

## POPULATION GENETICS OF WESTERN MEDITERRANEAN INSULAR LIZARDS

by

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The islands have attracted a great deal of attention to the evolutionary biologists ever since Darwin (1859) gave strong support to the theory of evolution by taking various remarkable examples from the Galapagos Islands. This stems from the fact that terrestrial organisms living in the oceanic islands are greatly constrained in their dispersal by intense marine barriers, which frequently provide all the necessary requirements for rapid processes of genetic divergence often associated with speciation.

The inter- and intraspecific genetic variability of organisms inhabiting some oceanic archipelagos have been recently subjected to a deep scrutiny by multidisciplinary approaches, using allozymes, serologic tests, DNA analyses, chromosomes, and behavioral traits, to set up comparisons with the classical morphological characters. Many species of *Drosophila* of the Hawaiian Archipelago (Carson *et al.*, 1967; Carson and Kaneshiro, 1976; Carson, 1983; Hunt and Carson, 1983), and several species of terrestrial vertebrates from the Galapagos Islands (reviewed by Patton, 1984), are among the most outstanding instances of this type.

Although the continental islands, that is those connected by the marine platform to the near mainland, have significantly less endemism than the oceanic ones, they can commonly provide

valuable tools for studying the effects of insularity on the genetic structure of populations. Indeed the marine barriers isolating populations of the continental islands may also be noteworthy, but since these islands, usually share a past geological record of terrestrial connection with the mainland, it allowed a regular genetic exchange between conspecific populations of both sides at the time when bridges were present. Whether these populations reached the status of a new species or not, it mostly depends on the time elapsed since the breakage of the last terrestrial bridge, on possible migrations, and on intrinsic characteristics of populations.

Two endemic species of lizards are found in the Balearic Islands, *Podarcis lilfordi* Gunther of Mallorca and Menorca (Gymnesies), and *P. pityusensis* Boscá of Eivissa and Formentera (Pityuses Islands). While the former is only living in the small islands and islets neighboring the Gymnesies, the latter live both in the main Pityuses themselves and in their surrounding islets. These Balearic lizards are highly polytypic species with great numbers of the so-called "subspecies" (Colom, 1978; Salvador, 1984), one for almost each insular entity that they colonize. An electrophoretic survey of the genetic variability for allozymes has been carried out in several insular populations of *P. lilfordi*, mostly coming from the Cabrera subarchipelago, close to the southeastern coast of Mallorca (Ramón *et al.*, 1986), and in the counterpart populations of *P. pityusensis* (Guillaume and Cirer, 1985; Cirer and Guillaume, 1986). We describe herein the electrophoretic results obtained in four populations of *P. lilfordi* from small islands and islets close to the coast of Menorca, and in one population of *P. hispanica* from the Columbrets Islands. *P. hispanica* is an allied species to the previous Balearic lizards, which is very likely their phyletic ancestor, having a widespread Iberian distribution. These findings are discussed with the preceding ones (Ramón *et al.*, 1986) to get a better understanding of the genetic structure and differentiation of the insular lizards of the three checked species.

