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Population genetics in the American Tropics

18. The genetic structure of peripheral *Drosophila pseudoobscura* from Colombia *

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Summary. There are several Colombian populations of *Drosophila pseudoobscura* which have begun to show divergence. The temporal samples of Torobarroso, one of the local populations identified, demonstrate genetic "resourcefulness" and selective opportunism by fluctuating mortality. The data suggest that both balanced selection and mutational origin are necessary to account for the frequencies of drastic genes encountered. In genetic isolates there seems to exist alternatively a mutational component and a balanced – selection component. These components overcome the damage in the first instance and in the second instance, profit from the recessive load.

Key words: Genetic load – Balance and mutation theory – Lethal equivalence – Selection

Introduction

Since the discovery of *Drosophila pseudoobscura* on the Altiplano of Bogotá, its special genetic structure has been evident (Dobzhansky et al. 1963). There are several isolated colonies of this species on the high (2,700 meters) plateau in the Central Cordillera of the Colombian Andes which are separated from the main body of *Drosophila pseudoobscura* by 1,500 miles. It is likely that the initial migrants in Colombia started a single colony of a few individuals which, in time, diverged as they spread across the Altiplano of Cundinamarca, Boyacá and Santander, an area of similar ecological conditions covering about 40,000 km². The high lands of Guatemala are similar but far from identical to their Colombian counterparts. Although in the 1950's we failed to find *Drosophila pseudoobscura* either in tropical lowlands or in the mountains, it is highly probable that the species was present. In the sixties, more thorough field investigations (Polanco et al. 1982) found many populations, and in the seventies, several more were added to the list. Moreover, we have chromosomal data (unpublished results) which confirm the findings of Dobzhansky et al. (1963) that Colombian populations are a depauperate version of those found in Guatemala, in so far as SC (= Santa Cruz) and TL (= Tree Line) inversions are concerned.

The Colombian population is chromosomally quite different from those of the main species distribution in the United States and Mexico. Furthermore, in Colombia, *Drosophila pseudoobscura* is not restricted to human environments, but it is limited to the high Andean plateau of Cundinamarca, Boyacá and Santander. Although others have presented these flies as a single population, there are at least fourteen populations with sufficient eco-genetic peculiarities to merit special attention if one is interested in studying their peripheral status (Hoenigsberg et al. 1972, unpublished results). Because pioneering works (Dobzhansky et al. 1963) show different results and interpretations from ours (Hoenigsberg et al. 1969, 1974), it appears desirable to clear up misunderstandings and erroneous ideas about this species in Colombia. Moreover, the results presented here suggest that there are several different processes operating in *Drosophila pseudoobscura,* and that these present new situations in terms of lethal equivalence and recessive penetrance.

Materials and methods

The flies were attracted with fermenting oranges (*Citrus sinensis*), papayas (*Carica papaya*), strawberries (*Rubus glaucus, Rubus urticaefolia*), bananas (*Musa paradisiaca, Musa sapien-*

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* This paper is dedicated to Charles Darwin in his centennial

Table 1. Seasons, generations elapsed and relative sizes of collections at the three localities. Relative sizes are expressed as large (200–300 individuals), medium (100–200), small (50–100) and very small (10–20)

Samples	Season	Generations (days)	Relative size
Torobarroso			
1	rainy	1 (0)	medium
2	dry-rainy	5 (103)	very-small
3	rainy	11 (240)	medium
4	dry-rainy	19 (406)	very-small
5	rainy	27 (587)	medium
6	dry-rainy	45 (993)	very-small
10	dry	50 (1123)	medium
11	dry-rainy	57 (1267)	very-small
12	rainy	60 (1327)	large
Santillana			
1	rainy	1 (0)	small
2	rainy	7 (151)	small
Aguas calientes			
1	dry	1 (0)	large
2	dry	12 (267)	large

tum), and pineapples (*Ananas sativus*) which were sprinkled with a yeast suspension and left on the ground for a minimum period of 4 days before sampling was done. Each locality had from 3–6 large baited areas 50 meters apart. Sampling was done by sweeping with a net until no more flies were found. Males and females were separated immediately.

