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# Relative influence of natural selection and genetic drift, along 104 years, on a population in Caceres Province (Spain)

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#### RESUMO

As alterações ocorridas nas populações espanholas nos últimos 100 anos, permitem-nos detectar variações significativas nos seus padrões genético e evolutivo. Sendo assim, tudo isso se reflete no papel prioritário da Selecção Natural nos dois primeiros períodos em estudo. Durante o último período, a Deriva Genética é o agente evolutivo mais forte. A melhoria das condições sanitárias, culturais e sócioeconómicas (menor fertilidade e mortalidade pré-reprodutiva), assim como o despovoamento rural (que provoca um maior isolamento da população estudada), determina a substituição, como agente microevolutivo principal, da Selecção Natural pela Deriva Genética na povoação de Barrado.

Palavras-chave: Selecção natural; Deriva genética; População humana; Barrado.

### ABSTRACT

The changes occured in the rural spanish populations along the last 100 years, allow us to detect significant variations in their genetic and evolution patterns. In this case, all that is reflected in terms of the priority role played by Natural Selection along the first and second periods of the study. Along the last period, Genetic Drift is the stronger agent of evolution.

The improvement of sanitary, cultural and socioeconomic conditions (lower prereproductive mortality and fertility), together with the rural depopulation (which leads to a higher isolation of the studied population), determine the replacement of Natural Selection by Genetic Drift as main microevolutive agent in the town of Barrado.

Key-words: Natural selection; Genetic drift; Human population; Barrado.

#### INTRODUCTION

The spanish town of Barrado is located at the N-E of the province of Cáceres, in the foothills of the Sierra de Gredos, specifically in the Sierra de

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San Bartolomé. The climatic conditions in this area are very different from the ones in the centre and south of the province; so, it is not possible to find, in the geographical region in which Barrado is located, the orographic and meteorological clichés typical of Extremadura.

The population of the village of Barrado (oscillating between 650 citizens in Winter and 1000 in summer) has an agricultural based economy. Concerning with this, there are important advantages because of the altitude in which the town is placed (700 m above the sea level), together with its northern situation (which provides some fair weather and relatively high hydric resources) and the quality of the cultivable soil. Because of those circunstances, the population of Barrado stares into the future without many fears, since, at present, it enjoys a hopeful economical prosperity.

However, as has been pointed out in other studies, this situation has not been the same always. Only very recently have change to better the socioeconomic and cultural conditions of this population (GONZALEZ, 1985: GONZALEZ, PRADO, 1985). In this paper, we shall analyse some factors closely related to such affirmation.

## MATERIAL AND METHODS

From the parish files of Barrado, 2,774 certificates of baptism were collected, together with 2,043 death certificates and 603 marriage certificates. They all are dated between 1st-I-1880 and 31st-XII-1983.

Afterwords, the family reconstitution method was applied. It consists of puting together in the same record card all the data of each single family unit. «Family unit» means husband, wife and their sons and daughters. This proceduree is very close to that described by FLEURY & HENRY (1976); though it has been modified and simplified in some aspects, in order to maximize the number of families covered by this study without making errors (GONZALEZ, 1985).

In this way, a total number of 729 families were completely or partially reconstituted. After a selection process, only 403 families were considered complete, and, hence, suitable for the study.

Besides that, other necessary data were obtained from the Town of Barrado and the I. N. I. (Instituto Nacional de Estadística).

Once the data had been treated properly, the study of the following parameters was done:

— Index of Chance for the Selection;

$$I = I_f + I_m = \frac{V_f}{\bar{x}^2} + \frac{P_d}{P_s}$$

where: If is the index of potential selection due to fertility.

 $I_m$  is the index of potential selection due to differential mortality.

 $\bar{\mathbf{x}}$  is the mean number of offsprings per family.

V<sub>f</sub> is the population variance in the number of descendents.

 $P_d$  is the proportion of individuals who die before reaching the reproductive age (fixed by us in 15 years).

P<sub>s</sub> is the proportion of survivors at that age.

- Effective Size (Effective Population Number):

$$N_{e} = N_{wi}^{(t)} = \frac{K_{i}^{(t)} \times N_{i}^{(t)} - 1}{\frac{N_{i}^{(t)} - 1}{N_{i}^{(t)}} \left(\frac{V_{i}^{(t)}}{K_{i}^{(t)}} + K_{i}^{(t)} - 1\right)}$$

where: N<sub>i</sub><sup>(t)</sup> is the number of parents of the population «i» in the generation «t».

