

An analysis of nonrandom mating between geographic strains
of the housefly, Musca domestica L., from
Western United States

A Thesis
Presented to
the Faculty of the Department of Biology
University of Houston

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
Kay T. Kimball
May 1976

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Abstract

The geographic variation in components of mating behavior of the housefly, Musca domestica L., was studied. Specifically, determinations were made as to whether differences in mating success among geographic strains could possibly isolate natural populations by limiting gene flow within the species. It was found that mating success for males varied significantly among these strains. While this did not prevent random mating in every case, it would decrease gene flow from southern into northern populations. Assortative mating and the "minority effect" were found to be not significant.

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Introduction

Geographic variation in morphological characters has been reported in many species including some plants, birds, fish, mammals, and quite often in insects (Mayr, 1963). While slight differences in morphology may not prevent mating among individuals from allopatric populations, behavioral and physiological differences may be the by-product of this genetic divergence. Thus, in the course of genetic divergence among geographic strains, many species have undergone divergence in mating preferences, including the Arctic skua (O'Donald, 1959), the white-throated sparrow (Lowther, 1961), the domestic fowl (Lill and Wood-Gush, 1965), and nineteen species of *Drosophila* (see Anderson and Ehrman, 1969, for review).

The deviations from random mating can occur in several ways: homogamic or assortative mating (preference for one's own genotype), heterogamic or disassortative mating (preference for another genotype), increased male or female vigor (increased numbers of matings for one or both sexes of a strain), and frequency dependent mating (an advantage in mating for minority males). This latter process increases the fitness of a genotype when it is rare and decreases it when it is in the majority. Petit (1958) was first to report frequency

dependent mating success in the species Drosophila melanogaster and it has now been reported in seven species for Drosophila: D. melanogaster, D. pseudoobscura, D. persimilis, D. willistoni, D. tropicalis, D. equinoxialis, and D. funebris (Petit and Ehrman, 1969; Borisov, 1970); and in Tribolium castaneum (Sinnock, 1970). While there was some initial skepticism that this effect occurred only in small artificial mating chambers, it has now been substantiated for Drosophila in the relatively unconfined spaces of a large room (Ehrman, 1970) and in nature (Borisov, 1970).

In conjunction with a larger effort in our laboratory to examine the population dynamics of the housefly, Musca domestica L., this study examined whether random mating occurs between widely separated geographic strains of this species. If such departures occur in spite of the apparent uniformity in phenotype and level of dispersal of the housefly, this would indicate that alteration in mating behavior is a selectively powerful evolutionary mechanism.

Materials and Methods

Because of the widespread distribution of this species in the United States, adequately sampling the species without increasing the total number of potential crosses prohibitively is difficult. To circumvent this, the results of a concurrent study of morphological variation were utilized to sample from localities representing maximal morphological diversity. Five localities were then selected, each representing a morphometrically homogeneous subset of localities, to establish five populations: Craigmont, Idaho (I); Kingman, Arizona (A); Redding, California (C); Osborne, Kansas (K); and Sheldon, Texas (T).

The method of direct observation described by Elens and Wattiaux (1964) and Ehrman (1965) was used to measure mating preferences in a 15 x 15 x 4-cm plexiglass observation chamber. For each mating the following records were made: 1) the type of male, 2) the type of female, 3) the time the mating began and ended, and 4) the location of the mating in the chamber so that no mating was recorded twice.

For the mating experiments the flies were raised at near optimal density in 60ml bottles each containing 80-100 eggs and 18g of CSMA larval medium (see Bryant, 1969, for details

of medium preparation). The emerging adults were removed from the jars at least every 12 hours and the sexes placed in separate holding cages. After four days the flies were lightly anesthetized with CO₂ and the end of one wing was clipped on flies of one strain for identification with clipping alternated between strains among replicates. The two strains were then introduced into separate sides of the mating chamber separated by a partition. After an acclimation period of one hour the partition was removed and the matings recorded for three hours. Three different ratios of the strains two at a time were tested: 1) 10X:10Y pairs; 2) 16X:4Y pairs; and 3) 4X:16Y pairs. Five replicates of all possible pairs and ratios of the five strains were tested.

Results

The departures from random mating for the 10X:10Y pairs are shown in Table 1. For each combination of two strains the five replicates were pooled and the four types of mating (XX, XY, YX, and YY) were tested using a chi-square test for goodness of fit to random mating. It was evident from these tests that some nonrandom mating was occurring and that further breakdown would elucidate these trends. Utilizing a methodology suggested by Bryant (personal communication), three independent components contributing to departures from random mating can be partitioned in a chi-square analysis: unequal male vigor, unequal female vigor, and assortative mating. Differences in male vigor among strains was shown by comparing the number of males mating in each strain regardless of type of female, i.e., (XX+XY) vs. (YX+YY), leading to a chi-square with one degree of freedom. Similarly, a chi-square value for female vigor can be derived from the numbers of matings of each type of female with the same assumption that equal numbers of females from each strain will mate regardless of the male partner, i.e., (XX+YX) vs. (XY+YY). The numbers of heterozygous vs. homozygous matings then test for the presence of assortative mating, also producing a chi-

Table 1. Number of matings for each cross and departures from random mating (10:10).

XxY	Number of Matings					Chi Square Tests ¹			
	XX	XY	YX	YY	Total	Random Mating ²	Assortative Mating ³	Male Vigor ³	Female Vigor ³
IxK	31	29	17	24	101	4.62ns	.80ns	3.57*	.25ns
IxC	27	25	21	24	97	.77ns	.26ns	.51ns	.01ns
IxA	26	23	17	24	90	2.00ns	1.11ns	.71ns	.18ns
IxT	28	28	18	21	95	3.23ns	.09ns	3.04+	.09ns
KxC	26	21	14	20	81	3.59ns	1.49ns	2.09ns	.01ns
KxA	22	31	24	21	98	2.49ns	1.47ns	.65ns	.37ns
KxT	32	34	18	18	102	8.90*	.04ns	8.82*	.04ns
CxA	30	23	21	25	99	1.81ns	1.22ns	.49ns	.09ns
CxT	37	21	17	23	98	9.27*	4.94*	3.31+	1.02ns
AxT	25	22	22	29	98	1.35ns	1.02ns	.16ns	.16ns

¹Significance levels for tests: ns = not significant at $P > .10$; + = $P < .10$; * = $P < .05$;
 ** = $P < .01$.

²Degrees of freedom for tests = 3.

³Degrees of freedom for tests = 1.

square value for departure from random mating for that pair (three degrees of freedom).

Calculation of male vigor for each set of replicates (Table 1) led to an unexpected observation in the data: the frequency of males mating was depressed whenever wings were clipped. A comparison between mean number of male matings with wings clipped and unclipped per three hour replicate for each strain showed a depression for both strains in every experiment except one, the depression being greater than 50% in one case (Table 2). When the number of clipped and the number of unclipped male matings were pooled over the four crosses for each strains, the depression ranged between 13% and 29%. To compensate for this, the numbers of male matings were adjusted for every pair mating. The adjustment for each strain was calculated by multiplying the mean number of unclipped matings per replicate (Column 3, Table 3) by the total number of replicates for that strain. This expected number of matings, if males were unclipped (Column 4), was divided by the actual number of males mating for each strain over all replicates and strains (Column 5). The adjustment value for each strain was then multiplied by the actual number of matings for each pair according to the type of male involved. New matings for each

Table 2. Number of males mating per replicate.

XxY	X Males		% Depres- sion	Y Males		% Depres- sion
	Clipped	Not Clipped		Clipped	Not Clipped	
IxK	9.0	14.0	35.7	7.0	10.0	30.0
IxC	8.0	12.0	33.3	7.0	12.0	41.7
IxA	8.3	12.0	30.6	7.0	9.0	22.2
IxT	10.3	12.5	17.4	6.5	8.7	25.0
KxC	8.0	11.5	30.4	4.0	8.7	53.9
KxA	10.5	10.7	1.6	8.7	9.5	8.7
KxT	12.3	14.5	15.0	6.5	7.7	15.3
CxA	8.5	12.0	29.2	8.0	11.0	27.3
CxT	11.7	11.5	- 1.5	7.0	8.7	19.5
AxT	9.0	9.7	6.9	9.7	11.0	12.1
Strain		% Depression				
Idaho		29.1				
Kansas		19.0				
California		22.6				
Arizona		17.4				
Texas		13.0				

Table 3. Calculation of adjustment for wing clipping.

