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Author(s): Alan T. Ohta

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COADAPTIVE GENE COMPLEXES IN INCIPIENT SPECIES OF
HAWAIIAN *DROSOPHILA*

ALAN T. OHTA

Department of Genetics, University of Hawaii, Honolulu, Hawaii 96822

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The concept of coadaptation was first defined by Dobzhansky (1948; 1950), but in the broader context in which it is presently used it is probably best defined by Wallace (1968, p. 305): "Genes are said to be coadapted if high fitness depends upon specific interactions between them." The coadaptation of alleles into tightly linked systems was demonstrated in *Drosophila pseudoobscura* and *D. persimilis* by Prakash and Lewontin (1968; 1971). Their results showed that different chromosomal inversions had different allelic frequencies, as well as different alleles, associated with them. Allard and his coworkers have presented evidence for coadaptation in both a wild and a cultivated species of plant and have demonstrated that the coadaptation has occurred in response to environmental parameters (Allard et al. 1972; Clegg et al. 1972). Coadaptation has also been shown to have evolved in response to a given set of genetic environments (Hartl 1977; Kuhn 1971; Templeton et al. 1976).

This study deals with the detailed character of the postmating isolation present between individuals from six populations of Hawaiian *Drosophila* using hybridization tests among stocks representing each population. The pattern of postmating isolation observed in these tests indicates that two different sets of coadaptive gene complexes have evolved among five of these populations. Furthermore, it appears that the coadaptation has evolved in response to sharp differences in the breeding site ecology of these populations.

Approximately 100 species of Hawaiian *Drosophila* form a close phylogenetic unit which is commonly called the "picture-winged" species group (Carson et al. 1970). Nearly all of these species are narrow endemics and are found on a single island or volcano only. The subject of this paper, *D. grimshawi* Oldenberg, is a conspicuous exception; the six populations used in this study are derived from five of the six accessible major islands of Hawaii (i.e., Kauai, Oahu, Maui, Molokai, and Lanai). The sixth island, Hawaii, is the habitat of a very *grimshawi*-like population which has nevertheless been judged to be a distinct but very closely related species, *D. pullipes* Hardy and Kaneshiro. The only external characters observed which distinguish between these species are the coloration of the legs and pleurae; those of *D. pullipes* are black, those of *D. grimshawi* yellow (Hardy and Kaneshiro 1972).

Cytological studies (Carson and Stalker 1968; Carson and Sato 1969; Carson et al. 1970) showed that the polytene chromosomes of all of the *D. grimshawi* populations and *D. pullipes* were homosequential, all of them having the standard chromosomal sequence. However, most *D. grimshawi* populations from the Maui complex of islands (Maui, Molokai, and Lanai) display a polymorphic inversion sequence in chromosome 4 (inversion 4a), whereas the other *D. grimshawi* populations and *D. pullipes* are monomorphic for the standard chromosomal sequence. No metaphase chromosome differences are known among any of these populations. Thus Clayton (1971) and Clayton et al. (1972) have reported that *D. grimshawi* and *D. pullipes* display a simple five rod and one dot haploid chromosomal complement. There is no evidence for the existence of differential blocks of heterochromatin.

Montgomery (1975) reared the adults of *D. grimshawi* and *D. pullipes* from field collected substrates containing *Drosophila* larvae. He discovered an ecological difference among the populations. Maui complex *D. grimshawi* were reared from substrates representing 12 different plant families including 10 endemic and two introduced species. In contrast, *D. grimshawi* from Oahu and Kauai and *D. pullipes* from Hawaii were reared only from the rotting bark of *Wikstroemia* trees (Hawaiian name Akia). Thus, *D. grimshawi* from the Maui complex are considered to be "generalists" and *D. grimshawi* from Oahu and Kauai and *D. pullipes* are considered to be "specialists" in their ovipositional behavior.

MATERIALS AND METHODS

All possible reciprocal crosses were made between four stocks; three of *D. grimshawi* (Oahu, R87G α ; Maui, G1; Molokai, R83B13) and one *D. pullipes* (Hawaii, R13Q). Certain crosses involving the Kauai (T49T120) stock were also made but the Lanai stock (T59T20) was not used in this study.