 $K_{i}^{(t)}$  is the mean in the number of descendents.

 $V_{i}^{(t)}$  is the variance in the number of descendents.

- Coefficient of Breeding Isolation:

$$C = N_e \times T_i$$

where: Ne is the effective size.

T<sub>i</sub> is the effective rate of inmigration.

#### **RESULTS AND DISCUSSION**

#### Index of Chance for the Selection

The index of chance for the action of Natural Selection (I) is a method for measuring the role of selection on a certain population. CROW (1958) divides I into two factors, because selection may act both through differential fertility and through differential viability.

It should be remembered that, the higher is the value of I, the higher will be the theoretical chance for the action of selection. The result of our study, divided in periods, are shown in Table 1.

In Table 2 (from FUSTER, 1982) values of  $I_f$ ,  $I_m$ , I and the proportion  $I_m/I$  are shown. These data were obtained from several populations and from very different periods of time.

When comparing both tables, we can realize that the results obtained in Barrado could be considered as high, mainly in a first and second periods of the study.

In Spain, only a case is known in which the action of selection has been studied data starting in the last century. It is the work done by FUSTER (1982) in the village of Los Nogales (Galicia). The levels of I described there, are

will reprint	1880-1930	1931-1983	1880-1914	1915-1949	1950-1983
P <sub>d</sub>	449.75	184.23	539.41	375.98	84.29
P <sub>s</sub>	500.25	815.77	460.59	624.02	915.71
$I_m$	0.999	0.226	1.171	0.603	0.092
V <sub>f</sub>	11.444	4.193	10.654	11.049	2.146
$\frac{V_{f}}{\bar{x}^{2}}$	35.647	10.465	32.308	27.259	7.252
$I_f$	0.321	0.401	0.330	0.405	0.296
Ι	1.320	0.627	1.501	1.008	0.388

TABLE 1. I,  $I_m$  and  $I_f$ 

clearly below the results derived from our analysis, mainly because of the component  $I_m$ . This is due to the fact that, until late XXth century, the mortality described for Barrado (GONZALEZ, PRADO; 1985) is the highest amongst all the others studied in spanish populations.

The comparison with the Maragatería (BERNIS, 1974), and the population of Las Alpujarras (LUNA, 1981) is much more difficult, because those are studies done by poll into contemporaneons populations and, consistently, there is a generational overlapping. However, it can be said that the level of  $I_m$  obtained in Barrado is close to that described for the Maragatería, and higher than the one from las Alpujarras. In the other hand, the  $I_f$  value for the Maragatería is much higher than the figures for Barrado, being the latter much closer to the value described for the population of Las Alpujarras.

The levels of  $I_f$  obtained in Barrado are very close to these described for the japanese or australian populations; but they below those ones from nearer populations (like the french one) for similar periods of time,

The comparison of  $I_m$  deserves a separate mention. First of all, it must be remembered that, at the same time that a population improves its cultural, socioeconomic and demographic conditions, a clear decrease appears in the index  $I_m$ . This phenomenon also happened in Barrado; there is a remarkable reduction in the value of  $I_m$  when comparing each period of the study with the following one. However, in the first and the second parts of this study, the values obtained for  $I_m$  may be considered as high, as a result of the unfavourable conditions in which the population develops. It can be stated that the level of  $I_m$  obtained for Barrado, between 1880 and 1914, is outstandingly higher than the one described for other modern populations. And also, that it surpasses amply those values obtained for many populations supposed to be in earlier steps of development than the rural spanish population of that period.

So, a quite high value of I has been found, specially until the midle of the present century. Such a fact is attributable to the high contribution of  $I_m$  (as set out above), due to the children's mortality and prereproductive mortality which beat the area precisely until the midle of the XXth century (GONZALEZ, 1985). The fall in the index of chance for the selection, through

