% lighter than either parent
12.	SV/ST × SV	86	16.3% SV but darker yellow ground color
13.	GU/SV × SV	111	20.0% SV
			9.0% GU
14.	BA/SV × SV	203	18.2% SV
			2.9% close to BA
15.	GU/GR × GR	95	31.5% GR
			8.4% close to GU
16.	GR/GU × GR	182	22.0% GR
			15.3% close to GU
			1 female lighter than either parent
17.	GR/BA × GR	212	10.0% GR
			1.3% very close to BA
			3.3% lighter than either parent

SUMMARY OF ISOLATING MECHANISMS

Island populations that can be tested in the laboratory are unique in that they show genetic differences produced through time and isolation unaffected by selection for or against isolating mechanisms after two closely related populations meet. They show that isolating mechanisms do evolve as a by-product of adaptation.

Sexual isolation is rather completely absent in the dunni subgroup. This may indicate that behavior phenomena are under a more general genetic control than other mechanisms and may be the last mechanism to evolve in allopatric populations through time. No sexual preference tests have yet been attempted.

Gametic mortality is only fairly common. Jamaica males produce no hybrids with all other islands although insemination takes place regularly. St. Lucia males and females show a high frequency of dead sperm with PR and ST to the north and SV and GR to the south.

All cases of zygotic mortality in the subgroup are more or less in direct relation to the geography of the islands. This phenomenon is probably not completely fortuitous and illustrates increasing genetic divergence through space (but see Discussion). The best example is the sex-ratio cline exhibited when the Y chromosome of Guadeloupe interacts with the X chromosome from islands to the south of GU (except Martinique), producing fewer males at each step. Since this was discussed in the previous paper only new information will be added here. Jamaica must be placed at the extreme end of the cline in the sense that the X-JA, Y-GU combination is almost completely lethal. The stage at which most of the males die, at least in the case of SV \times GU, is the critical period of emergence from the pupal case and also the pupal stage. The majority of males remain half-way emerged until they die. The remainder die before the pupa case is opened. The Y chromosome from St. Kitts as far as it has been tested behaves similarly to the GU Y but does not give such an extreme cross-lethal effect. The Y chromosome from Martinique has a very extreme lethal effect in combination with the X's of SL, BA, SV and GR resulting mostly in female progeny. Comparisons are summarized in Table 13.

TABLE 13

Per cent males from tests showing cross-lethal effects in relation to geography

Females	SK	Males GU	MA
SL	..	19.4	9.1
BA	28.3	20.0	2.8
SV	26.0; 33.1*	8.3	0.3; 0.6*
GR	..	0.9	0.4; 1.1*
JA	0	0.3	..

* Two mass matings.

Martinique and Barbados females show a maternal effect with the X's of SV and GR in that the sex ratio favors the males and more so with GR than SV. The gene or gene complex in the GR X behaves as a dominant lethal in MA cytoplasm resulting in death of all the female progeny. The phenomenon here compares favorably with the maternal effect in *D. montana* females to *texana* male reported by Patterson and Griffen (1944) in the virilis group which was a better analysis since the reciprocal hybrids were fertile. The reciprocal crosses (SV and GR \times BA males) give a relatively normal sex ratio. The two islands of Barbados and Martinique may be compared in their maternal effect:

BA \times SV:	63.0% males	MA \times SV:	62.2 to 70.2% males (2 tests)
BA \times GR:	72.7% males	MA \times GR:	91.7 to 100.0% males (2 tests)

Male sterility is by far the most common isolating mechanism in the subgroup. All hybrid males from interspecific crosses are sterile, although there have been several interspecies tests which gave a few second generation hybrids but they in turn were sterile. The one interesting case that did give at least one fertile male in which later progeny were fertile was the SV \times GU test as reported in

the first paper. The cross has been repeated many times since then and again one fertile male was produced. The results will be presented elsewhere.

Complete female sterility is found only in hybrids involving Martinique, however not all the possible combinations were tested. All other islands have at least one combination that produces partially fertile females with males of another interspecific island (Figure 3). There is no well-defined correlation of hybrid female fertility with the geography of the islands.

It should be emphasized that prediction is not possible for the combining abilities among the different islands and perhaps this is a special type of isolating mechanism. For instance Martinique males will produce hybrids with GU, BA and SV females separately but not in the "triple" combination females (Table 7). In other words any combination of genes does not work and each island has its own balanced system. The genotype as a balanced system has been emphasized by Stone, in Patterson and Stone (1952).

The isolating mechanisms illustrated above are no different than those already reported for *Drosophila* but they are proof that such systems may arise in isolation as a consequence of general adaptation. (See Discussion.)