The flies were collected in three different localities (Torobarroso, Santillana and Aguas Calientes) within the Altiplano area of Bogotá. Collections were made in alternate seasons (= rainy-dry) in Torobarroso, in the rainy season in Santillana, and in the dry season in Aguas Calientes. At Torobarroso the samples studied are numbered 1, 2, 3, 4, 5, 8, 10, 11, 12. At some collections (= 6, 7 and 9) not all the individuals were drained off, and these were omitted from this study. Our collecting techniques with repeated sweepings until no flies are found over the bait, permit us to have a general appreciation of the approximate population size. We have classified samples as large, when 200–300 individuals are caught after repeated sweepings with the nets until the bait is exhausted; medium, when 100–200 are caught; small, when 50–100 are collected; and finally very small, when only 10–50 individuals are found after repeated sweepings remove all flies from the bait area (Table 1). We are aware that this method is not very precise for estimating population size but the approximation was sufficient for our present purpose. A more exact estimation of the number of individuals in each locality is currently being carried out. In addition, attention was paid to the number of generations that elapsed between samples. While there would be seasonal differences in generation time, 22 days was taken as the average generation interval (Table 1).

Bogotá is located on a high, cold plateau in the Central Cordillera of the Colombian Andes. The various samples taken in Torobarroso represent different generations of a single population. They also represent different weather conditions, i.e., alternating periods of rainy and dry conditions. The average temperature during the rainy season is 14 °C and during the dry period 18 °C–20 °C. These same conditions hold for Aguas Calientes and Santillana. Only two samples were taken from each of these areas, one in a dry period and the other in a rainy period. Torobarroso and Aguas Calientes were done simultaneously while Santillana's sampling was completed six months afterwards.

There are some topographical differences which may be worthwhile considering. For example, Torobarroso is hilly country while the other two sites are flat lands separated by a

Table 2. Percent lethal, semilethal, and quasinormals (subvital, normal and supervitals) in the 2^d chromosomes of *Drosophila pseudoobscura* from the Altiplano of Bogotá, Colombia. *N* stands for the number of chromosomes analyzed

Sample	*N*	% lethal	% semilethal	Quasinormal		
				% subvital	% normal	% supervital
Torobarroso						
1	193	7.77	17.62	18.14	76.58	5.37
2	245	2.45	4.49	4.05	42.11	3.84
3	330	7.27	10.00	19.22	75.73	5.05
4	333	6.91	9.01	16.85	79.40	3.75
5	390	5.13	18.97	14.92	83.83	1.25
8	333	0.90	9.61	9.18	88.60	2.22
10	237	5.06	18.14	16.60	78.65	4.75
11	216	2.31	7.41	6.43	91.45	2.12
12	153	9.15	13.07	26.47	67.23	6.30
Aguas calientes						
1	487	5.75	17.66	21.19	77.27	1.54
2	450	0.88	10.44	7.93	90.00	2.07
Santillana						
1	440	0.02	10.91	10.20	87.73	2.07
2	354	1.13	9.04	9.18	87.88	2.94

Table 3. Average viabilities of the wild type class of homozygotes and of heterozygotes for the second chromosomes of *Drosophila pseudoobscura* from the Altiplano of Bogotá. *N* indicates the number of chromosomes sampled from each collection. The standard deviation of each mean is presented. Drastics are included in homozygotes but not in heterozygotes

Populations	*N*	Homozygotes	*N*	Heterozygotes
Torobarroso				
1	193	19.76±0.6840	319	23.09±0.3371
2	245	25.57±0.5073	452	25.92±0.3287
3	330	20.85±0.5010	442	24.29±0.2705
4	333	21.33±0.4817	440	24.83±0.2824
5	390	19.68±0.4833	511	25.38±0.3537
8	333	21.74±0.4735	591	24.58±0.2891
10	237	20.50±0.6441	264	23.95±0.4014
11	216	24.89±0.5730	401	27.00±0.3769
12	153	20.67±0.8106	328	24.54±0.2770
Aguas calientes				
1	487	18.04±0.3970	587	23.94±0.2658
2	450	22.14±0.3904	482	24.73±0.3237
Santillana				
1	440	21.97±0.3988	516	25.15±0.3041
2	354	22.42±0.4699	538	24.81±0.2994
Σ	4161	21.32±0.4700	5871	25.94±0.2694

mountain. Aguas Calientes has underground hot springs with dense forest and orchards, and although Santillana and Torobarroso do not present these special characteristics they may be described as humid. Intuitively, one may say that Aguas Calientes should be able to harbor dense populations while the other two cannot.