Strain	Mean number matings all strains		Expected number of matings if males unclipped	Actual number of males mating	Adjust- ment
	Clipped	Unclipped			
I	9.00	12.70	254.0	217	1.171
K	9.36	11.56	231.2	207	1.117
C	8.10	10.90	218.0	190	1.147
A	8.20	9.70	194.0	179	1.084
T	7.67	8.82	176.4	166	1.063

pair were then corrected to the original total number of matings for the combination of the two strains.

A noticeable difference in male vigor can be seen in the actual number of males mating (Table 3). The number of Idaho males mating was 31% greater than the number of Texas males. The adjustment values indicate that more vigorous males (ones who mate more often) were more affected by the wing clipping than the relatively weaker strains. In fact, when the adjustment was applied to the actual number of males mating for each strain and each was then corrected so that the total number of matings were unchanged, a chi-square test showed a significant difference among strains in total matings ($X^2 = 15.49^*$).

The number of matings for females of each strain was also tested for a depression in female vigor when wings were clipped. The differences in the clipped and unclipped means, with one exception (CxT), ranged from 1 to 1.5 matings and were nearly as often negative as positive (eleven positive and nine negative increases). The pooled number of matings shows percent changes from -5.0 to 8.6%, therefore female matings were not adjusted for wing clipping.

The number of matings for each cross (with males adjusted for wing clipping) and the results of the chi-square tests for

random mating, assortative mating, male vigor and female vigor are shown in Table 4. Significant departures from random mating in the Kansas x Texas matings can be attributed to greater vigor in Kansas males. This agrees with the overall difference in vigor shown in Table 3. Both assortative mating and male vigor were significant in the California x Texas cross because of a very large number of homogamic matings by the more vigorous California males. The significant differences in male vigor for the Idaho x Kansas and Idaho x Texas crosses also reflect the trend for overall male vigor (Table 3). Differences in male vigor are apparently the primary sources for departures from random mating in the 10:10 matings.

The 16X:4Y pairs were tested in the same manner as the 10X:10Y ratios with the number of matings first adjusted for the effect of wing clipping on males, and departures from random mating were partitioned into the three components. The expected number of matings for each chi-square test reflected the frequency of that genotype in the mating chamber. The results are given in Table 5.

In the 16 California:4 Idaho cross, a very large number of disassortative matings between Idaho males and California females gave a significant chi-square value for assortative mating and also for male vigor. It is unlikely that this

Table 4. Number of matings adjusted for wing clipping for each cross and departures from random mating (10:10).

XxY	Number of Matings					Chi Square Tests ¹			
	XX	XY	YX	YY	Total	Random Mating ²	Assortative Mating ³	Male Vigor ³	Female Vigor ³
IxK	31.6	29.6	16.5	23.3	101.0	5.49ns	.77ns	4.49*	.23ns
IxC	27.3	25.2	20.8	23.7	97.0	.93ns	.26ns	.66ns	.01ns
IxA	26.9	23.8	16.3	23.0	90.0	2.67ns	1.07ns	1.45ns	.15ns
IxT	29.1	29.1	17.0	19.8	95.0	4.99ns	.08ns	4.82*	.09ns
KxC	25.7	20.8	14.2	20.3	81.0	3.28ns	1.50ns	1.76ns	.02ns
KxA	22.3	31.4	23.6	20.7	98.0	2.79ns	1.49ns	.91ns	.39ns
KxT	32.6	34.6	17.4	17.4	102.0	10.30*	.04ns	10.22**	.02ns
CxA	30.8	23.6	20.4	24.2	99.0	2.31ns	1.24ns	.97ns	.10ns
CxT	38.1	21.7	16.2	22.0	98.0	10.97*	5.04*	4.75*	1.18ns
AxT	25.3	22.2	21.8	28.7	98.0	1.26ns	1.01ns	.09ns	.16ns

¹Significance levels for tests: ns = not significant at $P > .05$; * = $P < .05$; ** = $P < .01$.

²Degrees of freedom for tests = 3.

³Degrees of freedom for tests = 1.

Table 5. Number of matings adjusted for wing clipping for each cross and departures from random mating (16:4)

XxY	Number of Matings					Chi Square Tests ¹			
	XX	XY	YX	YY	Total	Random Mating ²	Assortative Mating ³	Male Vigor ³	Female Vigor ³
IxK	61.7	11.1	16.4	4.8	94.0	1.48ns	.32ns	.39ns	.54ns
KxI	60.2	10.9	17.6	8.3	97.0	6.73ns	.31ns	2.71ns	.00ns
IxC	63.3	14.1	13.8	5.9	97.0	1.41ns	.48ns	.00ns	.02ns
CxI	50.7	16.9	23.3	3.0	94.0	6.44ns	5.05*	3.83*	.09ns
IxA	60.6	18.2	10.3	0.9	90.0	4.30ns	.01ns	3.19+	.09ns
AxI	49.9	10.8	14.8	8.5	84.0	8.69*	.09ns	3.12+	.44ns
IxT	57.1	20.4	15.7	3.7	97.0	1.94ns	1.24ns	.00ns	1.43ns
TxI	58.7	15.7	18.3	4.3	97.0	.74ns	.41ns	.67ns	.02ns
KxC	47.7	16.9	16.3	5.1	86.0	2.94ns	1.73ns	1.30ns	1.67ns
CxK	40.4	11.1	23.6	4.9	80.0	12.54**	4.76*	12.23**	.00ns
KxA	68.4	9.1	12.7	7.8	98.0	7.75+	4.33*	.05ns	.48ns
AxK	49.7	15.9	11.3	8.2	85.0	7.98*	.00ns	.44ns	3.69+
KxT	63.5	16.1	10.6	5.8	96.0	2.57ns	.77ns	.54ns	.47ns
TxK	53.2	15.8	27.9	3.1	100.0	10.95*	6.30**	7.63**	.08ns
CxA	65.8	12.1	13.4	6.7	98.0	3.24ns	1.59ns	.01ns	.04ns
AxC	62.2	14.8	15.7	6.3	99.0	1.44ns	.07ns	.29ns	.10ns
CxT	60.8	14.2	9.4	5.6	90.0	3.07ns	1.39ns	.62ns	.23ns
TxC	53.7	14.7	23.2	8.4	100.0	9.90*	1.57ns	8.44**	.59ns
AxT	68.2	16.0	9.8	4.9	99.0	2.88ns	1.56ns	1.61ns	.09ns
TxA	62.7	11.9	18.3	7.1	100.0	3.78ns	.15ns	1.80ns	.06ns

¹Significance levels for tests: ns = not significant at $P > .10$; + = $P < .10$; * = $P < .05$; ** = $P < .01$.

²Degrees of freedom for tests = 3.

³Degrees of freedom for tests = 1.

involved a strong dislike for one's own genotype, because the increased vigor of Idaho males has been shown twice in the 10:10 ratios (IxK and IxT). It was also demonstrated in the 16 Idaho: 4 Arizona and 16 Arizona:4 Idaho crosses where the greater vigor of Idaho males gave chi-square values of 3.19 and 3.12 ($.05 < P < .10$). In these two cases where Idaho males were in the minority, the heterogamic mating with California females and the homogamic mating with Arizona present caused the number of Idaho male matings to be high. Thus, assortative mating as a general cause for mating differences is unlikely. The fact that the Idaho males mate much more often than expected while in the majority (IxA) as well as when in the minority (AxI) also dispels the idea of a significant minority effect for this strain.

In the 16 Texas: 4 Kansas and in the 16 California:4 Kansas crosses, the high numbers of the Kansas male x other female matings yielded significant chi-squares for assortative (disassortative) mating. This is similar to the 16 California: 4 Idaho cross discussed above where the chi-square for male vigor in Kansas was also significant (as seen in the trend for total male mating, i.e., $I > K > C > A > T$).

The 16 Texas:4 California cross was the only example of a possible minority advantage. Here California males mated more

than expected in both homogamic and heterogamic mating; however, they also were significantly more active in the 10 California:10 Texas cross.