THE SPECIES CONCEPT IN THE DUNNI SUBGROUP

There are six types of analysis reported on the dunni subgroup in this and the previous publication in order to distinguish similarities and differences between the island populations. The first three are genetic: fertility relations, metaphase configuration, and inversions. The last three concern the phenotype: abdominal color pattern, body size and male genitalia. The six characteristics are not superimposed upon one another in random fashion but tend to show relationships, and the relations are generally in accord with the geographic position of the islands. Figure 4 shows three main divisions. The first and sharpest division separates Puerto Rico and St. Thomas from all other islands in all characteristics except for the standard gene arrangement which is common also to SV, GR and JA. Actually the metaphase configuration of these two islands are different, which

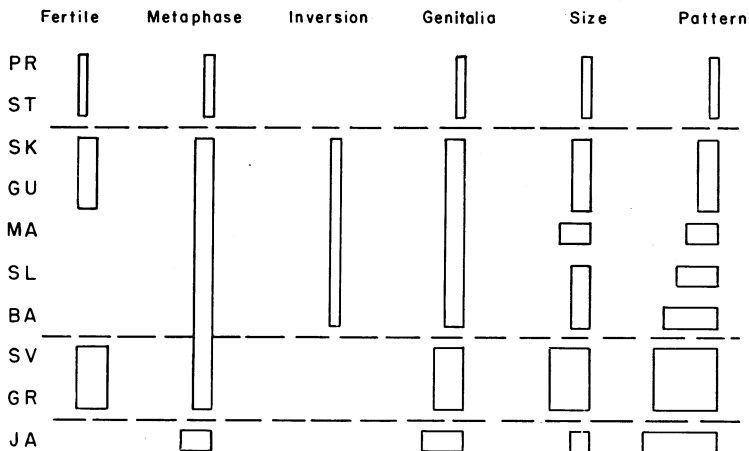


FIG. 4. Comparative characteristics in the dunni subgroup. Equal width of bars indicates equality within each class.

is not indicated in the figure. The fertility relations beyond a fertile F_1 are too diverse to include and will be discussed later. The hybrid inviability effects have already been discussed and are shown to be in accord with the spatial relations of the islands.

The second division separates the central islands from St. Vincent and Grenada in all characters but the metaphase type of 2 V's, a rod and a dot. The third division separates Jamaica in all characters except the gene arrangement and size. It is thus not difficult to establish three good species on the five most differentiated islands: *D. dumni* in Puerto Rico and St. Thomas; *D. similis* in St. Vincent and Grenada; *D. belladumni* in Jamaica. The five central islands offer more of a challenge.

To a taxonomist working with only morphological characters, they would seem to represent a complex of subspecies that show a cline in the amount of pigment, since there are no good differences even in the male genitalia (Figure 1). There is not one instance in *Drosophila* taxonomy that is familiar to the author where closely related species cannot be differentiated by genitalia. A good case in point is the taxonomically difficult tripunctata group in Middle and South America which consists of 45 described species and many more undescribed forms. The shape and coloring of the body are so similar in many instances that identification is possible only by dissecting out the genitalia. As far as has been tested, there is a direct correlation between the ability of two forms to hybridize and produce fertile progeny with the similarity in male genitalia and vice-versa. Patterson (1957) mated 11 population stocks of the tripunctata group in 110 crosses. Two of the stocks had identical male genitalia and they were the only stocks that produced fertile hybrids in reciprocal crosses. It is well known that sibling species in the willistoni group, obscura group and melanogaster group can all be differentiated by genitalic structure.

Biologically, however, the complex consists of one island that is genetically isolated from all the others, Martinique, and two islands that are completely inter-fertile, St. Kitts and Guadeloupe. The central islands at once represent good biological species but also good morphological subspecies (Mayr, 1948). The subspecific category implies inter-fertility, allopatry and, usually, ecological similarity. Although many of the hybrid females are semifertile, continued out-crossing to other island males produces fewer and fewer offspring and in some cases the systems become so unbalanced that no offspring survive. A trinomial designation would clearly indicate that each form lives on a separate island. The ecological requirements are probably quite similar on each island and this is reviewed in the discussion.

The species category, of course, implies rather strict reproductive isolation, which is typical of most of the island crosses. It is more important to emphasize the hybridization ability of those forms that can be tested in the laboratory than to emphasize their morphological and ecological characteristics. The similarity in phenotype, except for abdominal pattern, and apparent similarity in ecology among the populations of the five islands is regarded not as a result of present day gene exchange, but as a result of the absence of any selection pressure to make the change necessary. Accordingly, the complex of five islands is divided

into four species: *D. arawakana*, St. Kitts and Guadeloupe; *D. caribiana*, Martinique; *D. antillea*, St. Lucia; and *D. nigrodunni*, Barbados.

On the other hand, the fact that six of the seven species in all of the 10 islands are potentially capable of exchanging genes through partially fertile hybrid females with at least one other species, and in the case of *arawakana* and *similis* with four other species, has little taxonomic value and only serves to show closeness of relationship which can easily be deduced from examination of the phenotypes in the first place. Also the recent evidence that a certain strain from the Everglades, Florida, of *D. acutilabella*, which is not included in the dunni subgroup, produces partially fertile hybrid females with Barbados, reduces the value of this type of fertility for taxonomic purposes. *D. acutilabella* is the pivotal species in the cardini group since Stalker (1953) has shown that it will hybridize with more cardini group species than any other form. If *acutilabella* were included in the dunni subgroup, then this category, if based completely on back-cross fertility relationships, would vanish. However, the dunni subgroup is a useful division genetically and morphologically and the line is drawn to exclude *acutilabella*.