Individual wild – caught males (+i/+j) were mated singly with Δ//Ba gl (Delta/Bare glass) females from the laboratory. The F_1 heterozygous males were crossed individually to several Δ//Ba gl females in order to secure Δ//+ and Ba//+ heterozygotes for the same wild type chromosome in the F_2. The progeny collected were crossed in two ways: (1) Δ//+i females and Ba//+i males from the same culture were mated (sibs) in order to study the second chromosome in the homozygous condition. If the wild chromosome (+i or +j) does not contain genes which decrease the viability of the homozygotes, we should recover the following genotypes in equal proportion: +i//+i, Δ//+i, Ba//+i, and Δ//Ba. However, if there are loci which depress viability, there will be a proportional decrease in wild type adults (+i//+i). (2) The other kind of cross is the one between Δ//+i and Ba//+j from different F_2 cultures but from the same sample. The resulting genotypes +i//+j, Δ//+j, Ba//+i, and Δ//Ba, again expected in equal proportions, serve as a control (=heterozygotes) since only random combinations (+i/+j) of wild type chromosomes are present. The average viability of these controls represent "normality" relative to which homozygous viability is expressed. All flies were grown in the standard banana – agar medium and incubated at 22 °C.

Using (i) for allelism, (U) for mutation rate, and our previous estimates (Torobarroso collection 1, 1972) 0.046 and 0.002 respectively, the estimated and the calculated values for the elimination of lethal genes through allelism, homozygous and heterozygous genotypes were made. Since Q^2 stands for the homozygote frequency, the rate of allelic elimination could be represented by iQ^2. And, since pq stands for heterozygote frequency and h is the degree of dominance of lethal gene, then $hQ\,(1-Q)$ represents the fraction of heterozygotes eliminated; finally hQ^2 is the homozygous elimination. Therefore:

$$U - iQ^2 = hQ\,(1 - Q) + hQ^2$$

which means that the mutation rate minus allelic elimination is equal to total genotypic elimination. Then we calculate h (=dominance):

$$h = \frac{U - iQ^2}{Q}\,.$$

Table 4. Estimates of total, environmental, binominal and genetic variances of natural populations of *Drosophila pseudoobscura's* second chromosomes. While St^2, Se^2, and Sg^2 are to be multiplied by 10^{-4}, Ss^2 should be multiplied by 10^{-8}

Populations	Homozygous			
	St^2	Se^2	Ss^2	Sg^2
Torobarroso				
1	89.84	0.53	27.84	89.30
2	63.05	0.49	3.14	62.5
3	82.84	0.70	1.58	82.1
4	77.32	3.87	1.53	73.4
5	91.08	1.11	1.30	89.9
8	74.44	4.48	7.38	69.96
10	97.92	1.19	23.02	96.73
11	70.60	3.46	16.94	67.14
12	99.89	2.52	43.17	97.37
Aguas calientes				
1	76.60	1.13	3.33	75.46
2	68.43	0.910	4.04	67.52
Santillana				
1	69.82	0.45	5.21	69.36
2	77.94	4.78	9.44	73.16
	Heterozygous			
Torobarroso				
1	36.13	0.66	10.53	35.47
2	46.98	0.47	1.20	46.5
3	32.34	0.15	0.94	32.2
4	35.14	1.38	0.88	33.7
5	63.95	3.27	0.85	60.7
8	49.33	0.32	2.39	49.01
10	42.38	0.25	17.29	42.12
11	56.82	3.77	6.26	53.05
12	25.09	0.12	7.08	24.97
Aguas calientes				
1	41.40	0.24	2.16	41.26
2	50.40	0.49	3.03	49.90
Santillana				
1	47.63	0.15	3.43	47.48
2	48.14	0.55	3.87	47.59

Results

We have tested 4,161 second chromosomes for their viability performance in double dose (=homozygotes) and 5,871 random heterozygous combinations. Since the mean viability of the heterozygotes is "normal" by definition, we have for each sample a "normality". The array of viability classes studied begins with lethals, or those chromosomes which in homozygous condition produce 0–10% wild type, while semilethals are those loci with 10–50% viability relative to the "normal" viability of that sample (lethals + semilethals = "drastic"). Finally, those genetic variants showing more than 50% of the "normal" viability are classified as quasinormals.