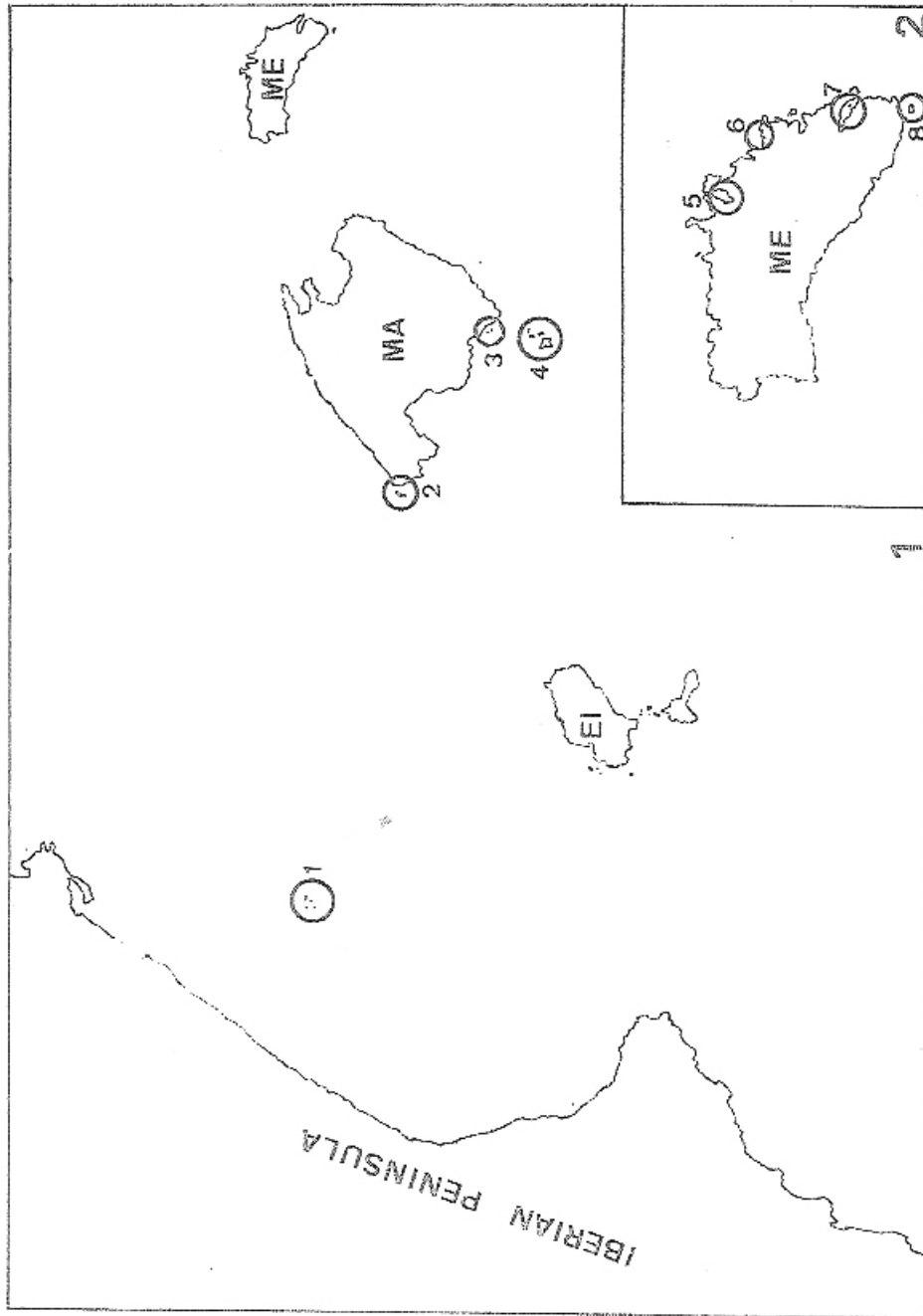
## MATERIAL AND METHODS

The populations studied in the present analysis and those examined before, for comparative purposes, are reported in *Table 1*. The geographical location of these populations is indicated in *figures 1 and 2*. The lizards were caught by traps or by hand directly and were frozen at  $-40^{\circ}\text{C}$  immediately on arrival to the lab and kept in the freezer until their analysis. Horizontal starch gel electrophoresis was used as in our previous study (Ramón *et al.*, 1986) of pooled homogenates of heart, liver, kidneys, and testes or ovaries, in 0.2M Tris adjusted to pH 7.2 with 1N HCl. The techniques given by Selander *et al.* (1971) were followed with some minor changes, to reveal the electrophoretic patterns of *lactate dehydrogenase* (LDH), *xanthine dehydrogenase* (XDH), *malate dehydrogenase* (MDH), *isocitrate dehydrogenase* (IDH), *glutamate oxalacetate transaminase* (GOT), *phosphoglucosomutase* (PGM), *phosphoglucosomerase* (PGI), *albumin* (ALB) and *esterases* (EST).