If subspecies are to be considered, it would be more legitimate to establish them within the three species that are distributed on six islands. Every one of the six islands has its own characteristics in its behavior in crosses with other island populations. St. Thomas differs from Puerto Rico in having a J-shaped X chromosome without satellites instead of a rod with satellites. St. Kitts differs from Guadeloupe by a heterozygous short inversion in the basal left arm of chromosome II. There is no assurance, however, that the inversion does not also exist in the island of Guadeloupe. The St. Kitts Y chromosome does not give as severe a sex-ratio with other island X's as does the Guadeloupe Y. The St. Vincent X chromosome differs from the Grenada X by being semi-lethal instead of lethal in Martinique cytoplasm.

Also, the populations of four of the six islands can be differentiated by visible morphological traits. St. Thomas has a grayish abdominal ground color and Puerto Rico is more yellowish. St. Kitts females have much shorter wings than body while Guadeloupe females have only slightly shorter wings than body. St. Vincent and Grenada are similar in appearance. To name the inhabitants of these two islands as separate subspecies is an obvious act of "splitting" to any taxonomist, but it has value in showing that they are in some way different from one another.

Accordingly, Puerto Rico becomes *D. d. dunni* and St. Thomas is *D. d. thomasiensis*. Guadeloupe becomes *D. a. arawakana* and St. Kitts becomes *D. a. kittensis*. St. Vincent is *D. s. similis* and Grenada is *D. s. grenadensis*.

Most assuredly the conclusions reached in the discussion of what constitutes a subgroup, a species and a subspecies in the island populations will not be accepted by all readers, but the author has attempted to be consistent. Nature will not be pigeon-holed and therein lies the species problem.

DISCUSSION

Perhaps the best approach to a description of the genetic characteristics of the dunni subgroup is to compare them with closely related forms on the South

American continent and in Middle America. The one comparison most significant in the cardini group is that the large land masses have evolved seven species while at least eight species are confined to the West Indian islands, seven in the dunni subgroup plus *D. acutilabella*. *D. cardini* ranges from Chile to Mexico, the Greater Antilles, and some of the islands of the Lesser Antilles, and thus is considered to be a continental form. Obviously the total land mass of the islands is only a very small fraction of the mainland indicating the effects of isolation and initially small populations to promote differentiation.

There is a little information on the ecology of the cardini group, especially in respect to "animals of different kinds". In the islands, the dunni forms are the subdominant *Drosophila*, being outranked only by *D. willistoni*. Table 2 in the first publication shows a surprising amount of consistency in the frequencies of the dunni forms taken in the month of January in baited forest samples from three of the four islands: Puerto Rico 22.2% (351); St. Kitts 25.2% (515); St. Lucia 23.8% (579); Barbados 5.3% (322). The numbers in parenthesis are the total numbers of *Drosophila* collected in each sample. Also, the fact that no two dunni forms are found on the same island attests to their ecological similarities.

Two population samples from the continent, both taken in December, will suffice to illustrate that the other cardini group species are ecologically different from the island species and from one another. One baited sample from Trinidad, which is effectively a part of the South American continent, taken in a Mora forest at Sangre Grande yielded 1,136 individuals of which *D. polymorpha*, the most common of the five species in the group in Trinidad, made up 1.7%. It was the eighth species in abundance out of 29. The other sample taken in the Arima Valley of Trinidad yielded 1,273 individuals of which *polymorpha* made up 1.2%. It was the ninth most abundant species out of 15.

The dunni forms have found their niche in the islands. If interspecific competition is operating to produce more cooperative genotypes, it is less severe on the islands and is typical of island ecology in general. It is also quite possible that *willistoni* has replaced the dunni forms as the dominant species by later invasions on the islands.

The taxonomic difficulties encountered in the island types have been discussed earlier. There are no taxonomic difficulties with the cardini group on the mainland, at least in morphology of the male genitalia, Figure 1, even though almost all members look superficially very similar in size, shape and general coloring.

The unusual species relationships of *D. cardini*, *acutilabella* and *belladunni* were pointed out in the previous paper. In Florida, *cardini* and *acutilabella* are very difficult to separate; in fact, there is no reliable criterion by which the females may always be distinguished. In Jamaica, *acutilabella* and *belladunni* are morphologically very similar and the females cannot be distinguished with perfect accuracy. However, *D. cardini* can easily be identified from *belladunni*. It is the opinion of the author that both sets of species may be considered as sibling species. Apparently different genotypes are responding in a similar manner to the same environment. If it is true, then the evidence is good that the particular abdominal patterns are adaptive.

Comparison of frequencies of inversions between island and mainland forms, as far as they have been tested, show that the former are more depauperate of

inversions, as one would expect in island populations. A much better comparison of this type has been made in the West Indies for *D. willistoni* by Dobzhansky (1957). Smaller islands usually have fewer inversions.

The isolating mechanisms isolating the mainland forms, as far as they have been tested, are more rigid and efficient than those in the *dunni* subgroup. Zygotic mortality may prove to be the most common type. Sexual isolation is also prevalent (Stalker, 1953; Streisinger, 1946). Streisinger tested interspecifically five strains of *cardinoides*, two strains of *polymorpha* and one strain of *neocardini*. The species were sexually isolated from one another. Stalker found *cardinoides* and *neocardini* females sexually isolated from each other and from *cardini*, *parthenogenetica*, and *acutilabella* males. *D. cardinoides* females were inseminated by *polymorpha* males but no hybrids were produced. *D. acutilabella* females from Florida produced various numbers of hybrids with *cardinoides*, *cardini*, *parthenogenetica* and *polymorpha*. The only fertile hybrids were those with *cardinoides* males. The only species with which *acutilabella* is sympatric in these tests is *cardini* and, thus, it is not surprising to find them not as sexually isolated. The other combinations usually produced dead eggs or larvae. Table 8 shows the tests of Barbados, St. Vincent and Grenada with other members of the *cardini* group. No hybrids were produced in the majority of cases, although insemination usually took place in all crosses.