Control and experimental crosses were made in a similar manner using 3–4 wk old males and females, which were aged separately. Thirty pair matings were made for each reciprocal combination in 30 cm³ shell vials (25 mm \times 95 mm) which were changed at weekly intervals. Each vial contained 2 ml of "yeastless" Wheeler-Clayton media (Wheeler and Clayton 1965) and a folded Tomac kerchief soaked in *Clermontia* extract. The extract of *Clermontia*, an endemic Hawaiian genus of the family Lobeliaceae, elicits oviposition in many Hawaiian *Drosophila* and inhibits fungal growth. Specialist females will oviposit only when a small piece of properly rotted *Wikstroemia* bark is added with the *Clermontia* extract.

The males of each pair were removed after 3 wk, dissected, and checked for motile sperm. If either member of the pair died during this interval, the vial(s) was discarded and a new pair started. The females were allowed to oviposit for five more weeks before dissection to check for insemination.

The vials containing eggs were held for 1 wk and examined for larvae. The larvae were allowed to develop in two vials of up to nine mated pairs per cross. After 3–4 wk these larvae were placed in glass jars about one-eighth full of moistened sterilized sand into which the larvae burrowed and pupated.

The F₁ adults eclosed after 3–4 wk and were counted and sexed. The sexes were

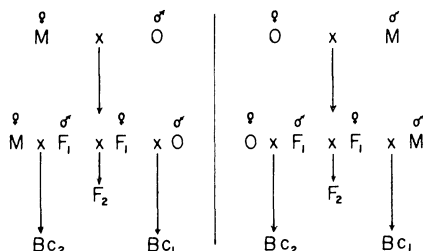


FIG. 1.—Outline of the hybridization procedure. M = Maui stock; O = Oahu stock.

aged separately for 4 wk, which is the approximate time required for 100% of the males to attain sexual maturity. These adults were then used for F_1 and backcrosses and the remainder were dissected and scored for sperm motility and maturity of the ovaries.

Crosses of F_1 adults consisted of 30 pair matings of: F_1 males crossed with F_1 females, F_1 males crossed with females of the parental female stock, and F_1 females crossed with males of the parental male stock (fig. 1). Progeny from the F_1 and backcrosses were obtained using the same procedure described above. The adults were again aged separately by sex and the flies dissected after 4 wk.

Up to 200 adults of each sex were dissected per cross. These were obtained from up to nine different pair matings of the same cross. Therefore an average of 20–25 flies were dissected per pair, which was an insufficient sample for tests of homogeneity between pairs within a cross.

The frequencies of males with motile sperm and females with mature ovaries were calculated within each cross; $R \times C$ contingency χ^2 's were calculated within each set of crosses, one set constituting the parental cross and the subsequent set F_1 and two backcrosses. If a significant χ^2 value resulted, a pairwise comparison was made to determine which of the crosses within the set had contributed to the significant deviation.

RESULTS

For convenience, the crosses completed are divided into two categories: the crosses made between ecologically similar stocks (i.e., specialist \times specialist, generalist \times generalist) and those between ecologically differentiated stocks (i.e., generalist \times specialist). To simplify the nomenclature, stocks from different islands are represented by letters; H = Hawaii, K = Kauai, M = Maui, R = Molokai, O = Oahu. All crosses are reported with the maternal parent first and the paternal parent second. In F_1 designations the first letter refers to the maternal and the second to the paternal parent. Thus, an F_1 progeny of the cross Oahu $\text{♀} \times$ Hawaii ♂ (O \times H) is designated $F_1\text{OH}$ and the F_1 progeny of the reciprocal cross (H \times O) $F_1\text{HO}$.

