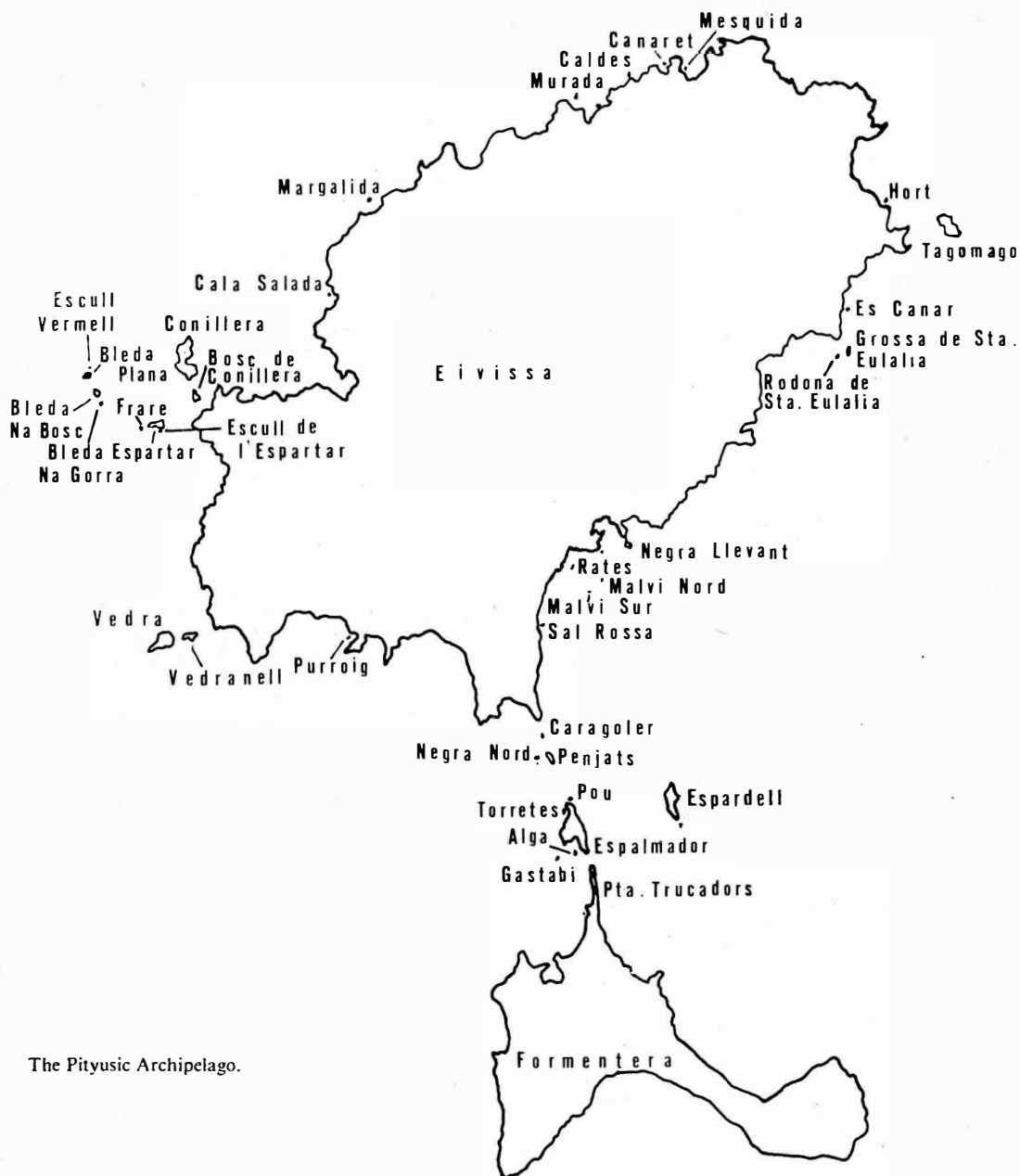


THE HERPETOLOGICAL JOURNAL



The Pityusic Archipelago.