Mr. David Futch has recently hybridized many newly obtained stocks in the *cardini* group (Futch, this Bulletin). He has confirmed that *acutilabella* will readily hybridize with the majority of the other species. However, if only the tests between the six species restricted to the mainland are considered, then five tests out of 30 produced hybrids. The species on the mainland, whether sympatric or not, are genetically more isolated than those which inhabit separate islands. Four of the five tests that were fertile included the *cardinoides-procardinoides-parthenogenetica* triad.

In island populations that have no closely related forms within each island (Jamaica and Grenada are exceptions), there is no selective pressure within these species to reinforce the evolution of isolating mechanisms. Hence, those that are found take on special meaning, that is, are either by-products of selection pressure of a different kind (in this case of the physical environment) or show genetic divergence by distance along a migration route, since several examples of gametic mortality and all examples of zygotic mortality (cross-lethal genes) are correlated with the spatial relations of the islands. The initial genetic divergence in the X chromosome causing cross-lethality and semi-lethality in the male hybrids, once initiated, might tend to accumulate with increasing distance by the addition of new alleles or modifiers as differently balanced systems were created on each newly invaded island. If the migration of the *dunni* subgroup started from Grenada and went north through the islands to Guadeloupe and St. Kitts, and Barbados was colonized from St. Lucia, then the sex ratio clines are in agreement with the migration route. Puerto Rico and St. Thomas fit only the cline with Martinique females, but this appears to be fortuitous since the males from the two stocks usually throw a low frequency of hybrid males with most other island females. Puerto Rico and St. Thomas are now believed to have been colonized from either Grenada or St. Vincent because they do not own inversion

3R. Also, the fact that St. Lucia females show complete gametic mortality with Puerto Rico and St. Thomas on the one hand, and Grenada and St. Vincent on the other, fits the picture. In this sense, then, increasing genetic divergence with distance could account for the results. If the migration routes were more disjunct in the middle and southern islands, then the clines in sex ratio must be attributable to the selection of the physical environment.

Mainland (1942) demonstrated a general east-west cline in sexual isolation and fertility between the several subspecies of *D. macropsina* and of *D. subfunnebris* in continental United States. He attributes these differences to genetic differentiation by distance. Patterson and Stone (1952) discuss this and other cases in more detail.

A more direct indication that selection is acting in a general step-wise fashion is the increase in dark pigment in the southern islands. Rensch (1960) has stated that geographical variation can at times be a consequence of successive loss of alleles in the course of migrations and expansions of small peripheral populations without selection operating at all. He gives as an example the reduction from polymorphism to monomorphism in color pattern in the terrestrial snail, *Papuina*, in New Britain, as the probable course of migration is traced from the west to the eastern tip of the island, where the snail does not occur. That such events occur is undoubtedly true, but it is also probably true that marginal populations are under more extreme selection pressures and cannot afford major gene polymorphism (Carson, 1959).

If the dumni forms spread by island-hopping, as they probably did, then at each step variability was lost. That variability has been regained and rebalanced as each island population expanded is evidenced by the isolating mechanisms and the variability in phenotypes in some of the inter-island hybrids. Ernst Mayr has laid the theoretical foundation for explaining why marginal island populations are not only different from one another and from large central island or mainland populations but different in a new way (1954). Such populations are not just variations on a single theme but are qualitatively different even when the environment is ostensibly similar among the small islands. Mayr emphasizes the drastic change in the genetic environment that must take place when a few individuals or one fertile female is removed from an area of active gene flow to an area where inbreeding suddenly becomes the only means for survival. There results a sudden change in the selective value of many genes simultaneously, a veritable "genetic revolution". This may be true, but if a single female, previously fertilized by one male, is transplanted, there still remains a maximum of four alleles at each locus to give variability by crossing over and recombination.

The establishment of the dumni forms as a separate subgroup is indication that its members are distinct from the remainder of the cardini group. The long paramedian markings that extend the length of each tergite on the abdomen is a qualitatively new character. *D. belladumni* is an exception. It owns an abdominal phenotype found only in the Jamaican *D. acutilabella*. Mayr is, of course, correct in stating that a genetic revolution need not take place every time a few individuals are isolated. Among the factors which will allow it to occur at the most rapid rate, however, Mayr lists two which can be measured in the cardini group. The first is a "shift into a vacant ecological niche somewhat different from the

parental one". The previous discussion on ecology has shown this to be true. The second condition is "if the parental population was particularly variable and subject to much gene flow." The second condition could also have been true in this case.