Significant assortative mating occurred in the 16 Kansas:4 Arizona cross for both strains but was not seen in the 10:10 ratio. Thus, the primary source of departures from random mating was again differences in male vigor, i.e., the more vigorous males mate more often than expected when in the minority as well as when in the majority and in equal proportions. Idaho males demonstrated greater vigor with every other strain: 10I:10K; 16C:4I; 16I:4C; 16A:4I; 10I:10T. Kansas males were significantly more vigorous when rare with California and Texas and in 10:10 mixtures with Texas; and California males were significantly more vigorous than Texas when rare and in equal mixtures.

The mean copulation times for homogamic pairs of each strain are shown in Table 6. Because these times are from the 10X:10Y matings, the other strain present in the chamber is indicated. A mean copulation time for each strain with mating times pooled over all replicates and all strains is also shown. Table 7 shows the means of copulation times for heterogamic matings. The mean of each type of heterogamic mating in the 10X:10Y matings and an overall heterogamic mean for each female

Table 6. Means of copulation times (in minutes) in homogamic matings for each cross and over all crosses.

Other Strain Present	Idaho (IxI)	Kansas (KxK)	California (CxC)	Arizona (AxA)	Texas (TxT)
Idaho		83.6	70.4	71.8	71.8
Kansas	79.3		65.4	73.9	93.2
California	69.0	67.6		66.1	77.4
Arizona	61.9	72.7	69.4		86.2
Texas	81.9	84.1	68.8	92.0	
All strains	73.0	77.2	68.7	76.0	82.0

Table 7. Means of copulation times (in minutes) in heterogamic matings for each cross and over all crosses.

Males	Females					
	Idaho	Kansas	California	Arizona	Texas	All Females
Idaho		76.2	68.3	74.3	78.4	74.4
Kansas	78.8		75.0	74.2	81.0	77.3
California	82.4	68.3		64.5	81.8	76.0
Arizona	64.7	75.2	72.3		86.0	75.1
Texas	77.9	90.6	90.0	85.0		86.2
All Males	75.8	77.8	75.5	75.4	81.6	

and each male with times pooled over all strains are given.

The pattern of the homogamic means is as follows:

$T > K > A > I > C$. For the heterogamic matings the patterns are

$T > K > I > C > A$ for females (the last row on the table) and

$T > K > C > A > I$ for males (the last column on the table).

Although the order changes for the last three strains (A, I, and C), the differences among these means is very small.

Discussion

Geographic variation in mating behavior among these strains was demonstrated in two ways: assortative mating and differences in male vigor. Assortative mating must be evaluated first because metabolic differences among strains can only be expressed when sexual isolation is weak or does not exist. Assortative mating accounted for 37.4%, while male and female vigor was 62.6% of the departures from random mating, pooled over all strains in both 10:10 and 16:4 combinations. However, the significant chi-square value for assortative mating can be caused by higher than expected numbers of homogamic or heterogamic mating. The latter occurred in three of these five significant tests. In all five cases it was the more vigorous male that was involved in the higher number of homogamic or heterogamic matings; and in four of the five, the significant assortative matings were one-sided (caused only the more vigorous males). This caused the chi-square test for male vigor also to be significant for these four pair combinations. The exception was 16 Kansas:4 Arizona where both types of homogamic matings were higher than expected. Assortative mating is therefore not strong enough to be a general factor in geographic variation among these strains, although

it occasionally occurs.

The differences of male vigor, however, permeated the entire experiment. In every significant test in both the 10:10 and 16:4 ratios the males from Idaho and Kansas mated more than those from California, Arizona and Texas. While this variation in vigor does not prevent random mating in many cases, it would tend to decrease gene flow from southern into northern populations. It would certainly enhance the spread of genes from northern flies introduced in a southern locality.

The only males exhibiting an advantage when in the minority (in 16:4 ratios) were Idaho, Kansas, and California. All three also exhibited an advantage when in the majority and in the 10:10 ratios for the same crosses.

The mean copulation times for homogamic matings which ranged from 82.0 to 68.7 minutes were as follows: $T > K > A > I > C$. This pattern did not change for females or for males (in heterogamic matings) implying that copulation times are determined by both sexes to some extent. Once copulation begins for a pair they move about the chamber very little unless disturbed by other flies. All females not engaged in copulation are courted almost constantly by the available males, and the females who escape copulation are usually very active in

rejecting males. This may account for the large numbers of disassortative matings among more vigorous males and females of the other (less vigorous) strain. When the first matings are over (about the end of the first hour), the more vigorous males are again free to court these more active females. The total number of females mating over all the experiments varied from 185 (Idaho) to 196 (Texas) reflecting that almost all females eventually mated and few mated more than once during the experiment. Within the three-hour experiment almost all of the 200 possible matings for females of each strain eventually occurred.

Thus, males who mated earlier were able to copulate more often over a given period of time because virgin females were still available. Fulker (1966) reported that Drosophila males who mated more quickly on the first occasion copulated more often, more successfully, and left more progeny. Parsons (1974) also concluded that mating speed is the most important component of fitness for Drosophila males paralleling the increased number of matings of the sexually vigorous males here.

Summary

Houseflies from five localities in the United States representing maximal morphological diversity were sampled, and laboratory populations were established. Virgins were randomly selected from flies raised under optimal laboratory conditions, and five replicates of each combination of the five strains were used so that assortative mating, increased male or female vigor, and frequency dependent mating, when present, could be detected. The number of male matings were adjusted to compensate for a depression caused by wing clipping.

Significant differences in male vigor were seen in the total number of matings over all strains as well as among pairs of strains. Differences in female vigor were not seen. The more vigorous males mated more often than expected when in the majority, in the minority, and in equal proportions, and the significant departures from random mating always followed the same pattern: flies from northern populations mated with greater speed and more often than flies from southern populations.

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- Table 1. 16 Idaho x 4 Kansas
- Table 2. 16 Kansas x 4 Idaho
- Table 3. 16 Idaho x 4 California
- Table 4. 16 California x 4 Idaho
- Table 5. 16 Idaho x 4 Arizona
- Table 6. 16 Arizona x 4 Idaho
- Table 7. 16 Idaho x 4 Texas
- Table 8. 16 Texas x 4 Idaho
- Table 9. 16 Kansas x 4 California

Appendix II. (continued)

Table 10.	16 California x 4 Kansas
Table 11.	16 Kansas x 4 Arizona
Table 12.	16 Arizona x 4 Kansas
Table 13.	16 Kansas x 4 Texas
Table 14.	16 Texas x 4 Kansas
Table 15.	16 California x 4 Arizona
Table 16.	16 Arizona x 4 California
Table 17.	16 California x 4 Texas
Table 18.	16 Texas x 4 California
Table 19.	16 Arizona x 4 Texas
Table 20.	16 Texas x 4 Arizona

Table 1. 10 Idaho : 10 Kansas. Duration of each mating from time 0 to 180 minutes.

Repli- cate	TxT		TxA		AxT		AxA	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	70	0	55	0	75	0	70
	0	95	0	70	0	75	0	75
	0	95	0	70	15	100	0	75
	55	135	0	75	25	70	0	95
	70	135	0	100			0	95
			0	100				
2			135	165				
	0	70	0	100	0	80	0	70
	50	150	40	105	0	85	0	70
	70	*	80	180	0	110	0	90
	75	145	110	145	70	145	0	90
	150	*			105	*	40	100
3							40	170
							85	170
	0	75	0	75	0	75	0	75
	15	85	0	75	45	120	0	85
	15	105	0	75	45	145	45	*
	45	135	15	90	60	135	95	*
4			75	*				
	0	55	0	65	0	65	0	70
	0	65	0	65	0	80	0	75
	0	65	0	75	0	90	0	90
	0	75	15	70			65	150
	0	90	45	115				
5	65	150	65	155				
	80	*	75	175				
			130	*				
	0	65	0	65	10	80	0	80
	0	75	0	65			0	110
	0	75	0	65			10	110
	0	80	70	145			45	110
	0	90	75	155				
	10	100						
	20	85						
	90	180						
	90	*						
	115	*						

* Mating in progress at end of experiment

Table 2. 10 Idaho : 10 California. Duration of each mating from time 0 to 180 minutes.