Tables 1 and 2 present the results of inter- and intrastock crosses between ecologically similar stocks, and tables 3 and 4 present the results of those crosses between ecologically differentiated stocks. Some crosses utilizing F_1 's fell short

HYBRIDIZATION OF ECOLOGICALLY SIMILAR POPULATIONS

Cross	No. of Pairs	No. P ₁ ♂♂ with Motile Sperm	No. P ₁ ♀♀ Inseminated	No. Pairs Producing Larvae	n	% ♂ Progeny with Motile Sperm
R × R	30	28	26	25	116	90.5**
F ₁ RR × F ₁ RR	30	30	28	27	135	98.5**
M × M	30	30	28	26	87	96.6
F ₁ MM × F ₁ MM	30	28	18	16	23	100.0
H × H	30	28	28	25	49	91.8
F ₁ HH × F ₁ HH	30	28	28	26	40	97.5
O × O	30	30	28	22	48	93.8
F ₁ OO × F ₁ OO	30	28	20	12	22	90.9
M × R	30	28	23	20	197	97.9
F ₁ MR × F ₁ MR	30	30	30	29	179	98.3
F ₁ MR × R	30	29	28	27	198	99.0
M × F ₁ MR	30	30	30	30	174	99.4
R × M	30	28	22	22	177	93.2*
F ₁ RM × F ₁ RM	30	29	28	27	175	95.4*
F ₁ RM × M	30	25	24	24	167	99.4*
R × F ₁ RM	30	24	23	23	178	94.9*
H × O	30	30	23	10	17	0
F ₁ HO × F ₁ HO	8	0	0	0
F ₁ HO × O	5	5	5	5	8	12.5
H × F ₁ HO	11	0	0	0
O × H	30	28	14	12	116	6.9**
F ₁ OH × F ₁ OH	30	0	0	0
F ₁ OH × H	30	30	17	4	6	0**
O × F ₁ OH	30	8	8	3	8	87.5**
K × O	30	29	26	18	152	98.1
F ₁ KO × F ₁ KO	30	30	26	22	147	96.6
F ₁ KO × O	30	29	20	17	87	95.4
K × F ₁ KO	30	30	15	6	24	100.0
O × K	30	29	25	15	74	98.7
F ₁ OK × F ₁ OK	30	29	26	25	128	99.2
F ₁ OK × K	30	28	27	23	137	98.5
O × F ₁ OK	30	30	30	7	83	100.0

NOTE.—H = Hawaii; K = Kauai; M = Maui; O = Oahu; R = Molakai; ... = no data; P₁ = flies used in pair matings; n = no. of male progeny dissected. For details see text.

* P < .05.
** P < .01.

TABLE 2

PAIRWISE COMPARISONS OF CROSSES WITHIN SETS OF CROSSES FROM TABLE 1 SHOWING SIGNIFICANT DEVIATIONS IN THE PERCENTAGE OF MALE SPERM MOTILITY

Comparisons	χ^2	df
Set RR	8.13	1**
RR vs. F ₁	8.13	1**
Set RM	8.47	3*
RM vs. F ₁80	1
RM vs. Bc ₁	9.03	1**
RM vs. Bc ₂47	1
F ₁ vs. Bc ₁	5.26	1*
F ₁ vs. Bc ₂05	1
Bc ₁ vs. Bc ₂	6.08	1*
Set OH	48.46	2**
OH vs. Bc ₁44	1
OH vs. Bc ₂	45.73	1**
Bc ₁ vs. Bc ₂	10.50	1**

NOTE.—Bc₁ = F₁ ♀ × parental stock ♂; Bc₂ = parental stock ♀ × F₁ ♂.* $P < .05$.** $P < .01$.

of the normal 30 pair matings. This was caused by the low number of progeny produced in the parental cross.

The number of P₁ males with motile sperm indicates the proportion of unsuccessful matings due to male sterility. For example, in cross F₁HO × F₁HO the F₁ males lack motile sperm and therefore produce no offspring, although the females appear to be fertile and capable of backcrossing. Sperm motility is used to indicate fertility, a relationship that has been confirmed in these flies.

The differences observed between the number of inseminated females and the number of fertile males provides a very rough indication of the amount of pre-mating isolation existing among the stocks. A more precise study of the degree of pre-mating isolation, using the male-choice technique, was completed and the data reported elsewhere (Ohta 1978).