*Table 1. Sampled populations of Western Mediterranean Podarcis lizards.*

species	island group or main isle	insular sample
<i>P. hispanica</i>	Columbrets Is.	Columbret Gran (CG)
<i>P. tilfordi</i>	Menorca	Sargantana (Sa)
"	"	Gran d'Addaia (GA)
"	"	Rei (Re)
"	"	Aire (Ai)
"	Mallorca	Dragonera (Dr)*
"	"	Moltón (Mo)*
"	"	Guardia (Gu)*
"	Cabrera subarchipelago	Foradada (Fo)*
"	"	Pobra (Po)*
"	"	Conillera (Co)*
"	"	Esclutasang (Es)*
"	"	Rates (Ra)*
"	"	Cabrera (Ca)*
<i>P. pityusensis</i>	Mallorca (introduced population of Mirada in Palma de Mallorca)*	-----

\*Ramón *et al.* (1986)



Figures 1 and 2. Geographic sources of the checked insular *Podarcis* lizards. MA = Mallorca, ME = Menorca, EI = Eivissa, 1) Columbretes Islands, 2) Dragonera, 3) Dragonera, 4) Cabrera subarchipelago, 5) Sargantana, 6) Gran d'Addaia, 7) Rei, and 8) Aire.

## RESULTS

Eighteen protein loci were analyzed in the four insular populations of *P. lilfordi* and in the only one of *P. hispanica*. The existence of the six esterase loci was tentatively presumed from the number and location of the electromorphs in the zymogramms but it remains to be proved by experimental rearing and crossing of the lizards. The allelic frequencies and mean heterozygosities for these loci and populations are given in *table 2*. Only one system, *Got-2*, was found monomorphic in the two presently studied species of *Podarcis* lizards. *Pgm-1* and *Pgm-2* were monomorphic in the Menorca populations of *P. lilfordi* but not in that of *P. hispanica* from Columbrets. *Xdh*, *Mdh-1*, *Mdh-2*, *Got-1* and *Alb* displayed monomorphism in the population of *P. hispanica* contrary to at least some of those of *P. lilfordi*. The *Xdh* and *Alb* fixed alleles of *P. hispanica* from Columbrets were unique and therefore critical for distinguishing this species with regard to *P. lilfordi*. The average frequency of heterozygous individuals per locus and mean heterozygosity per population ( $\bar{H}$ ) were calculated to get a reliable measure of the genetic variation for soluble proteins. It stands out that the mean heterozygosities vary strikingly among loci depending on the degree of polymorphism. Also, a wide variation in the mean heterozygosities was evidenced among populations, ranging from  $\bar{H} = 0.134$  to  $\bar{H} = 0.208$ .

## DISCUSSION

The electrophoretic data gathered in the present analysis can be used to scrutinize the genetic structure of these insular populations of *Podarcis* lizards in Western Mediterranean as an attempt to reveal the main factors involved in their differentiation. The allelic frequencies and mostly, the level of heterozygosity per population, are valuable tools to ascertain the possible role of the founder effects, genetic drift, migration, selective forces, and to evaluate any consistent interrelationship between the genetic inde-

Table 2. Allelic frequencies and mean heterozygosities (H) in the eighteen surveyed loci of insular lizards. CG = *Columbreis Gran* (P. hispanica), Sa = *Sargentana*, GA = *Gran d'Addaita*, Re = *Rei*, Ai = *Aire* (P. ilfordi), s = silent alleles.