Repli- cate	IxI		IxG		CxI		CxG	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	70	20	70	0	60	20	90
	0	80	50	100	15	110	55	100
	0	80	65	145	50	110	55	130
	0	90	95	150			115	165
	70	115	100	180				
	100	*						
	130	165						
2	0	80	0	70	0	90	0	75
	40	110	40	110	0	95	0	80
	50	120	40	115	0	120	0	95
	95	155	80	165	15	95	0	110
					70	*	40	110
					110	*	110	155
3	0	60	0	75	0	60	0	60
	0	75	0	75	0	60	0	75
	0	85	20	100	0	75	0	75
	60	130	50	110	180	*	0	80
					180	*	15	60
					180	*	75	165
4	0	50	0	50	0	65	0	75
	0	60	0	60	30	100	0	75
	0	65	0	90	30	165	0	84
	50	120	15	60			30	100
	60	100	50	85				
5	0	50	0	75	0	75	0	50
	0	55	20	75	0	75	0	60
	0	75	55	115	55	140	65	130
	0	75	65	125			90	160
	10	75	90	165				
	20	70	100	175				
	45	130	100	*				

*Mating in progress at end of experiment

Table 3. 10 Idaho : 10 Arizona. Duration of each mating from time 0 to 180 minutes.

Repli- cate	IxI		IxA		AxI		AxA	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	70	0	60	0	60	0	70
	0	90	0	70	0	70	0	70
	15	70	0	90	0	135	165	*
			0	135	15	60		
					25	70		
2	0	60	0	60	0	70	0	65
	0	70	0	60	30	65	0	70
	140	180	0	110	110	170	0	70
			20	110	150	180	0	110
							65	110
3	0	55	0	75	0	60	110	130
	0	60	15	75			0	60
	0	60	150	*			0	75
	0	75	75	150			20	75
	10	75					25	105
4	25	75					10	145
	60	140					60	125
	0	70	0	60	0	70	0	75
	0	75	0	60	0	115	60	165
	0	80	0	75	45	115	70	120
5	45	105	0	80			80	*
	75	165	15	60				
	115	170	55	*				
	115	170						
	0	60	0	75	0	90	0	60
5	0	60	0	90	10	95	25	75
	80	110	10	75	50	90	150	*
	90	115	40	90	95	175	155	*
	100	150	100	*			170	*
	100	170						

*Mating in progress at end of experiment

Table 4. 10 Idaho : 10 Texas. Duration of each mating from time 0 to 180 minutes.

Repli- cate	IxI		IxT		TxI		TxT	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	80	0	70	0	65	0	65
	0	95	0	70	0	115	0	65
	45	115	0	75	70	135	0	70
	55	110					0	75
	60	120					65	*
	90	*						
	115	*						
2	0	95	0	75	0	75	40	95
	75	140	0	80	0	90	40	95
	75	180	0	90	30	115	95	115
	180	*	0	90	40	115	180	*
			9	90	40	125		
			0	115	125	*		
			55	145				
3	0	115	0	60	0	100	45	110
	25	105	0	65	30	100	55	140
	60	140	0	75	30	100	75	175
	85	180	0	85	115	*	85	155
	140	*	0	85	150	*		
			75	135				
4	0	75	0	70			0	80
	0	80	0	85			30	100
	0	90	0	95			135	*
	0	90	15	115				
	75	165	30	100				
	85	*	135	*				
	180	*						
5	0	80	0	60	0	65	0	60
	65	145	0	65	40	95	0	80
	70	155	0	70	80	155	0	80
	70	135	50	120	155	*	15	60
	90	155	180	*			95	165

*Mating in progress at end of experiment

Table 5. 10 Kansas : 10 California. Duration of each mating from time 0 to 180 minutes.

Repli- cate	KxK		KxC		CxK		CxK	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	60	0	60	0	65	0	60
	0	60	0	75	30	75	160	*
	0	75	30	65	90	135		
	15	75	80	160				
	50	100	115	*				
2	0	90	0	60	0	60	30	150
	15	80	30	90			60	110
	25	110	40	180				
	30	110	70	145				
	60	120	140	*				
	60	170	160	*				
	90	180						
3	0	60	0	100	0	90	0	75
	0	60	50	110	0	95	0	85
	50	120	75	150	10	75	0	95
	120	150			20	50	40	75
	160	*			100	*	75	115
4							105	*
	40	120	0	70	0	85	20	95
	80	155	0	95	0	90	20	105
	85	145	20	105	0	90		
5			105	*	90	*		
	0	60	0	60	40	100	0	60
	0	65	15	70			15	65
	0	75	80	170			15	100
	45	115					60	90
	100	155					65	120
	105	150					85	*
							105	125
							170	*

*Mating in progress at end of experiment

Table 6. 10 Kansas : 10 Arizona. Duration of each mating from 0 to 180 minutes.

Repli- cate	KxK		KxA		AxK		AxA	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	10	110	0	60	0	55	0	90
	45	110	0	60	0	80	65	115
	70	125	0	70	70	140	115	*
			0	90				
			15	85				
			55	110				
			95	170				
			95	*				
			115	*				
2	0	70	0	60	0	55	45	110
	35	80	0	60	0	60	70	140
	60	140	0	60	0	60		
	70	140	0	115	0	70		
			15	80	15	80		
			60	110	15	110		
			80	140				
3	0	60	15	65	0	80	0	90
	0	70	75	135	0	90	40	120
	0	75	90	*	15	75	50	140
	0	80			60	110	55	110
	0	80					75	125
	0	90					95	*
							105	145
4	0	75	0	75	0	60	0	90
	0	90	0	75	0	75	15	90
	0	90	0	75	0	90	70	165
	75	150	0	90	0	90	90	150
			50	110	15	90	170	*
			90	165				
5	0	60	0	60	0	70	0	60
	0	70	0	80	0	105	0	85
	60	115	0	85	15	85	30	110
	85	165	0	120	30	130		
	100	165	60	165	60	140		
			100	*	60	160		

*Mating in progress at end of experiment

Table 7. 10 Kansas : 10 Texas. Duration of each mating from time 0 to 180 minutes.

Repli- cate	KxK		KxT		TxK		TxT	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1.	0	85	0	60	0	95	0	70
	0	85	0	75	0	105	0	100
	0	85	0	80	20	150	30	120
	0	100	75	150	45	105	135	*
	30	115	90	160	45	120		
			100	*				
2.			180	*				
	0	60	0	75	30	115	0	105
	0	70	15	85	30	155	0	145
	0	75	15	85			15	90
	0	95	75	145				
	0	110	85	165				
	0	120	95	175				
	15	85	180	*				
3	95	*						
	110	*						
	0	80	0	80	0	90	0	90
	0	90	0	80	80	165	70	140
	40	105	0	90	130	*		
	80	150	0	90				
	110	*	0	100				
	135	*	0	115				
4	155	*	20	90				
			100	*				
	65	120	0	70	0	75	0	100
	65	155	0	75	0	100	0	80
	75	155	0	75	15	115	40	115
	80	*	0	80	85	155	90	*
5			65	150	115	*		
			75	*				
	0	80	0	75	0	105	0	75
	0	90	0	80	60	130	0	90
	0	130	40	105	85	180	0	90
	30	105	75	135			0	100
	90	150	100	*			125	*
	100	*	100	*				
	105	180						

*Mating in progress at end of experiment

Table 8. 10 California : 10 Arizona. Duration of each mating from time 0 to 180 minutes.

Repli- cate	CxC		CxA		AxC		AxA	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	70	0	55	0	75	45	120
	0	70	45	115	55	95	55	110
	0	75	55	100			80	130
	15	95	95	165			80	140
	24	95						
	35	75						
	45	140						
	75	145						
2	0	60	0	60	0	60	0	60
	0	70	0	60	0	70	15	60
	0	70	60	120	0	110	40	140
	15	60	70	140	15	90	60	130
	15	80			60	120	60	130
3	0	75	0	80	0	60	0	50
	35	105	25	100	0	70	0	150
	65	135	25	100	0	85	25	100
	75	135	35	105	10	60	40	100
	80	160	80	120	25	85	65	135
4			100	*				
	30	105	10	90	0	105	45	120
	30	105	105	180	10	90	45	120
	45	105	180	*	30	115	90	150
	60	170			60	105	90	*
5	115	*			105	*	105	*
							120	170
							150	*
	0	60	0	60	0	65	0	60
	0	60	0	60	0	65	0	60
	0	60	0	60	15	70	0	65
	25	75	60	105	15	70	70	165
	60	120	85	145				
	65	105	165	*				
	165	*						

*Mating in progress at end of experiment

Table 9. 10 California : 10 Texas. Duration of each mating from time 0 to 180 minutes.