The per cent lethal, semilethal and quasinormal second chromosomes of *Drosophila pseudoobscura* appear in Table 2. The quasinormal chromosomes broadly overlap the heterozygotes, and produce a lower mean viability. Quasinormals are further classified as normal, subvitals and supervitals (Wallace and Madden 1953). The estimate of the frequency of subvital chromosomes involves calculation of the total observed variance (St^2) of the viabilities of the homozygotes and of the heterozygote combinations for chromosomes from a given population and the breaking up of this total variance into its environmental (Se^2) and sampling (Ss^2) components in order to leave the "real" genetic variance (Sg^2). Then subvital chromosomes are defined as that part of the distribution array of the quasinormal homozygotes which lie more than two standard deviation ($2\ \sigma_g$) below the mean of the heterozygote array (Hoenigsberg et al. 1977). Tables 3 and 4 show the relevant data for the calculation of quasinormal chromosomes in Table 2. The average viability of the wild type class in homozygotes and in heterozygotes for the second chromosomes of *Drosophila pseudoobscura* appear in Table 3; clearly the homozygotes have a reduced average viability when compared to the heterozygous average. However, the extent of depressed viability is not always the same because, as we will see later, the number of non-lethal loci with some detrimental effect distributed along the chromosomes and monitored in lethal equivalent units (Greenberg and Crow 1960), can change considerably. While the overall mean percentage of drastics (=16.15%) is among the lowest on record, some samples are of course much lower (9.7 and 7.0%).

Another measurement of the genetic load which closely follows the degree of subvitality as it registers the Poisson distribution of the frequency of lethal loci along the homozygous chromosomes, is the amount of lethal equivalence (Crow and Temin 1964). The negative natural logarithm of the percentage of non-lethal chromosomes represents the number of non-lethal loci with some detrimental effect distributed along the chromosomes. Therefore, lethal equivalence manifests the average degree of subvitality (further details see

Table 5. Lethal equivalents in inbred and random heterozygotes of *Drosophila pseudoobscura* from three isolates in the Colombian Altiplano of Bogotá. *N* stands for the number of homozygous chromosomes, *homo B* is the inbred load, *let-eq B* is the lethal equivalence of the homozygous load, *hetero A* is the random load, *let-eq A* is the corresponding lethal equivalence of heterozygotes. Finally, the *B/A* ratio stands for the inbreeding over the random breeding load in lethal equivalence

Populations	*N*	*Homo-B*	*Let-eq B*	*Hetero A*	*Let-eq A*	*B/A*
Torobarroso						
1	193	0.7461	0.2929	0.9236	0.0795	3.6843
2	245	0.9306	0.0719	1.0368	0.0361	1.9917
3	330	0.8273	0.1896	0.9716	0.0288	6.5833
4	333	0.8408	0.1734	0.9932	0.0068	25.5000
5	390	0.7590	0.2758	1.0151	0.0151	18.2649
8	333	0.8949	0.1110	0.9832	0.0169	6.5680
10	237	0.7679	0.2641	0.9580	0.0429	6.1562
11	216	0.7778	0.2513	1.0800	0.0770	3.2636
12	153	0.9028	0.1023	0.9816	0.0186	5.5000
Aguas calientes						
1	487	0.7659	0.2667	0.9576	0.0433	6.1594
2	450	0.8867	0.1202	0.9892	0.0109	11.0275
Santillana						
1	440	0.8728	0.1360	1.0060	0.0060	22.6667
2	354	0.8983	0.1073	0.9924	0.0076	14.1184
Σ	4161	0.8385	0.1761	1.0924	0.0884	1.9921

Hoenigsberg et al. 1982; Wallace 1968). Table 5 presents a summary of these lethal equivalents. The last column of the same table indicates the ratio of the inbreeding over the random breeding load (=the depressed viability produced by heterozygotes).

On the other hand, Table 6 presents the amount of recessive elimination through allelism, mutation and genotypes on the basis of our data for the allelism of 41 alleles out of 911 combinations (=0.046). This value for allelism is likely to be an underestimate because the number of chromosomal permutations utilized represents the surviving group. Since for *Drosophila pseudoobscura* we recently estimated a mutation rate of 0.002, which is in some cases lower than the rate of elimination of lethal loci, we must conclude that some recessives are retained in the population. There are, however, cases in which the opposite happens: when the rate of elimination of harmful recessives through allelism exceeds the average mutation rate, we compute negative penetrance (=h), meaning that a greater proportion of deleterious loci have heterotic functions.

From the average viability of the wild type class in all homozygous chromosomes ("All homo") and from the quasinormal combinations ("Norm homo"), we calculated adaptive values (Table 7). Then the total, subvital, and lethal loads were calculated with the data expressed relative to the mean frequency of wild type flies of the heterozygotes. The homozygous load (Crow 1968) due to all deleterious loci is the total load, while the subvital load includes only the effects of the detrimental loci occurring on the chromosomes.