enzyme	CG (17)	SA (20)	GA (20)	RE (13)	H	Ai (20)	H	GA (20)	RE (13)	H	SA (20)	Ai (20)	H
LDH-1	1	.853	1	.963	.975		.813	.867		.675	.875	.828	
	2	.055		.036			.187	.233		.325	.925	.063	
	3	.059										.859	
	s		.261		.073	.049	.304		.444	0		.139	.302
EST-2	1	.979		1	.975		.125	.194		.154	.200		
	2	.022			.025		.875	.850		.846	.800		
	s		.058		0	.049	.316	.255		.260	.200	1	0
XDH	1		.267	.654	.334		.813					.300	
	2		.133	.345	.456	.456	.187	.300		.265	.850	.300	
	3						.304	.700		.615	.150	.200	
	s	0			.230	.439	.304		.430	.473	.150	.255	.320
MDH-2	1		.200	.115	.650			1		1	1		.950
	2		.200	.200	.456	.456	.031						
	3						.969						
	s	0				.434						.050	.695
TPI	1		.230	.143	.590		.969						
	2		.230	.307	.456	.456	.031				.975		.925
	3							1		.855	.025		
	s	0			.245	.596		.060		.203		.040	0
PGR-1	1			.962	.975								.138
	2			.038	.025								
	3						.031						
	s	0			.073	.073	.063			0			
PGR-2	1		1	1	1		.429						
	2												
	3												
	s	0				.434							
PGR-1	1		.979	.962	.975		.688				.675	.585	
	2		.022	.038	.025	.025	.194				.025	.075	
	3										.430	.475	
	s	0			.073	.073	.373			.454	.204	.492	.499
PGR-2	1			1	1								.205
	2						.140		.134	.149	.154		

xes and biogeographic or historic parameters of the prospected islands. Furthermore, the genetic divergence between populations and species of these lizards should be dealt with to get quantitative estimates for evolutionary and taxonomic considerations.

#### a) Genetic variation

The amount of genetic variation given as the mean heterozygosity per population is surprisingly much higher in the Western Mediterranean insular *Podarcis* lizards than the average for reptiles, and the values found in other Mediterranean congeneric populations more particularly (see *table 3* for references). These high mean heterozygosities are shared by most *P. lilfordi* populations in the present samples from Menorca small islands and in the previously analyzed ones from the Mallorca group (Ramón *et al.*, 1986). The *P. hispanica* population of Columbrets shows also a high heterozygosity, and the same could be said for those of *P. pityusensis* from the Pityusic Islands, recently reported by other

*Table 3. Mean individual heterozygosities in populations of Podarcis lizards.*  
(m) = mainland, (i) = insular.

species	heterozygosities	source
<i>P. lilfordi</i> (i)	0.040 - 0.212	Ramón <i>et al.</i> (1986) present work
<i>P. pityusensis</i> (i)	0.027 - 0.185	Cirer & Guillaume (1986)
<i>P. hispanica</i> (m)	* 0.050	Guillaume & Lanza (1982)
" (i)	0.168	present work
<i>P. muralis</i> (m)	0.012 - 0.021	Guillaume & Lanza (1982)
<i>P. tiliguerta</i> (i)	0.005 - 0.052	Guillaume & Lanza (1982)
<i>P. melisellensis</i> (i)	0.000 - 0.077	Gorman <i>et al.</i> (1975)
<i>P. sicula</i> (i)	0.029 - 0.057	Gorman <i>et al.</i> (1975)
" (m)	0.059 - 0.129	Gorman <i>et al.</i> (1975)
" (m)	0.022 - 0.049	Guillaume & Lanza (1982)
Average Reptilia	0.047	Nevo (1978)
Average Vertebrates (m)	0.087	Nevo (1978)
Average Vertebrates (i)	0.017	Nevo (1978)

authors (Guillaume and Cirer, 1985; Cirer and Guillaume, 1986).

It can be generally predicted a lower level of genic variation in islands than in the mainland, either due to founder effects and a decrease in the population size or to stronger selection pressures because of the great reduction in the potential ecologic niches available for the species of islands. This expectation is commonly agreed with the facts at least for the allozyme data of vertebrates with few exceptions (Nevo, 1978; Kilpatrick, 1981; Patton, 1984). Why the present *Podarcis* lizards deviate from this rule? There are at least three possible answers to this question. First, the selection pressures exerted by the predators of lizards would be clearly less in these small islands than in the large islands or the mainland since most mammals, birds and snakes living on the latter are not found in the former. The extinction of *P. lilfordi* in Mallorca and Menorca themselves would argue in favour of this view. This, by no means would exclude the presence of any predator, some seabirds like the gulls and even humans sometimes may act as predators over lizards in these small islands. However, much lower predation rates can reasonably be assumed on them than in the mainland or large islands, which would allow to reach great population sizes of lizards except in the least suitable or very tiny islands obviously. Second, the passive migration of lizards among geographically very close small islands, over drift masses of vegetables or inside canes, is likely to have occurred for instance in the Cabrera subarchipelago, but not in those islands far apart from potential sources of migration such as in the Columbrets islands or in the Dragonera to a lesser extent. Thus, the immigration by itself would not account for the high heterozygosities found in some insular populations of lizards. A third alternative, that of a selectionist explanation for the allozyme differences among populations will be discussed in more detail later.