Also, some differences are present between the number of inseminated females and the number of females producing larvae. In the majority of cases this stemmed from a refusal of oviposition by the female, the reason for which is unclear. However, eggs failed to develop in crosses H × M, H × O, F₁HO × O, F₁OH × H, O × F₁OH, H × R, and H × F₁RH (in seven, 10, one, four, two, four, and three pairs, respectively). More than 20 eggs were observed in vials after the male of each pair had been removed, but no larvae developed. Antigenic reactions in the females were discounted when motile sperm was found in the spermathecae of all the females and all females were observed to be fully inseminated.

The n number associated with the male sperm motility data represents the number of male progeny which were dissected for each cross. The asterisks show those sets of crosses for which a significant χ^2 value is obtained. The pairwise comparisons within a set of crosses showing significance are presented in tables 2 and 4 for tables 1 and 3, respectively.

TABLE 3
HYBRIDIZATION OF ECOLOGICALLY DIFFERENTIATED POPULATIONS

Cross	No. of Pairs	No. P ₁ ♂♂ with Motile Sperm	No. P ₁ ♀♀ Inseminated	No. Pairs Producing Larvae	n	% ♂ Progeny with Motile Sperm
O × M	30	29	8	5	12	100.0**
F ₁ OM × F ₁ OM	30	20	17	18	62	21.0**
F ₁ OM × M	30	30	27	27	137	45.3**
O × F ₁ OM	42	34	23	7	44	77.3**
M × O	30	30	30	30	173	94.2**
F ₁ MO × F ₁ MO	30	29	28	27	43	27.9**
F ₁ MO × O	30	30	29	27	91	46.2**
M × F ₁ MO	30	29	22	17	145	88.3**
R × O	30	30	24	24	190	90.0**
F ₁ RO × F ₁ RO	30	29	29	29	48	50.0**
F ₁ RO × O	30	29	26	24	105	59.1**
R × F ₁ RO	30	27	26	26	195	89.7**
O × R	30	30	15	12	82	93.9**
F ₁ OR × F ₁ OR	30	29	28	28	123	43.1**
F ₁ OR × R	30	30	29	29	155	62.6**
O × F ₁ OR	30	27	22	13	37	86.5**
H × M	30	30	22	9	4	0
F ₁ HM × F ₁ HM
F ₁ HM × M	5	4	4	3	53	37.7
H × F ₁ HM	1	0	0	0
M × H	30	29	15	11	108	0**
F ₁ MH × F ₁ MH	30	0	0	0
F ₁ MH × H	30	29	20	20	46	19.6**
M × F ₁ MH	30	0	0	0
R × H	30	27	14	14	133	69.2**
F ₁ RH × F ₁ RH	30	24	21	19	20	35.0**
F ₁ RH × H	30	27	26	25	59	32.2**
R × F ₁ RH	30	21	15	12	50	66.0**
H × R	30	27	10	5	3	0
F ₁ HR × F ₁ HR
F ₁ HR × R	4	4	3	3	28	35.7
H × F ₁ HR

NOTE.—H = Hawaii; M = Maui; O = Oahu; R = Molokai; ... no data; P₁ = flies used in pair matings; n = no. of male progeny dissected. For details, see text. ** P < .05. * P < .01.

TABLE 4

PAIRWISE COMPARISONS OF CROSSES WITHIN SETS OF CROSSES FROM TABLE 3 SHOWING SIGNIFICANT DEVIATION IN THE PERCENTAGES OF MALE SPERM MOTILITY