The *cardini* group shows more externally visible phenotypic variability than any other species group in the genus. Species like *D. polymorpha*, *neomorpha* and *parthenogenetica* are polymorphic for the abdominal pattern which is controlled by one or a few sets of alleles. However, at least in the case of *polymorpha*, the marginal populations in northern South America, Trinidad and Grenada are monomorphic light. It has recently been demonstrated by Mr. Patrick Blake of this laboratory that the light alleles in Trinidad, B.W.I., and Santa Marta, Colombia, are dominant to the dark allele in at least two strains from Brazil. In most areas of Brazil, three phenotypes exist, controlled by a single pair of alleles with no dominance (da Cunha, 1949). A full report on the study will be reported later.

D. cardini and *acutilabella* possess light and dark phenotypes. Stalker (1953) reports that in *acutilabella* the pattern is apparently controlled in a simple Mendelian fashion, the heterozygote being very close to the light form. Tests with *acutilabella* in this laboratory do not confirm his findings and it was not possible to establish any rules for inheritance. Sturtevant (1921) had the same trouble with tests on *D. cardini*. His conclusions were that the conditions under which the larvae develop determined the phenotype. The problem remains unsolved.

Inheritance of the color pattern in two races of *D. neocardini* has been reported by da Cunha (1955). The situation here resembles more closely the condition in the *dunni* subgroup. The two races are morphologically distinct and uniform (not polymorphic), but the first generation hybrids are variable from one parental type to the other. However, the lighter parental type is favored in much higher frequency than the darker form (23.5% vs. 0.8% females, $n = 498$). The data may be directly compared to the variable hybrids obtained from the test JA \times GU in Table 10. The light phenotypes are 20% and the dark phenotypes (=JA) are 0.4% of the total F_1 (238). Da Cunha's conclusion is that the two races are homozygous for the gene or genes controlling pigmentation but are heterozygous for factors which act as modifiers in the hybrid genotypes. The same conclusions apply to several of the *dunni* tests. Thus, there is now living in South America a species that is variable in the same way the *dunni* species are variable. A closer scrutiny of *neocardini* is thus warranted.

Figure 1 demonstrates that the three most similar species to the island forms according to male genitalia are *polymorpha*, *neomorpha* and *neocardini*. Examination of the salivary chromosome arm 3R indicates that each of the three species is homozygous for the standard arrangement as found in the two southern islands, the two northern islands and Jamaica. Hybrids of *acutilabella* with St. Vincent and Barbados show that no inversion in 3R is present in the former case but that the 3R inversion is present with Barbados. *Acutilabella* then also has the standard gene sequence. Also, hybrids of this species with *polymorpha* show no inversion in 3R. Therefore inversion 3RB probably originated on the central islands. This is a good indication that the central islands were not the first ones to be invaded either from the north or the south and is important since the central islands from Guadeloupe to St. Lucia are apparently geologically older than the islands on

either end of the chain in the Lesser Antilles (Beard, 1949). The degree of banding differences on 3R between the three species, as compared to a photograph of the 3R of St. Vincent, showed that *neomorpha* was most distinct (many bands could not be matched), *polymorpha* was next in distinctness (several to many bands could not be matched), and that *neocardini* was strikingly similar to St. Vincent (almost band for band). The geographic origins of the three strains are: *neomorpha*, Honduras; *polymorpha*, Trinidad; and *neocardini*, Brazil. The 3R arm has not yet been compared with the other species in South America.

Futch (this Bulletin) has contributed more evidence on the relationship of the *neomorpha-polymorpha-neocardini* triad of species to one another and to the *dunni* subgroup. He has found that of all the possible crosses, *polymorpha* and *neomorpha* will produce sterile hybrids and that *polymorpha* and *neocardini* will produce at least partially fertile female hybrids with *acutilabella*. This confirms the order of relationship written above. Futch has tested all members of the *cardini* subgroup with *belladunni*, *dunni* and *arawakana*. Aside from *acutilabella* which produced hybrids with *arawakana* and *belladunni*, *neocardini* is the only other species in the *cardini* subgroup that hybridized with the *dunni* subgroup. In two tests *neocardini* males produced eight sterile females and two sterile males with *belladunni* females. This confirms our interest in *neocardini*.

It is possible that the island complex could have arisen from *neocardini* or a species with the same characteristics. The northern limit of *neocardini* may be the Amazon basin. It is not found in Colombia except at Leticia, on the Amazon, and has not been taken in Trinidad. The island founders could have been carried by floating vegetation from the Amazon, or possibly the Orinoco, to the islands. James Bond, a well-known West Indian zoogeographer, in personal communication, described the very strong current he encountered, while swimming off the island of Tobago, that came from eastern South America and headed straight for Grenada. Beard (1949) has found the vegetational affinities of the Lesser Antilles to be with both Puerto Rico and South America. In relation to the latter he says that much beach drift on the islands today is derived from the rivers of eastern South America. The few recent and fossil mammals present in the Lesser Antilles according to Simpson (1956) have their relations with the present Trinidad and eastern Venezuela fauna, not the Greater Antilles. In a sense then, this fulfills the last of Mayr's condition, "that the parental population be subject to much gene flow", in that marginal populations may not be involved.

Invasion of the Lesser Antilles from Puerto Rico is, of course, also possible, as discussed in the previous paper, but does not now seem as likely in view of the similarity in banding pattern in the 3R chromosome between *D. similis* (St. Vincent) and *D. neocardini* (Brazil).