MacArthur and Wilson (1967) stated that the species diversity is positively correlated with the island size in their well-known model for island colonization. In the Jaenicke (1973) model of insular polymorphism the frequency of polymorphic loci is expected to be directly proportional to the area of the island. This



correlation can also be predicted both from the selectionist and the neutralist positions due to the correspondence between niche availability or simple population size with the genetic variation, respectively. Gorman *et al.*, (1975) developed a multiple regression analysis in several species of insular Adriatic lizards of the genus *Podarcis* – formerly included within *Lacerta* – to correlate the heterozygosities with some geographic parameters of these islands and they found a maximum value for the log of island area. Similar results were also obtained in other species of insular non-reptilian vertebrates (Kilpatrick, 1981; Patton, 1984). The same kind of analysis was also performed in our fourteen insular population samples of lizards which is illustrated in *figure 3*. The coefficient of correlation,  $r = 0.491$ , was not significant but did approach rather closely to the 0.05 level of significance. This deviation with respect to the predicted correspondence might be attributed to a lesser number of screened loci or sampled individuals in four populations than in the remaining (see Ramón *et al.*, 1986).

b) *Is there selection for the allozyme variants?*

Twenty years of allozyme research by gel electrophoresis have produced huge amounts of polymorphic data in a continuously increasing number of species, which have often been interpreted either from a selectionist or a neutralist viewpoint. Nowadays most authors give more credit or are even tight adherents to the theory of neutrality. A recent book by one of the most outstanding propounders of this theory (Kimura, 1983), discusses the “pros” and “contras” and provides an impressive support to the neutral features of polymorphic protein variants, although some doubts can still be raised after new insights into the problem (Gillespie, 1984).

Several tests have been devised to discriminate between both alternatives except that none of them is completely satisfactory (Lewontin, 1985). Nevertheless, the test by Lewontin and Krakauer (1973) is maybe the most frequently used with this aim in monophyletic populations. It states that under the hypothesis of