Comparisons	χ^2	df
Set OM	46.69	3**
OM vs. F ₁	28.07	1**
OM vs. Bc ₁	13.23	1**
OM vs. Bc ₂	3.32	1
F ₁ vs. Bc ₁	10.72	1**
F ₁ vs. Bc ₂	33.06	1**
Bc ₁ vs. Bc ₂	13.71	1**
Set MO	143.76	3**
MO vs. F ₁	98.48	1**
MO vs. Bc ₁	79.39	1**
MO vs. Bc ₂	3.59	1
F ₁ vs. Bc ₁	4.04	1*
F ₁ vs. Bc ₂	63.57	1**
Bc ₁ vs. Bc ₂	22.16	1**
Set RO	79.83	3**
RO vs. F ₁	41.42	1**
RO vs. Bc ₁	39.03	1**
RO vs. Bc ₂	.01	1
F ₁ vs. Bc ₁	1.01	1
F ₁ vs. Bc ₂	40.75	1**
Bc ₁ vs. Bc ₂	38.78	1**
Set OR	64.17	3**
OR vs. F ₁	54.75	1**
OR vs. Bc ₁	26.96	1**
OR vs. Bc ₂	1.82	1
F ₁ vs. Bc ₁	10.49	1**
F ₁ vs. Bc ₂	21.51	1**
Bc ₁ vs. Bc ₂	7.74	1**
Set MH	22.44	1**
MH vs. Bc ₁	22.44	1**
Set RH	27.77	3**
RH vs. F ₁	10.55	1**
RH vs. Bc ₁	21.92	1**
RH vs. Bc ₂	1.07	1
F ₁ vs. Bc ₁	.05	1
F ₁ vs. Bc ₂	5.61	1*
Bc ₁ vs. Bc ₂	12.39	1**

NOTE.—Bc₁ = F₁ ♀ × parental stock ♂; Bc₂ = parental stock ♀ × F₁ ♂.* $P < .05$.** $P < .01$.

Female ovary maturation data are omitted in the tables because only a slight reduction, if any, was noted in all crosses. This is consistent with Craddock's (1974) finding that hybrid sterility was primarily exhibited in the male, and not the female, hybrids of closely related Hawaiian picture-winged *Drosophila* species.

All intra- and interstock crosses and subsequent F₁ and backcrosses between ecologically similar *D. grimshawi* stocks produced completely fertile male progeny (table 1, fig. 2). The significant differences observed in the males of sets RR and RM are due to an increase in fertility of the F₂ and Bc₁ male progeny,

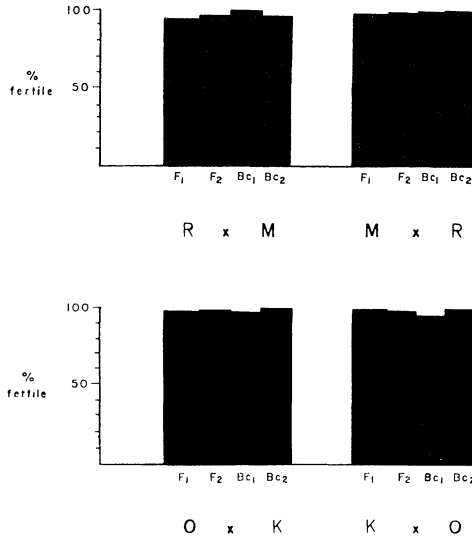


FIG. 2.—Hybridization of ecologically similar populations. Columns represent the percentage of fertile males among F_1 , F_2 , and backcross progeny in intraspecific hybridizations of *Drosophila grimshawi*; the first letter of each cross represents the females and the second the males used in the hybridizations; M = Maui; R = Molokai; O = Oahu; K = Kauai; Bc_1 = male progeny of $F_1 \text{ } \varnothing \times \text{parental stock } \delta$; Bc_2 = male progeny of parental stock $\varnothing \times F_1 \delta$.

respectively. The crosses of Oahu *D. grimshawi* with *D. pullipes* (Hawaii) showed extremely reduced fertility or complete sterility in the F_1 males, although the F_1 females appeared normal. However, backcrossing the few fertile F_1 males with parental females ($O \times F_1OH$) restored fertility in the male progeny.

Crosses of *D. pullipes* with ecologically differentiated *D. grimshawi* (table 3) again produced completely sterile F_1 males except in cross $R \times H$, which produced approximately 70% fertile F_1 males. Here again, fertility is partially restored in the backcross male progeny of F_1 males with parental females. Crosses involving *D. pullipes* females consistently produced few progeny (including $H \times O$ in table 1). This result is probably due to larval mortality. In these crosses oviposition and first instar larval development appeared to proceed normally. However, as the larvae developed they appeared to move very sluggishly through the medium and most did not survive through the third instar larval stage. The few larvae which were able to survive and pupate developed into adults, but all of the males were sterile.