The interpretation of a "genetic revolution" must take into account the amount of time involved for later differentiation by selection to occur, as Mayr well knew. The factors acting together, however, should produce qualitative differences.

Recent experimental studies by Dobzhansky and Pavlovsky (1957) and Dobzhansky (1960) indicate that genetic drift and natural selection may operate simultaneously, at least if the original material has more than the usual store of genetic variability. The authors have shown that replicate experimental populations initiated by a small number of founders (20) are more variable after 20

generations, for the frequencies of two different gene arrangements from different localities, then replicate populations started with 4000 flies, even though in both sets of experiments the cages are saturated after the first generation. This shows how each new founder group, arriving from a large population and expanding in numbers, can be genetically different after many generations even in the same environment. In different words, selection has a greater variety of genotypes from which to choose, in relation to initial population size, in the small founder cages. In this respect genetic drift and natural selection can operate simultaneously.

The authors have speeded up the evolutionary process by endowing the founders with more genetic variability than probably ordinarily exists in nature. The original hybrids were derived from Texas and California. Shifts in inversion frequencies do not constitute a genetic revolution, but they indicate how each new group of founders can be genetically different. There is some indication that genetic drift has operated in the dumni subgroup for the cline in abdominal pattern in the islands is not a perfect cline. The Martinique population has almost as much dark pigment as Barbados but the island is located north of St. Lucia, whose population is only slightly darker than the population from Guadeloupe.

Genetic drift must be more important in permanently small populations. Good observational data by Lowe (1955) on the vertebrate faunas of three islands in the Gulf of California of different sizes showed that the smallest island contained the highest frequencies of endemic species and subspecies, although the population sizes were not measured.

That only one major genetic revolution took place on the islands is evidenced by the basic similarity in phenotypes of most of the species, Jamaica being an exception. The similarities between the island forms and *neocardini* have been pointed out. In this sense the island species were preadapted for the type of differentiation under discussion. *D. polymorpha* inhabits Grenada, but it is still the same species.

Naturalists have observed for years that well-spread contiguous continental populations show the effects of selection only as geographical races while island populations show more drastic differences. It follows that gene flow, migration, is a very strong deterrent to selection. However, the observation that environmental selection may actually be different on islands was pointed out by Mayr (*op. cit.*) because the environment is different, especially the biotic environment. Islands have long been known to harbor unbalanced floras and faunas. The rarity of "animals of different kinds" (Andrewartha and Birch, 1958) is most evident in the Lesser Antilles. The largest number of species in the family Drosophilidae collected on any of the islands was 34 on the island of Guadeloupe in six collecting days. It is not uncommon to collect four to five times this number of species on the mainland in the same amount of time.

The consequences of these conditions, lack of migration and the absence of closely related species, are that island populations show the effects of selection by the physical environment more openly than do continental populations. The cline in phenotype in the dumni subgroup within approximately 700 miles illustrates the point. Also, the shorter wings on the flies from St. Kitts and Barbados, the two most "exposed" islands, illustrates the point. E. B. Ford and his co-

workers (1960, for review and references) are demonstrating that selection has a tight control on the number of spots on the underside of the hind wing of the Satyrine butterfly, *Maniola jurtina*. Also, the observation that on five small ecologically different islands in the Isles of Scilly the modal number of spots differs from one island to the next while on the three large islands, ecologically similar, the number of spots is the same, illustrates that selection is now operating. The spots are apparently under control of multiple factors, which makes it more difficult for genetic drift to be important.

The multitude of isolating mechanisms that have arisen in the dumni subgroup indicates that most of the island populations are genetically closed systems. That they are even more genetically closed than isolating mechanisms show is revealed by the fact that in no case has it been possible to obtain a phenotypically variable stock after several generations in any of the backcrosses even when the hybrid males are fertile after the first backcross. The great majority of hybrid combinations apparently do not work. The most extensive data concerns hybrids with St. Vincent and Guadeloupe. In several generations of mass breeding after the initial backcross to either St. Vincent or Guadeloupe, the total population cannot be distinguished from the parent to which it was backcrossed. Also, in two cases out of 10 attempts in the initial cross of SV females to GU males at least one hybrid male was fertile in each case. In both cases the hybrid stocks were carried many generations and were phenotypically like GU. When the hybrids were outcrossed to both parents, they were fertile to GU and sterile to SV. Also, the inversion 3R in both instances was homozygous for the GU type. This study will be reported in more detail at a later date.

Carson (1959) has used the term homoselection for small isolated populations. The phenomenon in the dumni subgroup may be termed interspecific homoselection, which undoubtedly is not a special property of island populations, but it is a constant property. This is in marked contrast to recent hybridization experiments with a few continental species of *Drosophila*. For instance, Mettler (1957) was able to establish a hybrid colony between *D. arizonensis* and *mojavensis* that had a combination of each species' inversions. Not all combinations worked but a new balance was maintained in some of them. Bruneau (1955) found the same phenomenon in several species of the virilis group. Carson (1959) reports that two out of four hybrid stocks in *D. bocainensis* and *parabocainensis* were interchromosomally balanced even after two and one-half years in the laboratory. A study of heterosis is supposedly not legitimate between species that show some sterility as some of the above cases do, but there is a little data for two island populations that are completely fertile. Table 14 shows, insofar as total number of offspring is a measure of heterosis, that none exists between St. Vincent and Grenada, either in mass matings or pair matings. The data were extracted from the first publication and the crosses were not made as a heterosis experiment. Each stock, originally composed of many males and females, had undergone about six generations in the laboratory before the tests were made.