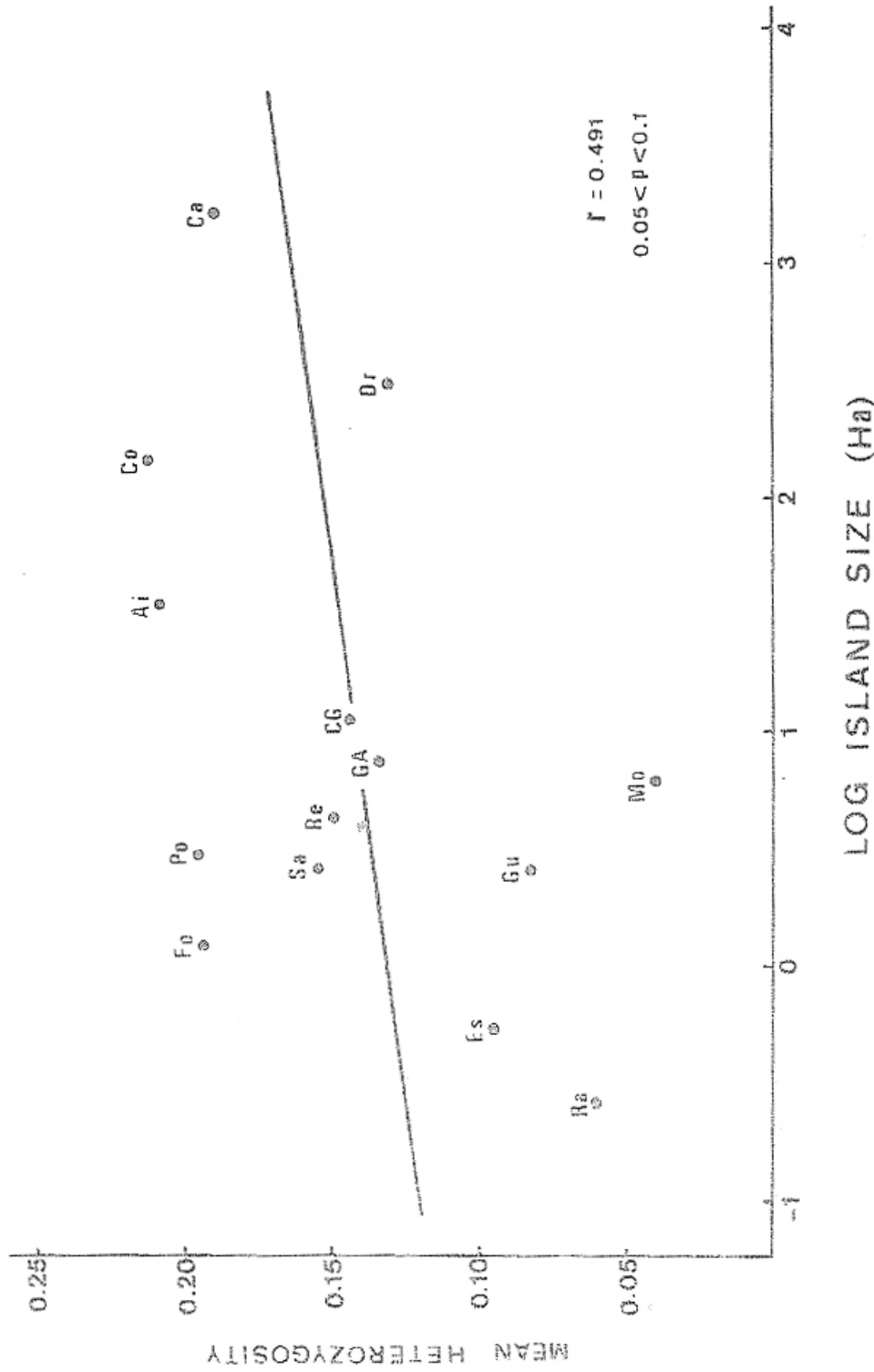


Figure 3. Mean heterozygosities per population plotted against log of island size in fourteen insular samples of *Podarcis lizards* (see Table 1 for the nomenclature).

neutrality the inbreeding should have a uniform effect over all loci. Therefore, using the standardized variance ( $F$  or  $F_{st}$ ) of the allelic frequencies (Wright, 1943) as:

$$F = \frac{\sigma_p^2}{\bar{p}(1-\bar{p})}$$

being  $\bar{p}$  the mean frequency of a determined allele in the checked populations and  $\sigma_p^2$  its variance, the heterogeneity of the  $F$  values is weighted by the following formula:

$$k = (n-1) S_f^2 / \bar{F}$$

where  $n$  is the number of populations,  $S_f^2$  the observed variance and  $\bar{F}$  the mean of means. When  $k > 2$  it implies selection and if  $k < 2$  neutrality can be invoked, but caution should be exerted in assuming  $k = 2$  as the critical figure since it can be higher sometimes (see Kimura, 1983). This is the same as calculating the ratio  $S_f^2 / \sigma_f^2$ , being  $\sigma_f^2 = 2F / n-1$ , when the ratio is  $> 1$  selection is involved but when it is  $< 1$  neutrality is suggested.