The remaining crosses in table 3 ($R \times O$, $O \times R$, $M \times O$, $O \times M$) produced completely fertile F_1 males and females with hybrid breakdown occurring in the F_2 and backcross males (fig. 3). The F_1 males of each cross are fully fertile (first bar), while there is a progression in the degree of breakdown of the males in subsequent crosses. The reduction in fertility is greatest in the F_2 males (second bar), significantly less (table 4) in the male progeny of the backcross to the parental males (third bar), and absent in the male progeny of the backcross to the parental females (fourth bar).

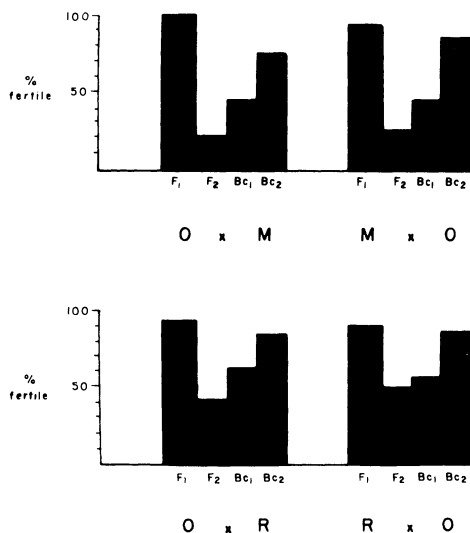


FIG. 3.—Hybridization of ecologically different populations. Columns represent the percentage of fertile males among F_1 , F_2 , and backcross progenies in intraspecific hybridizations of *Drosophila grimshawi*; the first letter of each cross represents the females and the second the males used in the hybridizations; M = Maui; R = Molokai; O = Oahu; Bc₁ = male progeny of F_1 ♀ × parental stock ♂; Bc₂ = male progeny of parental stock ♀ × F_1 ♂.

DISCUSSION

When ecologically similar populations of *Drosophila grimshawi* are crossed, F_1 's are fertile, F_2 's and backcrosses show a high degree of compatibility and no breakdown in fertility is observed (fig. 2). Such a statement, of course, does not apply to the crosses involving *D. pullipes* of Hawaii, which is more strongly differentiated than those populations considered to be conspecific with *D. grimshawi*.

The full compatibility observed in crosses of ecologically similar populations are not observed when ecologically different populations are crossed. Although F_1 males show full fertility, a striking feature of these crosses is that considerable breakdown, manifested by male sterility, occurs in the F_2 's. This also occurs in backcrosses in which the F_1 hybrid female is crossed back to males of her parental type. These effects are not observed in crosses between ecologically similar populations. Further, fertility breakdown does not occur when the F_1 male is crossed back to his maternal type. The following discussion interprets these interesting relationships.

These differences are considered to be due to the existence of different genetic coadaptations in the ecologically different populations. Thus, Brncic (1954) crossed strains of *D. pseudoobscura* from different geographical areas and obtained fitness values for each hybrid type. He showed that flies with two intact chromosomes from different localities gave the highest fitness. These were followed by flies with two intact chromosomes from the same locality, those with one

intact and one recombined chromosome, and those with two recombined chromosomes, which had the lowest fitness values. This progressive decrease in fitness was attributed to recombination breaking up the geographically related coadaptive gene complexes. Assuming that no crossing-over occurs in Hawaiian *Drosophila* males, as is the case for most *Drosophila*, then these data can be interpreted in much the same way.