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Four clear conclusions can be drawn from the three five day conditioning periods and four one day experiments; 1) palmate newts readily catch and eat frog tadpoles, 2) palmate newts almost totally reject toad tadpoles, 3) recognition of distasteful prey by palmate newts is not innate but learnt and 4) because palmate newts can learn to distinguish between palatable and unpalatable prey, frog tadpoles gain no long term (only short term) protection against newt predation through mixing with toad tadpoles.

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THE POLYMORPHISM OF *PODARCIS PITYUSENSIS* AND ITS ADAPTATIVE EVOLUTION IN MEDITERRANEAN ISLES

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ABSTRACT

The variation in morphological and colouring features shown by the insular lacertid populations of *Podarcis pityusensis* is discussed from the point of view of their adaptive advantages to specific insular ecosystems. Insularity factors, i.e. area and island-age, have been found to be related to average body size, and the average luminosity of each population. Populations tend to show a size increase, a greater morphological homogeneity and darker dorsal colouring on smaller and older islands. The advantages of larger size and melanism are discussed as well as their possible causes in the insular microecosystems of the Pityusic Archipelago. Genetic drift seems to play a secondary role, whereas a positive selection in favour of melanism and giantism is observed. Both features are not linked as cause and effect, but seem to share a common cause: isolation and time enough to allow selection to take place. Predation, though slight in degree, does exist, and seems to be one of the selective pressures favouring melanism, together with the parallel trend towards an increase in body size and the need to an effective thermoregulation during the early hours of the day.

INTRODUCTION

The great morphological variety, number of dorsal scales and body colouring shown by insular lacertids has often been analysed exclusively using taxonomical criteria, without considering the adaptative significance that could lie behind these variations in most of the available reports. It has even been stated that some

body size defining features (giantism and dwarfism in insular populations) or the number of dorsal scales showed a neutral selection (Radovanovic, 1954).

However, most authors nowadays accept that animal features are variable to a greater or lesser degree depending on their adaptative value. The adequate conditions for life in a specific environment must necessarily change if that environment changes.



Fig. 1 The Pityusic Archipelago.

Accordingly, the conditions particularly involved in the relationship of the living being with its environment are those endowed with a greater evolutionary plasticity. These features are associated with ectodermic organs, such as the skin, sensorial organs, etc. Functions related to interaction with the environment, except for cases where their stability is essential for the survival of the individual or species, are therefore very plastic. When very similar forms are being studied, i.e. subspecies or close varieties, the most important features are these being shaped at that precise moment by a known environment, whose ecological implications can be studied. These are relevant in terms of population genetics and ecology.

After exhaustive studies for taxonomic purposes (Cirer, 1987), which have provided a deep knowledge of all *Podarcis pityusensis* populations and their intrapopulational variability, this review is presented with the aim of establishing some of the general patterns of morphological variation, between both sexes as well as among the different populations of the species. These patterns are probably due to adaptation to insular environments.

This lacertid appears all over the Pityusic archipelago, south of the Balearic Islands, in the Spanish Mediterranean Sea (Fig. 1), comprising the Island of Ibiza and Formentera southwards (the only islands permanently inhabited by human beings), and a considerable number of islets varying greatly in area, height and distance from the biggest nearby island (Ibiza). All are located on a continental shelf not more than 80 metres deep and, accordingly, when the sea receded in the Quaternary glaciations formed a single piece of emerged land.

Not all biometric and scale number variables used in the foregoing taxonomic studies seem to be relevant to biogeographical studies; therefore, a small number of variables has been selected to avoid the 'background noise' caused by an excess of information. The features taken into account are mainly those related to general body shape and colouring, since they play a more relevant role in interactions with the environment and with other individuals — conspecific or not. The changing of these traits has been studied particularly in insular reptile populations, in which the adaptative significance of features such as gigantism, dwarfism, melanism and other hypertelic trends have been analysed (Sacchi, 1961).

DWARFISM AND GIANTISM AND ISLANDS

Both phenomena are clearly present in all the fauna living in small isles worldwide; among the reptiles, there are such classic examples as the giant turtles from the Indian Ocean Archipelagos, the giant monitors in Komodo, etc. Insular dwarfism has been registered more frequently among mammals and invertebrates, but there are also examples among reptiles.