Eleven polymorphic loci can be taken in the thirteen surveyed insular populations of *P. lilfordi* lizards to develop the Lewontin and Krakauer (1973) test on them. Among the sampled loci we have removed the *Est* ones since in most the presence of silent alleles did not allow an accurate identification of the individual genotypes. The  $F$  values for these loci are reported in *table 4* and it can be seen there that the  $k$  value is clearly smaller than 2 and the ratio  $S_f^2 / \sigma_f^2$  is also clearly smaller than 1. Consequently, the observed polymorphism for these eleven loci in the lizard populations is in agreement with the hypothesis of neutral variation. The differences detected in the  $F$  values among loci are understandable as caused by changes in the sizes of populations, genetic drift, inbreeding, and/or founder effects.

### c) Genetic distances and their evolutionary and taxonomic implications

The allelic frequencies in the eighteen electrophoretically analyzed loci provide also valuable information to measure the degree

Table 4. Standardized variances of allelic frequencies for eleven loci in thirteen insular populations of *P. lilfordi*.

<u>Ldh-1</u>	1.124	
<u>Ldh-2</u>	2.094	
<u>Xdh</u>	0.934	
<u>Mdh-1</u>	1.937	$\sigma_F^2 = 0.571$
<u>Mdh-2</u>	2.019	
<u>Got-1</u>	1.505	$k = \frac{(n-1) S_F^2}{F^2} = 0.976$
<u>Pgm-1</u>	2.585	
<u>Pgm-2</u>	2.571	$S_F^2 / \sigma_F^2 = 0.488$
<u>Ath</u>	1.802	
<u>Pgi</u>	2.217	
<u>Idh</u>	1.469	
mean	1.805	
variance	0.279	

of differentiation between insular populations both intra- and interspecifically. The genetic distances proposed by Nei (1972) for estimating identity (I) and distance (D) between populations have been applied to our five sampled populations of lizards, and four additional ones of the previously worked Balearic lizards are included as points of reference too (table 5). It is evident from the distance values that the *P. hispanica* from Columbrets is well differentiated from both Balearic lizards, *P. pityusensis* and *P. lilfordi*. Similar levels of genetic distances have been reported by Cirer and Guillaume (1986) between *P. pityusensis* and *P. muralis*, being the latter a species very allied to *P. hispanica* on morphological and biometrical grounds (Vives-Balmaña, 1982). Four species of *Podarcis* lizards including both *P. hispanica* and *P. muralis* have shown a broad range of Nei's genetic distances, from  $D = 0.206$  to  $D = 1.114$  (Guillaume and Lanza, 1982). Furthermore, the average of genetic distance between three species of *Podarcis* from Eastern Mediterranean was  $\bar{D} = 0.38$  (Mayer and Tiedemann, 1982). Therefore, the present figures of I and D

Table 5. *Nei's* genetic identities (above) and distances (below) between nine populations of the three studied *Podarcis* lizards, *P. hispanica* (CG), *P. pityusensis* (MU), *P. lilfordi* (GA RE, SA, AI, CA, DR, GU).

	CG	MU	GA	RE	SA	AI	CA	DR	GU
CG		.608	.555	.578	.536	.520	.570	.578	.553
MU	.497		.914	.800	.767	.764	.842	.912	.880
GA	.570	.205		.970	.900	.849	.870	.756	.833
RE	.531	.222	.029		.854	.811	.878	.755	.828
SA	.623	.256	.104	.156		.901	.921	.754	.846
AI	.652	.269	.162	.209	.103		.914	.759	.799
CA	.560	.171	.139	.130	.082	.089		.834	.965
DR	.546	.092	.279	.280	.281	.262	.181		.876
GU	.425	.127	.182	.188	.167	.223	.144	.131	

between *P. hispanica* and the two Balearic species of *Podarcis* are in good agreement with the rough general picture obtained in this genus.