Whenever F_1 females were used in crosses, fertility in the male progeny was significantly reduced. This effect may be attributed to the recombinational breakup of both linked and unlinked coadapted genes in the gametes of the female parent. The increase in fertility of the Bc_1 backcross males over the F_2 male progeny is probably caused by the "intact" set of chromosomes inherited by the Bc_1 backcross males from their parental parent. The Bc_2 backcross produced fully, or nearly fully, fertile male progeny, and this is attributed to the absence of recombination in the parental F_1 males. The slight reduction in fertility in this backcross compared with that of the F_1 males was nonsignificant in all sets of crosses (table 4). However, the consistency of the reduction in fertility in all four sets and their χ^2 values indicate that if a larger sample is taken statistical significance may result. In this case the reduced fertility would probably be caused by the breakup of nonlinked coadapted genes. The F_1 hybrid males of all sets of crosses showed complete fertility because of the two "intact" sets of coadapted gene complexes obtained from its stock parents. Therefore, it appears that the ecological differentiation observed within *D. grimshawi* caused the genetic divergence of the generalist from the specialist populations (or vice versa, although other evidence indicates that the generalist evolved from the specialist; Ohta 1978) which has led to hybrid breakdown and the formation of incipient species.

The higher fertility observed in the F_2 and Bc_1 backcross males of the Molokai and Oahu crosses as opposed to those of the Maui and Oahu crosses may be due to the 4a inversion sequence, present in the Molokai stock, preventing the breakup of coadapted genes in this region. If this is true, then some genes controlling male fertility should be found in this inversion. The Molokai stock was found to contain the 4a inversion as well as the standard 4 chromosome sequence, and before the hybridizations were started an effort was made to select for a homozygous standard 4 chromosome line from this stock, but all efforts failed. Therefore, this stock was maintained with the inversion polymorphism.

Certain of the facts appearing in the crosses involving *D. pullipes* of Hawaii deserve comment. The fertility observed in the F_1 hybrids of the $R \times H$ cross may be caused by the inversion polymorphism which persisted in the Molokai stock. The occurrence of these fertile F_1 hybrids, the persistence of the inversion polymorphism in the Molokai stock, and the association of the inversion with the increased fertility described above deserves further investigation.

Developmental failure of the eggs in the crosses previously noted may be due to the nonfertilization of the eggs. Patterson and Stone (1952) reported that the sperm of some species of *Drosophila* were unable to penetrate the membrane of the eggs of another species. Alternatively, the fertilized eggs may have died. This seems to be a more plausible explanation since all of the crosses involved are either with, or

the result of, crosses with *D. pullipes*, and this species is seen to decrease viability in some crosses.

SUMMARY

The degree of postmating isolation existing among allopatric populations belonging to two species of endemic Hawaiian *Drosophila* was investigated. *Drosophila grimshawi* is unusual among picture-winged Hawaiian *Drosophila* in that it is widely distributed in the archipelago with populations on the islands of Kauai, Oahu, Lanai, Molokai, and Maui. The second species, *D. pullipes*, is very closely related and is confined to the island of Hawaii. Kauai and Oahu *D. grimshawi* and *D. pullipes* are known to be ovipositional specialists, utilizing only one genus of plant. Populations of *D. grimshawi* from Lanai, Molokai, and Maui are generalists and oviposit on several plants of a number of different families.

Hybridizations among stocks representing four of the six allopatric populations (i.e., Oahu, Maui, and Molokai *D. grimshawi* and *D. pullipes*) were completed in all reciprocal combinations; and, in addition, Kauai *D. grimshawi* was crossed to Oahu *D. grimshawi*. The F_1 hybrid progeny were used to produce an F_2 and backcrosses to parental males and females.

Although crosses between ecologically different *D. grimshawi* stocks resulted in full F_1 male fertility, breakdown was observed in the F_2 and backcross males. This was not observed in crosses between ecologically similar populations. Fertility breakdown in these intraspecific crosses was consistently greatest in the F_2 's, followed by the backcross to the parental males, and least in the backcross to the parental females. This progressive breakdown, based on the assumption of no crossover recombination in Hawaiian *Drosophila* males, was attributed to the breakup of two differing sets of coadaptive gene complexes. It is further suggested that the coadaptive gene complexes of populations with the same adaptive peaks are identical or at least similar enough so as not to have yet evolved reproductive isolation.

The *D. pullipes* stock was found to produce completely sterile F_1 males when hybridized with all stocks except Molokai, in which approximately 70% of the F_1 males were fertile. Added to the hybrid sterility, crosses involving *D. pullipes* females showed a reduction in hybrid viability.

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