Repli- cate	Cx C		Cx Y		Tx C		Tx T	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	75	0	60	0	90	0	60
	0	75	0	90	0	90	15	75
	15	120	40	90	0	150	60	135
	75	145	40	165	15	125		
	160	*	90	155	90	165		
2			90	*				
	0	50	0	65	0	65	0	70
	0	65	0	70	0	85	0	85
	0	70	0	115	100	170	0	85
	25	100	65	120			0	90
	55	110	170	*			15	85
	60	105					80	165
3	85	155						
	180	*						
	0	55	55	120	0	95	0	90
	0	55	100	*	40	120	40	120
	0	55	115	*	95	*	45	120
	0	70					95	*
	0	75					135	*
4	25	70						
	55	135						
	0	55	0	60	0	75	0	55
	0	55	60	115	20	115	0	65
	0	60	65	155	65	170	0	65
	0	90	140	*			60	120
	60	125					75	140
5	65	140					75	140
	90	140						
	0	55	0	110	0	85	50	*
	0	60	50	120	0	85	60	150
	0	85	75	155	50	120	120	*
	0	85						
	30	80						
	50	130						
	55	105						
	60	155						
	85	175						
	90	*						

*Mating in progress at end of experiment

Table 10. 10 Arizona : 10 Texas. Duration of each mating from time 0 to 180 minutes.

Repli- cate	AxA		AxT		TxA		TxT	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	85	0	75	0	90	10	90
	45	*	20	135	10	105	15	110
	85	185	25	90	75	165	40	105
	140	*	26	100	105	*	40	110
			60	160				
			60	170				
			90	*				
2	25	125	0	80	0	80	0	70
	100	*	0	90	0	90	0	70
	165	*	0	90	40	110	0	90
			0	90	60	*	0	90
					80	170	40	115
					90	190	170	*
					125	*		
3	25	160	0	85	25	130	0	70
	40	145	0	100	75	155	0	75
	50	155			75	*	0	85
	50	160			106	160	0	85
	75	160			105	*	0	115
							20	100
							70	155
4	0	85	0	70	0	75	0	95
	20	70	0	75	45	120	0	120
	20	90	0	90	50	140	20	110
	60	145	0	90	120	*	20	120
	60	150	90	*			70	*
	175	*						
5	0	65	0	55	0	65	0	75
	0	65	0	60	0	75	0	65
	0	75	0	75			15	100
	0	100	0	105			15	115
	0	116					50	130
	60	170					70	165
	60	175						

*Mating in progress at end of experiment

Table 1. 16 Idaho : 4 Kansas. Duration of each mating from time 0 to 180 minutes.

Repli- cate	IxI		IxK		KxI		KxK	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	50	0	90	35	125	0	115
	0	90	35	125	90	130	60	90
	0	90	125	*				
	0	90						
	0	90						
	0	100						
	0	125						
	0	125						
	35	150						
	35	*						
	85	165						
	125	180						
	125	*						
2	25	135	0	90	0	60	0	60
	60	135	0	110	0	90		
	60	145			40	100		
	60	160			110	170		
	90	180			170	*		
	90	*						
	100	165						
	110	145						
	110	*						
	120	*						
	145	175						
	155	*						
3	0	60	0	85	0	75	0	85
	0	60	45	135	0	85		
	0	120			65	130		
	45	150			105	*		
	45	165						
	65	135						
	65	155						
	65	*						
	75	*						
	85	150						

Table 1. (Continued)

Repli- cate	IxI		IxK		KxI		KxK	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
4	0	60	65	120	0	65	65	105
	0	65	65	135	0	75		
	0	65			0	75		
	0	65			20	75		
	0	65						
	0	75						
	0	75						
	0	75						
	0	75						
	0	85						
	15	70						
	85	120						
5	0	65	0	65	0	65		
	0	65	80	160	70	135		
	0	65						
	0	65						
	0	65						
	0	75						
	0	75						
	0	80						
	0	90						
	10	80						
	20	70						
	20	90						
	55	125						
	75	125						

*Mating in progress at end of experiment.

Table 2. 16 Kansas : 4 Idaho. Duration of each mating from time 0 to 180 minutes.

Replicate	KxK		KxI		IxK		IxI	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	75	75	135	0	75	0	75
	0	75			0	90	75	165
	15	85			75	135		
	15	100						
	35	100						
	35	100						
	35	100						
	35	115						
	35	125						
	55	115						
	70	135						
	95	180						
	95	180						
2	0	80	0	60	0	80	90	180
	0	80	50	90	0	80		
	0	80			50	110		
	0	90						
	0	90						
	0	90						
	0	110						
	15	80						
	15	80						
	30	55						
	90	145						
	90	160						
	110	*						
3	0	75	0	120	15	120	150	*
	0	135	15	105	85	145		
	0	145	85	120				
	15	105	85	150				
	45	105						
	45	105						
	45	105						
	45	165						
	45	*						

Table 2. (Continued)

Repli- cate	KxK		KxI		IxK		IxI	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
4	60	150						
	105	*						
	105	*						
	120	*						
	0	65	0	65	0	65	155	*
	0	65	0	65	0	105		
	0	65	85	145	20	85		
	0	65						
	0	65						
	0	70						
	0	70						
	0	70						
	0	85						
	20	85						
5	65	135						
	95	*						
	0	75	0	90	0	65	0	65
	0	75			0	65	90	150
	0	90			0	65	145	*
	20	105			65	145		
	20	125			70	160		
	30	115			100	180		
	45	130						
	55	135						
	70	145						
	70	170						

*Mating in progress at end of experiment.

Table 3. 16 Idaho : 4 California. Duration of each mating from time 0 to 180 minutes.

Repli- cate	IxI		IxC		CxI		CxC	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	55	0	65	0	85		
	0	80	60	120	15	35		
	0	85	130	*	75	110		
	0	85			90	140		
	15	45						
	15	70						
	15	85						
	40	85						
	40	130						
	75	130						
	80	120						
	110	145						
	120	*						
2	0	65	0	75	0	75	0	75
	0	75	180	*	145	*	55	120
	0	75					90	160
	0	75						
	0	90						
	30	55						
	30	105						
	50	125						
	60	145						
	75	130						
	75	160						
	90	175						
	180	*						
3	0	55	0	55	0	75	0	80
	0	55	0	60	20	100		
	0	60	0	60				
	0	60						
	0	65						
	0	85						
	0	110						
	15	65						
	20	105						

Table 3. (Continued)

Repli- cate	IxI		IxC		CxI		CxC	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
4	65	135						
	65	165						
	75	165						
	0	60	20	90	0	60	40	105
	0	60	75	140	0	90	75	150
	0	75						
	0	90						
	0	90						
	0	90						
	0	90						
	15	75						
	30	90						
	30	120						
	90	165						
	90	*						
	90	*						
5	0	60	0	60	0	60		
	0	60	60	150	0	60		
	0	60	65	125	60	125		
	0	65	120	*	75	150		
	0	65						
	0	70						
	10	70						
	60	120						
	60	150						
	75	150						
	90	150						
	120	*						

*Mating in progress at end of experiment.

Table 4. 16 California : 4 Idaho. Duration of each mating from time 0 to 180 minutes.