In the Balearic Islands there are good examples of dwarfism, (terrestrial Gasteropoda) and gigantism (tenebrionid Coleoptera). Balearic lizards, like the ones in all other Mediterranean islands present no remarkable examples of gigantism or dwarfism, but they do show a trend towards increased body size when compared to similar continental populations or, more rarely, towards a decrease in body size. The average snout-vent length in *Podarcis pityusensis* populations is between 62 and 82.6 mm for males, and between 54.8 and 72.4 mm for the females. Whereas the continental populations of *Podarcis hispanica* measure between 52.0 and 58.2 mm for males, and 49.7 and 55.5 mm for females. And in *P. muralis* populations males are between 56.9 and 59.4 mm and females 57.9 to 61 mm. There is no doubt about the fact that *P. pityusensis* is bigger as a species than its continental congeners. The trend towards increased body size in insular lizard populations is clear in other Spanish localities (Columbretes Islands, islets of the Cantabric Coast, etc.).

In the major Balearic islands (the Gimnesians), *P. lilfordi*, the species nearest to *P. pityusensis*, is smaller, at least in some populations. However, its average size is also greater than that of the continental lizards.

Selection leading to large insular forms has been explained through different mechanisms, ranging from polyploidy to the role of islands as reducts. In the case of the Balearic Islands, the most plausible explanation is based on a reduction of predatory pressure, a shortage of food resources and an increase in intraspecific competitiveness. This situation is considered in the Case (1978) model, which seems to fit the data extremely well in our example.

INSULAR MELANISM

The evolution of melanism considers different evolutive models presently included in the field of insular biogeography. These models are based on the following causal hypotheses:

1. *Mimicry*. Evolution would work mainly on epidermic colouring features, which would be affected by a selection favouring cryptic colourings. The disadvantage of this hypothesis is that it cannot easily explain the trend towards melanism shown by many populations. In some other cases, it is not possible to see clearly which selective agent is involved.

2. *Vegetarianism*. Some authors (Eisentraut, 1949) have explained the trend towards melanism shown by many insular populations as a food adaptation to vegetarianism caused by an insect shortage in the islets. In that case the melanism would be a side effect of metabolic processes which would be the real aim of the selection. The main argument against this hypothesis is epidermic tinge diversity in populations with similar diets.

3. *Climate*. Other authors consider melanism to be a consequence of climatic factors and, more specifically, of an adaptation to the high sunshine levels that apparently occur in many islets. This hypothesis does not explain the diversity of tinges observed in populations located near each other and submitted to similar climatic conditions.

4. *Randomness*. This hypothesis is applied not only to melanism but also to all the typical features of insular populations. The evolution of such features would be determined by genetic drift, acting on very reduced populations with its genetic basis being limited due to the founder effect. This hypothesis has many supporters who have formulated it with varying nuances.

Insularity is considered by most authors as being a direct function of the distance from the continent and an inverse function of the logarithm of the area of the island (Soule, 1966; McArthur and Wilson, 1967; Clover, 1975). The area or its logarithm are also good indicators of the ecological diversity of an island. Distance does not appear to be a good indicator of insularity in the case of the Pityusic archipelago because of the features of its continental shelf. There are very close islands but with deep channels between them, and vice versa, remote islands with shallow water between; all islets made part of a single piece of emerged land until the end of the Würm glaciation.

The factor which seems best to define the isolation is the age of separation from the main island (Ibiza) (Cirer, 1982, 1987). Unfortunately this factor cannot be known with precision since we lack the geological studies of the area which would allow us to quantify it, but the separation of the Pityusic massif into the present diverse islets has its origin in the sea level changes occurring during the Würm. Therefore, the level of depth between each isle and the Island of Ibiza is an indirect index quite close to their age.

MATERIALS AND METHODS

Two analyses of *P. pityusensis* individuals were made according to morphometric and colouring variables. The first group of variables was analysed in the 41 current insular populations (Table 1). The available sample for colouring analysis could not be analysed as widely and the test covers only 17 of these populations.