The island populations then may be at a different level of fitness than many continental populations. They are not so flexible among themselves; they are under stronger environmental selection pressure since among other things there is little or no migration from distances greater than within each island to disrupt

TABLE 14

Total number of offspring of St. Vincent and Grenada and their hybrids

Two mass matings each of 20 females and 20 males	Pair matings showing average per pair
SV × SV : 2702	SV × SV : 105.9
GR × GR : 2483	GR × GR : 197.2
SV × GR : 2518	SV × GR : 92.3
GR × SV : 2754	GR × SV : 160.6

selection. The amount of time in isolation is of course important, but it is also important in the above examples from mainland populations.

That migration can disrupt selection has been abundantly illustrated by Brcic (1954), Wallace (1955) and Vetukhiv (1957, and earlier) for large continental populations such as *D. melanogaster* and *D. pseudoobscura*. The interpopulation hybrid heterosis, demonstrated by these authors, is usually lost in the next generation because of crossingover and recombination in the original hybrids. The influx of new genotypes by migration into a locally coadapted gene pool undoubtedly produces more variability but at the same time breaks up the integrated systems in all probability in proportion to the rate of migration.

Wasserman (1960) has excellent cytological data that the 12 species in the mulleri complex of the repleta group initiated their divergence as a mosaic of small semi-isolated desert populations. The unusual sharing of six inversions between the 12 species has led Wasserman to propose an important function of inversion differences between populations, *i.e.*, to reduce the effects of ill-adapted migrants by suppressing recombination.

The lack of heterosis between St. Vincent and Grenada is more similar to the report of Stone *et al.* (1954) for small isolated populations of *D. novamexicana* and *D. hydei* in the southwest. Stone measured egg production and egg hatch in interpopulation hybrids and found that egg hatch was improved, but there was no heterosis for total egg production in comparison to the controls. Also later generations did not fall below the parentals in egg hatch. Stone concluded that the egg-laying pattern is at its optimum in these small inbred populations, thus making it difficult to improve by outcrossing. The present author has collected *novamexicana* as well as the island flies and knows first hand that the latter have far larger populations. In fact, the largest collection of *novamexicana* amounted to only 58 individuals in several days' trapping. One, however, cannot measure the degree of homozygosity in each population so readily. St. Vincent and Grenada are two of the island types that give intermediate and uniform hybrid color patterns to most other islands. In this sense they are more homozygous than Guadeloupe for instance. Even so, they are no doubt more heterozygous than the extremely small, shrunken, isolated populations of *novamexicana*. Different kinds of genes and balanced systems are effective under different conditions. The absence of heterosis for egg production in both types of populations, so different in history and structure, may have basically the same underlying cause. They are under more strict control of natural selection since both types of populations are isolated populations.

There is one direct measure of the results of natural selection in island popula-

tions of various sizes. Stone *et al.* (1957) and Stone and Wilson (1958) measured the fertility, fecundity and viability of *D. ananassae* from four of the Marshall Islands and Ponape by inbreeding, crossbreeding and doublecrossing the progeny from three successive years of collecting (1955 to 1957) after thermonuclear tests on one of the island atolls (Bikini in 1954 and other lesser tests in 1956). Although the measurements and times of collecting were not as favorable as desired, there are some very dramatic recoveries in viability (egg development) within one year. Rongelap atoll, which received fallout, changed from 45 per cent (1955) to 83.7 per cent (1956) egg development. Bikini atoll, where the tests were made, changed from an average of 46.1 to 63.4 per cent egg development. The control islands did not change this much. Interestingly enough, egg production between the three years did not change in any population but inter-island hybrids did show a little improvement in two out of the three years.

It appears that the island populations in the cardini group have been drastically rebalanced only once, at the initial invasion from the mainland. The best evidence for this is the presence of a species on more than one island. For instance, St. Thomas was probably colonized from Puerto Rico (because its metaphase is more different than Puerto Rico's in relation to other dumni forms) but St. Thomas is completely fertile with Puerto Rico. The interfertility also between St. Kitts and Guadeloupe, St. Vincent and Grenada illustrates that an invasion from one island to an uninhabited island does not necessarily imply a drastic genetic rebalance on the part of the invader. Therefore, the populations that *are* sterile between themselves must have had more time to become different, barring differences in island ecologies.

The fact that no two species in the dumni subgroup exist on the same island may be explained in several ways. Either migration between islands is taking place and interspecific homoselection occurs for the phenotype of the island being invaded in each case or the ecological properties of each island population are so similar that competition would not allow the invaders to get a foothold. Perhaps both phenomena are at work, but in the case of Martinique, ecological barriers seem to explain the situation, since this island is sterile to all other island species and thus interspecific homoselection could not occur. The situation is in contrast to the secondary island invasions believed to have occurred in the evolution of the drepaniids in the Hawaiian Archipelago (Amadon, 1950) and the geospized finches in the Galapagos Islands (Lack, 1947). Both authors agree that most of the species initiated their divergence on separate islands even though at present there are 15 species of honeycreepers on Hawaii itself and 10 species of Darwin's finches on James, Albermarle and Indefatigable.