Repli- cate	CxC		CxI		LxC		LxI	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	60	0	80	0	70		
	0	60	0	80	0	90		
	0	70	90	170	0	95		
	0	80			100	*		
	0	80						
	60	130						
	60	135						
	90	*						
	170	*						
	180	*						
2	0	70	0	75	15	40		
	0	80	0	95	15	85		
	0	80	60	*	25	100		
	0	80			30	100		
	0	80						
	15	80						
	15	120						
	35	100						
	40	120						
	85	180						
3	160	*						
	0	55	0	60	0	60	0	60
	0	60	0	70	0	60	110	*
	0	60	0	80	0	60		
	0	60						
	0	70						
	0	70						
	0	70						
	0	70						
	0	110						
	20	100						
	40	*						
	70	140						
	75	165						

Table 4. (Continued)

Repli- cate	Cx C		Cx I		Ix C		Ix I	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
4	0	55	0	55	0	80		
	0	80	0	60	0	80		
	20	105	0	80	30	105		
	55	90	20	105	50	105		
	60	120	70	105	90	165		
	90	*			120	*		
	105	*						
5	0	50	0	65	0	60	0	60
	0	50	0	85	0	60		
	0	65	80	115	10	75		
	0	65			65	125		
	0	70			75	150		
	0	70			80	*		
	40	105						
	50	125						
	70	150						
	85	115						

*Mating in progress at end of experiment.

Table 5. 16 Idaho : 4 Arizona. Duration of each mating from time 0 to 180 minutes.

Replicate	IxI		IxA		AxI		AxA	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	60	0	45	0	45	0	60
	0	60	0	75	0	60		
	0	75	0	75	45	75		
	0	75						
	0	105						
	0	120						
	0	135						
	30	75						
	90	105						
2	0	60	0	60	0	60		
	0	60	10	90	60	90		
	0	60						
	0	120						
	0	130						
	0	175						
	0	*						
	10	90						
	45	*						
	90	110						
	90	110						
	110	*						
	175	*						
3	0	65	0	55	0	75		
	0	70	0	75	35	100		
	0	75	5	55	85	170		
	35	130	85	*				
	45	85						
	55	130						
	55	130						
	80	170						
	80	*						
	100	155						
	100	*						
	135	*						

Table 5. (Continued)

Repli- cate	IxI		IxA		AxI		AxA	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
4	0	60	0	60				
	0	60	0	60				
	0	60	55	110				
	0	60	80	100	0	80		
	0	60	80	135	0	85		
	0	60						
	0	60						
	10	60						
	25	60						
	55	90						
	55	135						
	65	90						
	85	140						
5	0	75	10	75	0	65		
	0	80	30	60				
	0	100	30	80				
	10	75	165	*				
	10	80						
	10	85						
	10	85						
	40	160						
	55	155						
	75	145						
	100	125						
	100	125						
	100	130						

*Mating in progress at end of experiment.

Table 6. 16 Arizona : 4 Idaho. Duration of each mating from time 0 to 180 minutes.

Repli- cate	AxA		AxI		IxA		IxI	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	60	0	60	60	90	0	60
	0	60	0	60	90	110	60	135
	0	60						
	0	60						
	0	60						
	0	60						
	90	135						
2	0	55	60	75	0	55	60	145
	0	55	60	145	0	55		
	0	55	155	*	55	105		
	0	55						
	0	60						
	0	75						
	0	75						
	0	115						
	30	75						
	55	120						
	75	*						
	90	160						
	125	*						
	0	60	5	95	0	60	85	155
	0	75	10	80	60	110		
	0	110			155	*		
	5	95						
	10	65						
	40	110						
	40	*						
	65	110						
	95	*						
	120	*						
	115	*						
	0	60	80	135	0	60	0	85
	0	60			0	80	80	170
	0	80					0	60
	0	80						
	20	105						

Table 6 (Continued)

Repli- cate	AxA		AxI		IxA		IxI	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
	35	100						
	60	90						
	60	120						
	65	100						
	120	*						
5	0	55	55	135	0	80	40	95
	0	55	65	125	0	80		
	0	65	80	165	40	130		
	0	75			140	*		
	0	95						
	15	80						
	15	80						
	40	110						
	80	135						
	80	165						

*Mating in progress at end of experiment.

Table 7. 16 Idaho : 4 Texas. Duration of each mating from time 0 to 180 minutes.

Repli- cate	IxI		IxT		TxI		TxT	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	55	0	60	0	60		
	0	70	0	65	0	60		
	0	70	20	100	0	65		
	0	80	60	165	0	90		
	0	85			0	90		
	0	85						
	0	100						
	60	*						
	60	125						
	70	*						
	80	165						
	90	*						
2	0	75	0	80	40	120		
	0	80	0	95	50	105		
	0	95	30	130	70	135		
	50	105	70	135	120	*		
	65	140						
	85	140						
	90	180						
	95	*						
	100	*						
	130	*						
3	180	*						
	0	90	0	60	55	140		
	0	140	0	90	145	*		
	20	90	20	75	45	115		
	30	105	65	165				
	45	140	160	*				
	55	135						
	20	90						
	90	150						
	90	165						
	140	*						
	145	*						

Table 7. (Continued)

Repli- cate	IxI		IxT		TxI		TxT	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
4	0	50			0	90	20	80
	0	70	30	90	85	160	80	130
	40	195	70	160	135	*		
	45	120	85	155				
	55	150	170	*				
	65	140						
	85	160						
	125	*						
	150	*						
5	0	70	0	75	60	130	0	60
	0	75	40	75	85	180	0	70
	0	110	75	120				
	25	75						
	40	100						
	60	140						
	75	145						
	75	150						
	75	170						
	135	*						
	140	*						
	160	*						
	180	*						

*Mating in progress at end of experiment.

Table 8. 16 Texas : 4 Idaho. Duration of each mating from 0 to 180 minutes.

Repli- cate	TxT		TxI		IxT		IxI	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	60	0	70	0	60		
	0	70	0	85	25	75		
	0	70			45	120		
	0	70			95	160		
	0	90						
	0	90						
	0	110						
	0	115						
	20	100						
	25	90						
	70	125						
	160	*						
	180	*						
2	0	80	70	160	0	85	0	75
	45	120	165	*	110	*	80	165
	65	120			170	*		
	70	150						
	75	170						
	85	165						
	90	170						
	90	*						
	115	*						
	130	*						
	180	*						
	180	*						
	180	*						
3	0	85	20	80	0	75		
	0	100	40	140	0	85		
	0	105	85	*	0	*		
	15	85	100	*	20	110		
	30	140			85	175		
	35	100						
	65	175						
	65	175						
	85	175						

Table 8. (Continued)

Repli- cate	TxT		TxI		IxT		IxI	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
4	85	180						
	110	*						
	165	*						
	0	85	5	90	0	70	0	85
	0	100	110	*	45	120		
	0	120	140	*	75	*		
	0	*	180	*	90	*		
	15	115						
	65	*						
	65	*						
5	75	165						
	100	180						
	0	70	0	60	0	70	0	80
	0	70	0	80				
	0	70	70	135				
	0	75	80	180				
	0	90						
	0	95						
	0	95						
	25	75						
	25	90						
	30	120						
	40	110						
	75	160						
	75	170						

*Mating in progress at end of experiment.

Table 9. 16 Kansas : 4 California. Duration of each mating from time 0 to 180 minutes.

Repli- cate	KxK		KxC		CxK		CxK		CxK	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	60	0	70	30	80	0	60		
	0	60	0	120	30	90	0	70		
	0	70			60	115				
	0	80								
	0	90								
	0	100								
	0	105								
	0	110								
	45	100								
	75	160								
	105	*								
2	0	60	80	115	0	60				
	0	60	80	155	10	90				
	0	75	105	150	30	*				
	0	90	105	170	75	150				
	100	180								
	120	170								
3	0	60	0	50	0	60	105	180		
	0	90	0	60	0	90				
	0	90	30	90	50	135				
	0	90	30	90						
	0	90	90	145						
	0	90								
	0	105								
	30	105								
	50	120								
	75	150								
	90	*								
	95	160								
4	0	75	0	85	0	75	0	70		
	0	80	55	150	55	110	45	125		
	0	90			80	165				
	0	95								
	0	110								

Table 9. (Continued)

Repli- cate	KxK		KxC		CxK		CxK	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
	40	95						
	65	95						
	100	175						
	105	160						
	135	*						
5	0	80	0	60	10	70		
	75	125	0	60	30	100		
	90	*	30	90				
	115	*	55	100				
	150	*						

*Mating in progress at end of experiment.

Table 10. 16 California : 4 Kansas. Duration of each mating from time 0 to 180 minutes.