Data of Studied Populations of *Podarcis pityusensis*

| Locality | N. Mal | N. Fem | Bl. Mal | Bl. Fem | Dlum. Mal | Dlum. Fem | Area | Age |
|---------------------|--------|--------|---------|---------|-----------|-----------|-------|------|
| Eivissa | 39 | 51 | 64.7 | 55.1 | 44.06 | 42.17 | 239.2 | 0.0 |
| Formentera | 49 | 41 | 73.6 | 63.3 | 34.33 | 35.48 | 91.1 | 8.1 |
| Pta. Trucadors | 12 | 13 | 64.4 | 56.7 | 42.07 | 45.42 | 3.6 | 8.1 |
| Rodona Illetes | 3 | 8 | 71.6 | 63.8 | | | 0.7 | 8.1 |
| Espalmador | 15 | 12 | 74.8 | 64.0 | | 37.75 | 11.8 | 8.1 |
| Gastabí | 16 | 6 | 67.5 | 61.8 | | 31.87 | 1.2 | 8.1 |
| Alga | 7 | 3 | 72.7 | 64.3 | 37.56 | | 1.1 | 8.1 |
| Torretes | 20 | 17 | 67.2 | 56.7 | 40.14 | 39.07 | 2.6 | 8.1 |
| Pou | 33 | 22 | 74.9 | 64.3 | 38.80 | 39.38 | 1.3 | 8.1 |
| Penjats | 30 | 22 | 76.5 | 66.5 | 39.63 | 35.16 | 3.0 | 8.1 |
| Caragoler | 12 | 5 | 64.6 | 60.7 | | | 0.8 | 7.8 |
| Espardell | 23 | 32 | 77.6 | 65.9 | 38.07 | 40.33 | 7.5 | 9.2 |
| Sal Rossa | 4 | 6 | 71.0 | 60.7 | | | 0.7 | 7.0 |
| Purroig | 26 | 1 | 69.0 | 64.2 | | | 0.8 | 7.0 |
| Negra Llevant | 3 | 3 | 75.8 | 58.0 | | | 0.7 | 7.8 |
| Negra Nord | 13 | 17 | 76.6 | 66.5 | 32.57 | 39.23 | 1.5 | 8.1 |
| Rates | 13 | 13 | 79.6 | 68.0 | | | 1.0 | 7.0 |
| Malví Nord | 12 | 13 | 79.4 | 70.4 | | | 0.9 | 9.0 |
| Malví Sud | 11 | 11 | 79.4 | 70.0 | | | 0.8 | 9.0 |
| Rodona Sta. Eulalia | 14 | 14 | 82.0 | 72.5 | | | 0.7 | 8.5 |
| Grossa Sta. Eulalia | 23 | 23 | 76.7 | 70.0 | | | 2.0 | 8.8 |
| Margalida | 2 | 18 | 72.0 | 65.9 | | | 1.0 | 10.8 |
| Es Canar | 22 | 10 | 78.1 | 68.5 | | | 0.8 | 8.5 |
| Tagomago | 23 | 35 | 77.6 | 65.0 | | | 7.7 | 9.5 |
| Hort | 14 | 16 | 72.6 | 66.9 | | | 0.8 | 7.8 |
| Mesquida | 10 | 6 | 73.9 | 68.8 | | | 0.4 | 7.8 |
| Canaret | 6 | 5 | 62.1 | 58.2 | | | 0.4 | 7.0 |
| Caldés | 24 | 13 | 68.8 | 60.8 | 38.34 | 40.31 | 1.5 | 7.0 |
| Murada | 26 | 36 | 74.0 | 65.2 | | 24.89 | 1.2 | 9.5 |
| Cala Salada | 16 | 8 | 73.0 | 56.7 | | | 0.9 | 7.8 |
| Bleda na Plana | 21 | 34 | 82.6 | 69.1 | 30.16 | 33.52 | 1.8 | 12.6 |
| Escull Vermell | 9 | 7 | 75.7 | 69.3 | | | 0.3 | 12.6 |
| Bleda na Bosc | 11 | 14 | 84.5 | 73.1 | | | 1.9 | 12.6 |
| Bleda na Gorra | 19 | 15 | 83.2 | 72.8 | | | 1.4 | 12.6 |
| Conillera | 23 | 26 | 75.1 | 65.5 | | | 9.9 | 7.8 |
| Bosc de Conillera | 15 | 10 | 68.6 | 62.9 | | | 3.8 | 7.8 |
| Espartar | 36 | 21 | 77.6 | 68.8 | 33.14 | 34.76 | 4.3 | 9.5 |
| Escull d'Espartar | 7 | 10 | 79.6 | 69.5 | | | 0.3 | 9.5 |
| Frare | 18 | 18 | 75.2 | 64.7 | 27.96 | 30.38 | 0.9 | 9.5 |
| Vedrá | 29 | 26 | 76.4 | 65.5 | 32.56 | 33.62 | 7.8 | 10.8 |
| Vedranell | 15 | 13 | 78.3 | 66.5 | | | 3.4 | 10.8 |