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POPULATION	I <sub>f</sub>	I <sub>m</sub>	I	<sub>m</sub> /	AUTHOR
Los Nogales 1871-1899	0.34	0.42	0.91	0.47	Fuster (1982)
Los Nogales 1900-1929	0.41	0.26	0.77	0.33	Fuster (1982)
Los Nogales 1930-1983	0.47	0.14	0.67	0.20	FUSTER (1982)
La Maragatería (comtem.)	0.60	0.35	0.95	0.40	Bernis (1974) <sup>1</sup>
Las Alpujarras (comtem.)	0.30	0.13	0.47	0.21	LUNA (1981) <sup>2</sup>
France (1830)	0.64	0.49	1.44	0.34	Jacquard (1974)
France (1900)	0.84	0.26	1.32	0.20	JACQUARD (1974)
Switzerland 1600-1650 <sup>3</sup>	0.73			-	Henry (1956)
Switzerland 1750-1800	0.49		<u></u> 1.1		Henry (1956)
Japan 1910	0.39	_		—	Matsunaga (1966)
Japan 1930	0.40	-	_	_	Matsunaga (1966)
Japan 1950	0.35	—		in-	Matsunaga (1966)
Australia 1900	0.40	0.25	0.75	0.33	CAVALI-SFORZA & BOOMER (1971)
New Guinea (Kiunga) <sup>1</sup>	0.44	0.47	1.41	0.33	Serjeantson (1975)
New Guinea (country) <sup>1</sup>	0.48	0.37	0.85	0.44	Serjeantson (1975)
New Guinea (urban) <sup>1</sup>	0.25	0.11	0.36	0.30	SERJEANTSON (1975)
Chile (urban, contem.)	0.45	0.15	0.67	0.22	Crow (1966)
Chile (country)	0.22	0.33	0.62	0.53	CROW (1966)
Chile (nomadic)	0.17	1.38	1.78	0.78	Crow (1966)
Brazil (Indian; Ayoreo)	1.56	0.33	2.41	0.14	Perez & Salzano (1978)
Brazil (Indian; Xavante)	0.49	0.41	0.90	0.46	Perez & Salzano (1978)
Brazil (Indian; Terena)	0.28	0.27	0.63	0.43	Salzano & Oliveira (1970)
Brazil (Indian; Cashinahua)	0.11	0.78	0.99	0.80	JONHSTON & KESINGUER (1971)
Mexico (San Pablo) <sup>2</sup>	0.31	1.63	2.46	0.66	HALBERSTEIN & CRAWFORD (1972)
Mexico (Tlaxcala) <sup>2</sup>	0.35	0.59	1.14	0.51	HALBERSTEIN & CRAWFORD (1972)
U.S.A (Indian; Uthe)	0.47	0.07	0.57	0.12	Түгев (1974)

TABLE 2. I,  $I_f$  and  $I_m$  in some populations (taken from FUSTER (1982))

<sup>1</sup>  $I_{f}^{*} = I_{f} / P_{s}$ <sup>2</sup> Fertile women

<sup>3</sup> Survival offspring

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diferential mortality, becames obvious when the temporal evolution of the quotient  $I_m/I$  is analysed: between 1950 and 1983, it means only 1/3 of the value reached between 1880 and 1914.

It all could be summed up by saying that, along a first period of 70 years, Natural Selection acts more efficiently through differential mortality. Only between 1950 and 1983 the effect of selection is exercised by means of differential fertility.

#### Breeding Isolation and Genetic Drift

The larger the degree of isolation and the smaller the size, the stronger is the action of Genetic Drift on a population.

LASKER & KAPLAN(1964) established, on the previous premise, the coefficient of breeding isolation (C). It is obtained as the product between the effective rate of inmigration and the effective population number.

The Genetic Drift's acting chance will be small when the value of C is higher than 50, and will be high when C is below 5.

Previously to the calculus of the effective population number  $(N_e)$ , we shall reckon the breeding size.  $(N_b)$ .

The estimate of breeding population number, in the periods 1880-1914 and 1915-1949 has been done following BERTRANPETIT (1981). This is due to the fact that it was not possible to obtain the population's distribution, by sex and age, for these periods. So, we calculated the proportion of married individuals in relation to the total number of members in the population. Afterwords, the obtained value was corrected when we took into account the possibility of those marriages to be fertile (see Table 3).

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	( 6671 2/5 °C 12 7 °C	1880-1914	0.45	1915-1949	1950-1983	-side	
-	Population size	530		741			
	Women in population				341		
	Married persons	270		284			
	Women between 15 and 45 years old				127		
	Proportion	0.509		0.383	0.372		
	Probability to get married				0.976		
	Probability to have a fertile union	0.934		0.950	0.956		
	N <sub>b</sub> Proportion	0.475		0.364	0.347		
	Population (harmonical mean)	591		774	816		
	Breeding size (N <sub>b</sub> )	281		318	283	1	
-							

TABLE 3. Measurement of Breeding Population Number

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Between 1950 and 1983, period for which there is not a reliable estimate of the proportion of married people, it has been possible to obtain the data by sexes and ages. It has been considered the proportion of women aged between 14 and 44 (accepted as the feminine fertile period) in relation to the total number of women in the population. Next, it was corrected on the basis of the rate of definitive celibacy (reckoned by GONZALEZ (1985), for the population of Barrado). It was also necessary to do a second correction because of the probability of these women to establish a fertile union (Table 3).