Table 6. Estimated and calculated values for the elimination of lethal genes through allelism, homozygous and heterozygous genotypes. The rate of allelism calculated for *Drosophila pseudoobscura* and used in these studies is 0.046 (41 out of 911 trials). Mutation rate is said to be 0.002

Populations	iq^2	pq	q^2	$hpq+2hq^2$	h
Torobarroso					
1	0.0029	0.1894	0.0642	0.3178 h	-0.0028
2	0.0002	0.0646	0.0048	0.0742 h	0.0242
3	0.0014	0.1429	0.0298	0.2025 h	0.0030
4	0.0012	0.1339	0.0253	0.1845 h	0.0043
5	0.0027	0.1829	0.0580	0.2991 h	-0.0023
8	0.0005	0.0941	0.0110	0.1161 h	0.0129
10	0.0025	0.1782	0.0539	0.2860 h	-0.0017
11	0.0004	0.0878	0.0094	0.1066 h	0.0150
12	0.0023	0.1728	0.0494	0.2715 h	-0.0011
Aguas calientes					
1	0.0025	0.1793	0.0548	0.2889 h	-0.0017
2	0.0006	0.1005	0.0128	0.1261 h	0.0111
Santillana					
1	0.0007	0.1110	0.0162	0.1434 h	0.0091
2	0.0005	0.0914	0.0103	0.1120 h	0.0134
Σ	0.0012	0.1354	0.0261	0.1876 h	0.0043

Table 7. Relative viability of the wild-type class for the second chromosomes of *Drosophila pseudoobscura* from the Altiplano of Bogotá (the wild-type class is divided by the double mutant class (△//Ba)) and the total, the subvital, and the "drastic" load in these natural populations

Populations	All homozygotes	Normal homozygotes	Normal heterozygotes
Torobarroso			
1	0.8010±0.095	0.9953±0.060	0.9431±0.060
2	1.2671±0.090	1.3455±0.061	1.1434±0.062
3	0.7817±0.089	0.8982±0.070	0.0997±0.071
4	0.8337±0.084	0.9749±0.071	1.0448±0.062
5	0.7489±0.087	0.9368±0.067	1.0924±0.066
8	0.7195±0.086	0.8807±0.076	1.0147±0.070
10	0.8333±0.099	1.0475±0.071	1.0958±0.065
11	1.1401±0.084	1.2438±0.066	1.2356±0.075
12	0.7706±0.099	0.9359±0.058	1.0027±0.050
Aguas calientes			
1	0.6676±0.087	0.8382±0.060	0.9855±0.064
2	0.8406±0.083	0.9129±0.068	1.0979±0.071
Santillana			
1	0.8425±0.084	0.9393±0.067	1.1315±0.069
2	0.9114±0.088	0.9928±0.076	1.0689±0.069

Populations	Total load	Subvital load	Drastic load
Torobarroso			
1	0.2219	0.0047	0.2172
2	0.2367	0.2968	-0.0601
3	0.2463	0.1074	0.1389
4	0.1819	0.0254	0.1565
5	0.2891	0.0653	0.2238
8	0.3292	0.1270	0.2022
10	0.1824	0.0464	0.1360
11	0.1311	0.2182	-0.0871
12	0.2606	0.0662	0.1944
Aguas calientes			
1	0.4041	0.1765	0.2276
2	0.1737	0.0911	0.0826
Santillana			
1	0.1714	0.0626	0.1088
2	0.0927	0.0072	0.0855

Discussion

Since Dobzhansky et al. (1963) did not present the complete data for the average viability of the wild type class in homozygous and in heterozygous combinations, adaptive values relative to heterozygous wild type flies cannot be computed. Therefore, there is no way to calculate the total subvital and lethal loads. Nevertheless, the estimated values for the frequency of non-lethal and non-semilethal second chromosomes which are subvital in homozygotes, correspond to approximately 42% of the area of a Gaussian curve which is about 1/2 the comparable estimate for California (=93.5 and 70.0%) and Texas (=89.6%) populations. Our comparable estimate is approximately 14% (Table 2). Therefore, the genetic load of subvital second chromosomes in the Colombian populations is the lowest ever found! Moreover, there are significant differences between the various Colombian populations and it would not be biologically meaningful to compare a Colombian population to a Guatemalan or Californian population. Some of our populations (=Torobarroso 12) have 26% subvital chromosomes, while others have 4% (=Torobarroso 2). Which is the representative one?