TABLE 1: N. Mal. = Sample size of males; N. Fem = Sample size of females; Bl. Mal. = Length snout-vent in males; Bl. Fem. = Same for females; Dlum. Mal. = Back luminosity in males; Dlum. Fem. = The same for females; Area = Square root of island surface in hectares (km² x 100); Log. Age = Logarithm of estimated separation time from the main [10 x (log A - 3)].

For the morphometric analysis the following measurements and counts were considered on each specimen:

— BL. Body length. This variable is a good indicator of size and shape, according to the result of previous factor analysis (Cirer, 1987).

— HW. Head width.

— PL. Pileus length.

— PW. Maximum Pileus width.

— LH. Length of the hindleg.

— W. Weight.

— DTS. The number of dorsal transversal scales.

— DLS. The number of dorsal longitudinal scales.

— L. The number of lamellae of the fourth hindleg toe.

— FP. The total number of femoral pores.

A t-student test for each variable was applied to the original data matrix obtained to determine the degree of sexual dimorphism in this species.

Moreover, the average coefficient of variation (ACV) has been calculated for each population. This coefficient shows us the degree of intrapopulation variability. The coefficient used by Soule (1972) has been chosen, because it seems to be adapted for comparing closely related species or populations.

$$ACV = \frac{\sum_{i=1}^p v_i}{p}$$

Where V_i is the coefficient of variation ($S_i * 100 / x_i$, x_i being the mean of the i th character) and p is the number of variables used, in our case $p = 10$.

Study of the evolutive variation of pigmentation in reptiles is still hindered by the difficulty in quantifying melanism. This problem has been solved by measuring average luminosities on live individuals, using a reflexion colour imeter in accordance with the method described in Cirer and Martínez-Rica (1986). Measurement of only one colour variable (dorsal luminosity) has been taken into account for this study, since it appears to be a good index of melanism. The populations studied, with their respective sample size are listed in Table 1.

A more detailed analysis of the relationship between certain variables and the main defining factors of the insular characteristics of each population was carried out. For this purpose body length and dorsal luminosity were chosen as dependent variables, supposing them to be directly influenced by evolutive trends towards insular giantism or melanism; the square root of the island area (because of the need to linearise a quadratic variable) and the logarithm of the estimated age of the separation of the islets from the island of Ibiza have been taken as independent variables. Each of the variables has been separately related to every factor, independently for males and females, to eliminate effects of sexual dimorphism. Separate multiple regression analyses have also been carried out, in which each dependent variable has simultaneously been related to both above-mentioned factors, so as to estimate the relative contribution of each of them to the joint regression.

RESULTS

Sexual dimorphism. Sexual dimorphism has been observed in each population and in the species as a whole. The difference between population means of males and females is highly significant in all cases in the variables determining size and shape (BL, HW, PL, PW, LH and W). The population means of scale number variables are not significantly different between males and females in most cases, though the number of dorsal transversal scales (DTS) is significantly different for most of the populations. However, all the scale variables show significative differences for the total of individuals belonging to the species.

Females are considerably smaller and less robust than males although they have a similar number of dorsal scales, which means that there could exist a difference in scale size. To prove this assumption a test with the resultant variables of quotients BL/DLS, W/DLS, BL/DTS and W/DTS was carried out, producing highly significative results in all populations showing that males have bigger dorsal scales than females, though similar in number.

The results allow us to state that *Podarcis pityusensis* shows a high degree of sexual dimorphism in shape and size, a slight or non-existing variation for the number of scales in some populations and very noticeable variation in dorsal scale size.