Repli- cate	CxC		CxK		KxC		KxK	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	50	0	60	0	60		
	0	60	0	65	0	75		
	15	60	40	100	0	90		
	15	75			0	120		
	30	90			15	105		
	45	90			60	160		
2	0	70	40	85	0	60	60	120
	0	90	50	110	0	90	155	*
	10	90	85	135	15	60		
	20	120			15	90		
	50	120			25	85		
	60	120			90	155		
	85	120			105	*		
	85	145						
3	0	60	0	90	0	65	0	80
	0	75	65	120	20	75	80	*
	0	105			20	105		
	20	130			90	135		
	65	120			140	*		
	65	150						
	90	160						
4	105	*						
	0	90	0	80				
	0	90	40	100	0	160		
	20	90	160	*	30	80		
	110	*			160	*		
	130	180						
5	175	*						
	10	60			0	60	45	105
	10	70			70	160		
	10	70			130	*		
	15	65						
	15	70						
	20	80						
	20	100						

Table 10. (Continued)

Repli- cate	Cx C		Cx K		Kx C		Kx K	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
	30	80						
	45	90						
	60	90						
	120	170						
	135	*						

*Mating in progress at end of experiment.

Table 11. 16 Kansas : 4 Arizona. Duration of each mating from 0 to 180 minutes.

Repli- cate	KxK		KxA		AxK		AxA	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	50	25	120	0	70	0	80
	0	60	125	*	30	80	135	*
	0	60			50	110		
	0	60			70	110		
	0	60						
	0	65						
	0	80						
	5	65						
	15	70						
	30	90						
	50	120						
	100	175						
2	0	75	0	75	0	75	85	170
	0	75			0	85		
	0	75	75	170	85	120		
	0	80	130	*				
	0	85						
	0	85						
	0	85						
	60	120						
	60	140						
	75	120						
	75	160						
	75	*						
	120	145						
3	0	75	180	*	0	100	45	90
	0	75			45	120	150	*
	0	75						
	0	75						
	0	75						
	0	75						
	0	75						
	20	75						
	30	90						
	30	90						

Table 11. (Continued)

Repli- cate	KxK		KxA		AxK		AxA	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
4	40	90						
	75	150						
	85	135						
	105	165						
	0	40			0	70		
	0	70	0	90	45	70		
	0	70	15	70				
	0	80	100	165				
	0	80						
	0	90						
	0	90						
	0	120						
	15	80						
	15	90						
	30	70						
	45	105						
	70	105						
	70	135						
5	0	60			0	70	0	75
	0	60			60	160	0	85
	0	60					80	150
	0	60						
	0	60						
	0	70						
	0	70						
	0	70						
	0	70						
	0	90						
	0	100						
	30	75						
	60	140						
	105	*						
	125	*						

*Mating in progress at end of experiment.

Table 12. 16 Arizona : 4 Kansas. Duration of each mating from time 0 to 180 minutes.

Repli- cate	AxA		AxK		KxA		KxK	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	75	0	60	0	55	0	60
	35	90	55	75	75	145	40	110
	40	125	135	*				
	40	150						
	60	120						
	75	130						
	75	130						
2	0	60	0	60	0	55		
	0	70	0	60	0	60		
	0	75	0	80	0	80		
	0	80	70	130				
	0	80						
	0	80						
	35	95						
	80	120						
	80	120						
	85	140						
	105	170						
	120	150						
	120	*						
3	20	100	0	75			0	75
	30	100	0	75			100	140
	45	100	0	75				
	75	140						
	75	150						
	100	125						
	100	180						
	100	*						
	125	*						
4	130	*						
	170	*						
	0	75	0	90	0	90	0	75
	15	75	90	130	0	90	15	90
	15	90					170	*
	30	110						

Table 12. (Continued)

Repli- cate	AxA		AxK		KxA		KxK	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
	30	115						
	45	105						
	55	115						
	60	115						
	105	165						
	105	165						
5	0	75	0	75	0	70	75	160
	0	85	0	75	0	70		
	0	85	0	85	0	75		
	0	100	0	85	30	100		
	15	100						
	15	120						
	30	105						
	75	*						
	120	*						

*Mating in progress at end of experiment.

Table 13. 16 Kansas : 4 Texas. Duration of each mating from time 0 to 180 minutes.

Repli- cate	KxK		KxT		TxK		TxT	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	65	0	70	0	70	70	180
	0	115	135	*	0	80	180	*
	25	90	180	*	0	105		
	25	100						
	35	95						
	70	135						
	70	145						
	70	145						
	70	145						
	70	170						
	80	175						
	80	*						
	160	*						
2	0	60	0	65	0	85		
	0	60	0	65	0	100		
	0	85	0	85	30	100		
	0	85	0	85				
	0	85						
	0	100						
	15	75						
	15	100						
	65	135						
	65	145						
	65	160						
3	0	75	0	60	20	85	90	145
	0	85	0	110				
	0	95	40	115				
	0	110						
	0	110						
	0	135						
	60	110						
	60	150						
	60	160						
	90	175						
	95	160						

Table 13. (Continued)

Repli- cate	KxK		KxT		TxK		TxT	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
4	95	165						
	95	175						
	120	*						
	0	75					25	95
	0	90	0	85				
	0	110	55	115	0	75		
	25	85	120	*	35	115		
	35	120			70	165		
	45	125			95	175		
	45	165						
	70	150						
	85	*						
	125	*						
	180	*						
5	0	60	0	90			0	105
	0	80	60	145			55	145
	0	80	80	175				
	0	80						
	0	90						
	0	90						
	15	90						
	25	90						
	25	100						
	30	90						
	45	150						
	55	125						
	80	155						
	80	180						

*Mating in progress at end of experiment.

Table 14. 16 Texas : 4 Kansas. Duration of each mating from time 0 to 180 minutes.

Repli- cate	TxT		TxK		KxT		KxK	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	75	0	80	0	75		
	0	75	0	90	45	145		
	0	80	40	115	65	165		
	0	90	45	130				
	0	95						
	0	115						
	20	125						
	30	115						
	45	120						
	80	175						
	85	160						
	120	*						
	135	*						
2	0	70	0	80	0	70	0	65
	0	70	80	*	0	80		
	0	70			0	80		
	0	80			80	175		
	0	80			95	165		
	0	95			165	*		
	0	95						
	15	80						
	30	100						
	45	135						
	80	165						
	80	175						
	100	*						
3	0	105	40	105	80	135	0	70
	0	130	55	105	70	115		
	0	150	125	*	20	115		
	20	70			0	55		
	20	80			0	105		
	40	125			105	150		
	55	125			130	*		
	70	165						
	105	165						

Table 14. (Continued)

Repli- cate	TxT		TxK		KxT		KxK	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
4	0	65	25	85	0	55	85	165
	0	85	35	105	0	75		
	25	85	70	135	25	90		
	25	95	35	105	60	130		
	35	120	70	135				
	40	135						
	55	125						
	90	150						
	165	*						
5	40	*	30	105	0	70		
	60	150	50	110	0	75		
	70	150	90	*	0	95		
	70	155	105	*	75	155		
	75	155			75	155		
	90	*			90	160		
	120	*			165	*		
	120	*						
	150	*						
	150	*						

*Mating in progress at end of experiment.

Table 15. 16 California : 4 Arizona. Duration of each mating from time 0 to 180 minutes.

Repli- cate	CxC		CxA		AxC		AxA	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	60	0	50	0	70	0	70
	0	70	0	70	55	125	0	70
	0	70						
	0	90						
	0	90						
	25	80						
	25	80						
	25	80						
	25	80						
	25	125						
	80	150						
	165	*						
2	0	60	30	110	0	75	85	145
	0	60	60	130	15	70		
	0	60			120	*		
	0	60						
	0	60						
	0	90						
	0	110						
	60	130						
	60	140						
	80	165						
	160	*						
3	0	55	0	70	10	70	0	75
	0	60	70	180	70	130	0	75
	0	65			90	170		
	0	65						
	0	85						
	25	110						
	30	130						
	45	105						
	45	105						
	60	120						
	65	130						
	105	170						

Table 15. (Continued)

Repli- cate	Cx C		Cx A		A x C		A x A	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
4	160	*						
	160	*						
	0	55	60	130	0	60	55	130
	0	60	70	130	0	90		
	0	60	130	*	70	130		
	0	70						
	0	70						
	0	70						
	0	90						
	0	120						
	0	120						
	30	115						
	90	165						
	90	170						
	125	*						
	130	175						
5	180	*						
	0	60	0	65	0	70	180	*
	0	60	65	135	0	85		
	0	65	85	155	110	180		
	0	75						
	0	75						
	0	85						
	15	85						
	15	110						
	60	150						
	70	115						
	120	*						
	165	*						
	180	*						

*Mating in progress at end of experiment.