It is also true that insects in general are more sedentary than birds. Zimmerman (1948), in his analysis of the insects of the Hawaiian Islands, has recorded that most of the species endemic to the archipelago are restricted to only one island or small part of one island. Of the 222 endemic species of carabid beetles, only five occur on more than one island. Eighty per cent of the anobiid beetles (140 species) are confined to one island. Zimmerman believes the island having the largest number of species of a particular group is the one in which the original colonization occurred. The restricted microenvironments of many of the insects of these islands accounts for the secondary isolation necessary for divergence.

The *Drosophila* under study in the Antilles have a much greater ecological latitude for they can be found in domestic as well as undisturbed sites in many areas of each island.

There is a little evidence that the presence of closely related species restricts genetic variability. Da Cunha *et al.* (1959 and earlier) have found that the frequencies of inversions in *D. willistori* are less in areas where several or all of the three other sibling species are present, especially in high proportions, than in ecologically similar areas, where they are absent or in low proportions. Ives (1954) suggested that the reason for the drop in frequencies of homozygous lethal second chromosomes from 65.3% (337 chromosomes) to 51.1% (131 chromosomes) over a period of nine years in *D. melanogaster* in Florida may have been caused by the observed rise in frequency of the sibling species, *D. simulans*, from 15% (300 males) to 86% (990 flies). The dumni forms have no sibling species with which to compete in any of the islands except Jamaica allowing in part a greater genetic, and thus ecological, latitude for each island type. This in turn supports the thesis that each form is restricted to its own island because of ecological barriers.

Incidentally, the drosophilid fauna in the Hawaiian Islands is extraordinarily rich. Zimmerman (1958) has estimated perhaps 300 species may eventually be described by Hardy and others, and rightly challenges: "Where else has such a drosophilid fauna developed?" In August, 1958, in Boquete, Chiriqui Province of Panama, Dr. Marvin Wasserman and the author collected 230 species in eight collecting days in an area of about two square miles, an area smaller than any of the main islands in Hawaii.

It is believed that the study of island populations of *Drosophila* has disclosed the relative importance of two major types of selection pressure, among many, that lead to differentiation. The first type is selection by the physical environment, that is, temperature, humidity, solar radiation, etc., the type of selection that produces differences in relation to the geography of the landscape inhabited by a similar group of organisms. Possible examples of such selection have been discussed previously, but the cline in phenotype is the best example. The cline in sex-ratio may also be an example. The examples do not appear to be fortuitous because of their regularity. The second type of selection pressure is that caused by the presence of closely related species. This type is absent on most of the islands and imparts to the populations certain characteristics usually otherwise present in species on the mainland. The first is the complete lack of sexual isolation between island populations. The second is the similarity in male genitalia among four genetic species in the five central islands. The third is the apparent similarity in ecology in most of the island populations. If the three latter characteristics are present solely because of recent habitation of the islands by the dumni subgroup, then it not only strengthens the thesis that physical environmental selection is operating but that it is working at a rapid pace.

Anderson (1960) has been able to isolate other selective forces operating on island populations of salamanders in the San Francisco Bay region. The lack of predators and competing species has allowed these forms to build up dense populations which resulted in reproductive inhibition and this in turn permits new modes of selection to operate by regulating population size.

Parenthetically, the role of peripheral populations in originating really new characters (evolutionary novelties) has recently been emphasized by Carson and Mayr. Oceanic islands harbor numerous examples of a radical change in function and sometimes structure. The genus *Drosophila* is not without representation since an entirely new ecological niche has recently been discovered (verifying an old museum label) for a species inhabiting Mona Island, west of Puerto Rico. *Drosophila carcinophila* is an ordinary-looking fly which apparently lives its entire life cycle on a cave-inhabiting land crab. The unusual story has been reported by Wheeler, 1960.

SUMMARY

Ten islands in the West Indies harbor seven closely related species and three of the species are newly described. The complex of species is a natural one and is known as the dumni subgroup of the cardini species group of *Drosophila*. Three two-island groups contain members which can be distinguished usually morphologically and always genetically in tests to other island strains. They are described as subspecies.

The similarities and differences between each island population are described and discussed on a genetic and morphologic basis. Comparisons are made with the cardini group species in Middle and South America. The original differentiation of the dumni subgroup can be explained by the thesis presented by Ernst Mayr that the change in the genetic environment in founder individuals and the subsequent different kind of selection pressure on island populations promotes novel differences. Some of the present-day differences between the island strains are believed to result from selection pressure of the physical environment. Many of the similarities are believed to result from the absence of closely related species.

The island populations are characterized as large, fairly heterogeneous but closed genetic systems. The majority of interspecies crosses produce sterile males. The one intersubspecies cross tested gave no heterosis for total number of progeny. The results are compared to several contrasting types of continental and other island *Drosophila* populations.

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This paper is presented in the memory of Professor John Thomas Patterson. Just 10 years ago in June, Dr. Patterson sent his last fledgling graduate student on his maiden collecting trip for *Drosophila*. Then, as now, the wealth of material contained a high potential for understanding organic diversity, reward enough for anyone, as he well knew.

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