Contrary to the above interspecific correspondances, the genetic distances between conspecific populations of *P. lilfordi* are greater than those reported within other species of *Podarcis*. The insular populations of *P. lilfordi* differ from each other in a range of genetic distances from 0.029 to 0.281 with a mean of  $\bar{D} = 0.167 \pm 0.015$  whereas those of *P. melisellensis* and *P. sicula* studied by Gorman *et al.* (1975) have ranges of distances from 0.003 to 0.116 and from 0.001 to 0.063, respectively. In an attempt to get an account on the observed genetic distances between populations of *P. lilfordi* they were correlated with the geographic distances (in Kms.) but the correlation value,  $r = 0.504$ , was found not significant. The paleogeographic record of island separation based upon the depth of the marine channels and the eustatic changes during the last pleistocene glaciation can be inferred after some geologic studies of the Western Mediterranean coast (Lumley, 1976; Pomar and Cuerda, 1979; Cuerda, 1983). Mallorca and Menorca, with a channel depth of about 90 m., became finally isolated around 22,000 years ago while Dragonera and the Cabrera subarchipelago were detached from Mallorca around 9,000-10,500 years ago, and the remaining small islands surrounding Mallorca and Menorca within the period of 5,000-8,000 years from present. Thus, greater genetic distances would be expected in the pairwise comparisons of Dragonera or Cabrera with the Menorca small islands populations than the latter between themselves. This is true for the average genetic distance between Dragonera and the Menorca islets,  $\bar{D} = 0.275 \pm 0.015$ , but not for that between Cabrera and the Menorca islets,  $\bar{D} = 0.110 \pm 0.013$ , since the average genetic distance of the latter between themselves is  $\bar{D} = 0.128 \pm 0.025$ . However, the origin of these small islands is quite recent so the time elapsed would not likely be reflected in terms of genetic distances. Although Cirer (1987) in her study on the insular populations of *P. pityusensis* claims that there is a correspondance between the insular age and the genetic distances we have been completely unable to prove it in the *P. lilfordi* populations.

A very interesting problem concerns the genetic and evolutionary interrelationships between the two Balearic lizards, *P. lilfordi* and *P. pityusensis*. The average genetic distance between the introduced population of *P. pityusensis* in Palma de Mallorca and the whole checked populations of *P. lilfordi* gives a rather low value,  $\bar{D} = 0.192 \pm 0.022$ , very similar to that found in comparing the *P. lilfordi* populations from Mallorca and Menorca islets,  $\bar{D} = 0.167 \pm 0.015$ . Based upon these genetic data the existence of two independent species of Balearic lizards is unjustifiable which supports also the assertion by Bischoff (1973) about the high likelihood of the  $F_1$  hybrids between the two lizards to propagate themselves. A sound taxonomic proposal would be keeping *pityusensis* as a subspecies of *P. lilfordi* simply on morphological and biogeographical basis and removing all the other described subspecies of both Balearic *Podarcis*, which would be no more than local races in many cases. Nevertheless, this proposal does not give a phylogenetic answer to the splitting of the Balearic lizard into two groups of islands, Gymnesies and Pityuses, whose separation can be roughly dated to 5-6 million years from present. Until very recently, the fossil remains of *Podarcis* had only been described from Mallorca and Menorca but they are now also known from the Upper Pleistocene of Eivissa (Alcover *et al.*, 1981), so the *Podarcis* lizards were living in all the main Balearic islands well before the human arrival. Because of this fact we are very much compelled to assume several events of migrations between the two groups of *Podarcis* to account for the high genetic homology found in the lizards from the Gymnesies and the Pityuses.

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### SUMMARY

Eighteen protein loci have been electrophoretically analyzed in one population of *Podarcis hispanica* lizards from the Columbrets Islands and in four others of *P. lilfordi* from islets close to the Menorca coast. These populations and almost all of those previously studied from Mallorca showed much higher mean heterozygosities than the average for reptiles. This fact could be tentatively explained firstly by the large population size effects and secondly by possible migration events on the genetic structure of a selectively neutral pool of allozymic alleles. The genetic distances allowed a sharp discrimination between *P. hispanica* and both Balearic *Podarcis*, but not between the latter two. Thus, *P. pityusensis* should be synonymized with *P. lilfordi* but having a possible taxonomic status of subspecies in agreement with the hybridization results got by other authors. Some possible correspondences between genetic distances and geographical parameters are also discussed.

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