The study of the genetic load of these marginal isolates of *Drosophila pseudoobscura* reveals another interesting situation. As a whole, the Colombian population carries the lightest genetic load ever found for *Drosophila pseudoobscura.* As already reported by Dobzhansky et al. (1963), geographical marginality does not explain the fact that it has such low subvital and lethal loads (Table 7) because the Guatemalan population is also supposed to be a marginal group and it has the heaviest load! On the other hand, Death Valley and San Jacinto in California have loads smaller than the Guatemalan population and yet they are part of the central distribution of the species. We have, however, demonstrated that there are several distinct colonies of *Drosophila pseudoobscura* within this vast Colombian area and they are spreading. These colonies appear to respond to ecological conditions which have determined their degree of divergence. For example, the rainy and dry conditions seem to have brought about the kind of genetic loads that appeared in Torobarroso. Interchanging summer and rainy season collections, we wanted to see if the genetic structure of an isolate could have in its genome the number of concealed variants which would allow an adequate response to such cyclic stresses. From the tables reported, it is evident that although they have structural (=chromosomal inversions) poverty, the populations sampled do retain "some" genetic variability that permits genetic responses as conditions change. It is speculative but highly probable that a high degree of inbreeding during periodic environmental stress can affect the equally periodic changes in load (Tables 7 and 1).

The lethal equivalence ratio (Table 5) cannot be vindicated as a means to decide between the balanced selection theory and the neutralist (=mutational) school because its algebra does not account for very small populations (Hoenigsberg et al. 1982). There are, however, other criticisms that make its theoretical application doubtful (Wallace 1968; Lewontin 1974). Nevertheless under certain conditions its application can be an advantageous way of measuring the damage produced by the genetic load (Crow and Temin 1964). Table 5 reveals that although most samples showed relatively low (1, 2, 11, 12) B/A ratios, others (Torobarroso 3, 4, 5, 8, 10; Aguas Calientes 1, 2; Santillana 1, 2) had high B/A ratios. Therefore, what was found to be a periodic, almost cyclical change in the genetic structure of the populations, also is shown by the B/A ratios. This makes the significance of the B/A ratio doubtful. Genetic isolates, relatively depauperate in variability, do not have the structural balanced lethal systems with which to respond. Whatever balance natural selection tries to establish may be periodically swamped by migrations from other nearby demes. Evidently, we have for marginal isolated *Drosophila pseudoobscura* evidence that the genetic load is not exclusively maintained by recurrent mutations. There are low and high values for B/A ratios which indicate that there are many changes in the genetic structure of isolated *Drosophila pseudoobscura* populations. While other reported and unpublished studies of non-isolated, although marginal populations of *Drosophila willistoni,* presented uniformly low values for B/A lethal equivalence ratios, indicating a non-mutational interpretation of conventional retention of a damaging concealed load, in our present data we have for the first time in the records, temporal changes in lethal equivalence which can be interpreted with both theories: some generations retain concealed recessives by virtue of their role in the heterozygous condition (heterosis), while other generations of the same population expose the mutational load to natural selection.

Furthermore, there is a seasonal effect on load structure apparently brought about by the ecological milieu in which the population thrives, so that the frequencies of drastics (lethal and semilethal) show regular oscillations from sample to sample (Table 2), as well as concomitant fluctuations in the average homozygote viabilities (Table 3). Finally, there are periodic changes in the degree of recessive dominance (=h) reported (Table 6), which also closely follow the kind of seasonal oscillations registered (Table 1). Rainy seasons in Torobarroso sustain medium sized samples, while relatively dry conditions reduce sample size considerably (Table 1). The result is that the frequencies of lethal chromosomes and other viability classes (Table 2), plus some of the components of the genetic load, show temporal fluctuations which cannot be explained with either the mutational or the balance load theories. Within *Drosophila pseudoobscura* from the Altiplano we get both phenomena: negative as well as positive values for penetrance. The population manipulates two parameters as expected: with a lower dominance a higher frequency of genotypes is eliminated, and vice versa, with a higher dominance a smaller number of genotypes is eliminated (Table 6). None of the populations sampled can be said to have a uniform behaviour in reference to the genotypes that can be eliminated by virtue of the detrimentals carried. Therefore, to utilize an average value for h as a representative value for the average degree of dominance, would be biologically meaningless.

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