The total number of individuals in the population has been calculated for the three periods. Starting from its value, we obtained the breeding population number through the harmonic mean of the available censuses.

On the basis of the results reckoned for the breeding size, we can proceed to estimate the population's effective size. The formula used is that from MORTON (1973), but, instead of the number of offsprings born alive, we have made use of the number of them who have reached the reproductive age (and, logically, its variance).

In Table 4 are shown the values of  $N_i$ ,  $V_i$  and  $K_i$ , together with the number of reconstituted families used in the calculus of this part of the study. The effective population number, and its proportion in relation to the total number of individuals in the population, are shown in Table 5.

Between 1880 and 1949, the variance in the number of descendents is higher than the mean, and, hence,  $N_e$  is smaller than  $N_b$ . Between 1950 and 1983, those proportions are the opposite.

The proportions of both the effective size and the breeding size in relation to the total number of individuals in the population, are clearly higher than those described in Formentera by BERTRANPETIT (1981), and in Los Nogales by FUSTER (1982).

In a parallel way, the estimate of the effective rate of inmigration was carried out. For that purpose, we calculated the frequencies of foreing parents (in percentage/100) on the total number of reconstituted families used in our study.

The effective rate of inmigration, the breeding size and the coefficient of breeding isolation are displayed in Table 6, for the three periods studied. In the periods 1880-1914 and 1915-1949, the values of C are very similar. The coefficient of breeding isolation remains almost constant, due to the increase in effective size, The later, counteracts the fall in the effective rate of inmigration.

Nevertheless, inmigration keeps falling until the end of the study, and between 1950 and 1983 there is a reduction in C in spite of the increase in  $N_e$ . Therefore, we face a population tending towards a gradual reproductive isolation.

When comparing the coefficient of breeding isolation amongst different populations we meet plenty of problems, because of the fact that there will always be a reliance on the pattern of populational association chosen by the author (parish, municipality, neighbouring villages, shire, etc).

Families	Ki	Vi	$N_i (= N_b)$		
1880-1914	142	2.803	3.496	281	
1915-1949	155	3.426	4.206	318	
1950-1983	88	2.583	1.655	283	

TABLE 4. Breeding population number  $(N_i = N_b)$  and families that were included in the study of  $K^i$  and  $V^i$ 

 

 TABLE 5. Effective population number and its percentage with respect to the total population

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Less secondar	Harmonical mean; population	N <sub>e</sub>	%
1880-1914	591	258	43.65
1915-1949	774	299	38.63
1950-1983	816	330	40.44

TABLE 6. Effective rate of inmigration  $(T_i)$ , effective population number  $(N_e)$ and coefficient of breeding isolation (C)

<ol> <li>Serie area data?</li> </ol>	Τi	N <sub>e</sub>	C
1880-1914	0.1217	258	31.40
1915-1949	0.1043	299	31.19
1950-1983	0.0455	330	15.02

In Formentera, BERTRANPETIT (1981) obtains a value close to 35, from an effective size of 573 individuals. In Los Nogales, FUSTER (1982) describes a figure for C of about 170, being  $N_e$  equal to 1,230; nevertheless, he obtains, in a certain parish of that municipality, a value of C close to 11 (10.8) from an  $N_e$  of 63. LUNA (1980) gives a coefficient of breeding isolation of about 104 for the population of Las Alpujarras, being  $N_e$  equal to 842 individuals.

In general, it can be noticed that the values of C are clearly higher than 5 in all the studies previously mentioned. Only FUSTER obtains a value of 10.8, but with a very small  $N_e$ .

We can consider that, in Barrado, the estimate of C offers a low value between 1950 and 1983. Such an estimate could lead to think of a possible action of Genetic Drift, mainly due to the high isolation of the population in terms of reproduction. Mutation, migration, selection and genetic dirft act on populations as microevolutive agents. The current research techniques do not allow an immediated analysis of mutation, and neither do they allow to quantify the contribution of migration in the genetic pool of populations. The two ways of maximum efficiency in order to study the evolution of current populations (and in recent periods of time) are those analysed in this paper.

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