Table 16. 16 Arizona : 4 California. Duration of each mating from time 0 to 180 minutes.

Repli- cate	AxA		AxC		CxA		CxC	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	75	0	55	0	60	0	75
	0	75	15	115	0	75		
	0	75			15	115		
	0	75						
	0	75						
	25	90						
	45	100						
	45	120						
	85	155						
	85	170						
	105	170						
	180	*						
2	0	60	0	60	0	60	40	90
	0	60	70	130	0	60		
	0	70	70	140	0	90		
	0	85						
	0	85						
	15	85						
	25	120						
	60	130						
	60	140						
	70	140						
	90	140						
	90	150						
	170	*						
3	0	70	0	70	0	70	0	75
	0	70	120	*	55	125	35	100
	0	85			150	*		
	10	70						
	30	90						
	70	140						
	75	115						
	125	180						
	125	*						
	140	*						
	180	*						

Table 16. (Continued)

Repli- cate	AxA		AxC		CxA		CxC	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
4	180	*						
	180	*						
	0	80			0	60	0	80
	0	85	0	80	45	100	165	*
	15	80	30	90	75	*		
	30	90	30	150	180	*		
	30	90	180	*				
	30	120						
	80	135						
	80	160						
	100	135						
	150	*						
	180	*						
	0	60	0	60	0	85		
5	0	70	0	80	0	85		
	15	60	70	105				
	25	100	180	*				
	60	120						
	60	170						
	70	145						
	75	165						
	100	*						
	105	165						
	120	170						
	145	*						
	180	*						
	180	*						

*Mating in progress at end of experiment.

Table 17. 16 California : 4 Texas. Duration of each mating from time 0 to 180 minutes.

Repli- cate	CxC		CxT		TxC		TxT	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	60	70	130	0	70	0	85
	0	60			90	*	0	100
	0	60					30	100
	0	65						
	0	75						
	0	85						
	40	100						
	40	115						
	60	120						
	70	145						
	75	145						
	160	*						
	180	*						
2	0	50	0	60	0	85	45	115
	0	60	75	150	10	95		
	0	60						
	0	60						
	0	75						
	0	80						
	0	80						
	0	135						
	10	75						
	95	165						
	115	*						
3	0	55	0	55	0	85	95	*
	0	55	0	60	15	85		
	0	55	15	65	20	115		
	0	65	85	160				
	0	80						
	0	80						
	0	80						
	20	80						
	30	115						
	60	140						
	95	145						

Table 17. (Continued)

Repli- cate	CxC		CxT		TxC		TxT	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
4	0	50	0	55	0	60		
	0	55	0	65	80	140		
	0	55	0	70				
	0	60	30	95				
	0	60	95	170				
	0	60						
	0	90						
	20	85						
	70	150						
	70	170						
	110	*						
	150	*						
5	0	60	0	50	95	160	0	85
	0	70	90	155				
	0	85						
	0	90						
	0	95						
	25	115						
	30	70						
	30	115						
	55	160						
	60	120						
	70	125						
	90	*						
	95	*						

*Mating in progress at end of experiment.

Table 18. 16 Texas : 4 California. Duration of each mating from time 0 to 180 minutes.

Repli- cate	TxT		TxC		CxT		CxC	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	60	0	80	0	55	0	60
	0	80	85	165	0	60	60	120
	0	80			0	75		
	0	100			60	120		
	0	100						
	40	100						
	40	110						
	75	125						
	75	135						
	75	155						
2	0	75	0	90	0	75	0	90
	0	75	15	90	0	115	75	130
	0	75			35	90	180	*
	0	75			115	*		
	0	80						
	10	75						
	15	80						
	35	95						
	45	130						
	75	*						
	75	*						
	90	135						
	90	155						
3	0	75	0	45	0	50	115	170
	0	95	0	100	0	70		
	20	125	25	110	180	*		
	40	105	40	115				
	40	125	65	115				
	85	*						
	105	*						
	120	*						
	135	*						
	180	*						
	180	*						

Table 18. (Continued)

Repli- cate	TxT		TxC		CxT		CxC	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
4	0	65	85	155	0	50	65	155
	0	80			0	50	75	125
	0	80			0	50		
	0	85			0	60		
	0	90			60	105		
	0	105						
	15	60						
	15	60						
	25	70						
	30	105						
	30	110						
	100	*						
5	0	70	45	130	0	70		
	0	85	55	115	0	85		
	0	95	85	145	55	130		
	0	95	85	160	70	160		
	0	180	115	175	95	*		
	40	120			175	*		
	70	120						
	85	175						
	120	*						

*Mating in progress at end of experiment.

Table 19. 16 Arizona : 4 Texas. Duration of each mating from time 0 to 180 minutes.

Repli- cate	AxA		A x T		TxA		T x T	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	70	0	70	0	70	0	80
	0	75	0	85	0	75	120	*
	0	85	70	120	0	80		
	0	90			0	100		
	20	105						
	40	105						
	40	120						
	40	150						
	85	140						
	90	*						
	105	*						
	120	*						
2	0	85	0	80	0	80		
	0	85	0	95	0	90		
	0	90	0	95	0	95		
	0	90	90	*	0	105		
	0	90			95	*		
	0	90						
	15	85						
	15	105						
	70	150						
	85	180						
	180	*						
3	0	65	0	65			70	*
	0	75	25	120				
	0	75	55	140				
	0	85						
	30	55						
	40	130						
	40	180						
	55	115						
	55	140						
	55	170						
	60	135						
	60	*						

Table 19. (Continued)

Repli- cate	AxA		AxT		TxA		TxT	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
4	85	130						
	105	*						
	140	*						
	180	*						
	0	75	0	75				
	0	80	45	115			25	100
	0	90					45	135
	0	90						
	0	100						
	0	100						
	25	75						
	25	105						
	45	90						
	45	125						
	75	150						
	75	*						
	85	175						
	100	*						
	105	*						
	180	*						
5	0	60	0	60	75	155		
	0	60	0	70				
	0	65	0	90				
	0	75	60	125				
	0	75						
	0	100						
	15	75						
	15	90						
	15	115						
	60	180						
	70	135						
	80	135						
	80	155						

*Mating in progress at end of experiment.

Table 20. 16 Texas : 4 Arizona. Duration of each mating from time 0 to 180 minutes.

Repli- cate	TxT		TxA		AxT		AxA	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
1	0	70	0	110	0	70	130	*
	0	70	155	*	0	90		
	0	70			20	85		
	0	85			90	*		
	0	90						
	0	105						
	40	130						
	70	140						
	75	140						
	75	180						
	85	175						
	85	175						
	180	*						
2	0	100			0	65		
	0	100	0	50	0	80		
	0	105	0	90	15	135		
	0	105	0	100	70	150		
	0	110	40	170				
	0	110						
	0	120						
	0	165						
	15	130						
	90	180						
	105	180						
	105	*						
	110	*						
3	0	80	75	*	0	100	120	170
	0	100	105	*	0	100		
	0	100			105	*		
	0	120			135	*		
	0	135						
	0	150						
	40	120						
	50	170						
	70	180						

Table 20. (Continued)

Repli- cate	TxT		TxA		AxT		AxA	
	Began	Ended	Began	Ended	Began	Ended	Began	Ended
4	70	*						
	70	*						
	85	120						
	105	*						
	0	85	0	85			105	175
	0	85	0	105	0	70		
	0	95	50	115	20	105		
	0	105			40	*		
	0	105						
	0	105						
	0	125						
	0	135						
	20	95						
	45	135						
	50	130						
	55	*						
	90	180						
5	0	55	65	135	0	45	0	45
	0	65			0	80	0	80
	0	65			70	155	50	105
	0	80					55	145
	0	155						
	15	65						
	15	115						
	15	130						
	50	115						
	55	130						
	105	165						

*Mating in progress at end of experiment.