Intrapopulation variability. The average coefficient of variation allows an estimation of the degree of polymorphism shown by the population. This rate has been related to insularity factors: the area and age of the isle were both found to be significant. Area was found to be positively significant and age negatively significant. The area of the isle is an indirect index of its ecological diversity, therefore small isles should have fewer different microhabitats available to lacertids, which would mean that fewer different lines of adaptation exist and this would result in a homogenisation of the populations. Inversely, in bigger islands, which are usually more diverse, species can respond with different morphologies whose viability depends on the different environments. On the other hand, Hespénhede (1973) points out that living beings having a greater variation in their alimentary habits show a greater polymorphism. Accordingly, in our case it can be expected that polymorphism increases in bigger isles where diet is bound to be more diverse; in contrast, ecologically more homogeneous islands, with a smaller diversity of potential prey will, keep population adapted to the isle's specific conditions, with narrower variability margins, and extreme individuals which have not developed optimal phenetic characteristics for their viability in that specific insular ecosystem will be eliminated.

We should also expect a greater morphological uniformity in those populations where evolution has acted over a longer period of time to adapt phenetic traits to an insular environment. Thus, smaller and/or older islands have more homogeneous populations because evolution, lack of population elements and environmental uniformity cause a decrease in polymorphism.

Trend towards giantism and melanism. We have tried to classify the relationship linking insular area and isolation time with the average size of all the populations of *Podarcis pityusensis* so as to find out which evolution model best fits our data. These are listed in Table 1. Obviously, the separation and assembly process of the isles has been recurrent, with variations in sea level accompanying glacial periods.

The simple regression analysis in Table 2 shows the existence of a clear relationship between the giantism index variable (BL) and melanism (dorsal luminosity) with the factors characterising insular environment. Size in males and females shows a strong positive relationship with the isle's separation age, as if the trend towards giantism could be shown more clearly because selection has been working for a longer time. Dorsal luminosity (naturally inverse to the degree of melanism) also shows a clear negative correlation with the isle's age in male specimens, while the correlation almost reaches a significative level in female specimens (94 per cent). With regard to this point, it should be pointed out that the number of populations whose averages of luminosity we know of is much lower than that which provided size measurements, and the relationship would probably be significant if we had been able to study each population in the same way. It seems evident that both melanism and size are features depending partially on the age of the isle and, in

| <i>Y</i> | <i>X</i> | <i>Z</i> | <i>Equation</i> | <i>Corr. Coef.</i> | <i>Signif.</i> |
|--------------------------------|----------|----------|-------------------------------|--------------------|-----------------------|
| (a) Simple regressions: | | | | | |
| Bl. Mal. | Area | | $Y = -0.037X + 74.74$ | -0.272 | 91% |
| Bl. Fem. | Area | | $Y = -0.041X + 65.48$ | -0.349 | 97% |
| Bl. Mal. | Age | | $Y = 1.588X + 60.65$ | 0.620 | >99.9% |
| Bl. Fem. | Age | | $Y = 1.384X + 53.1$ | 0.629 | >99.9% |
| Dlum. Mal. | Area | | $Y = 0.029X + 35.61$ | 0.412 | 83% |
| Dlum. Fem. | Area | | $Y = 0.023X + 35.91$ | 0.282 | 70% |
| Dlum. Mal. | Age | | $Y = -1.18X + 46.11$ | -0.698 | 99.4% |
| Dlum. Fem. | Age | | $Y = -0.935X + 44.22$ | -0.481 | 94% |
| (b) Three variable regression: | | | | | |
| Bl. Mal. | Age | Area | $Y = 1.90X + 0.027Z + 57.63$ | 0.614 | 73% (Z) >99.9% (X) |
| Bl. Fem. | Age | Area | $Y = 1.49X + 0.009Z + 52.05$ | 0.607 | 37% (Z) >99.9% (X) |
| Dlum. Mal. | Age | Area | $Y = -1.90X - 0.036Z + 52.94$ | 0.703 | 83% (Z) 99.2% (X) |
| Dlum. Fem. | Age | Area | $Y = -0.029X - 1.51Z + 49.66$ | 0.399 | 60% (Z) 93% (X) |

TABLE 2: Regression of Size and Pigmentation on the Insularity Indicators.

consequence, evolution seems to work accumulatively in them.

The relationship between the area of the isle and the variables of melanism and size is somewhat less clear than the one for age: it attains a significant level only in females, when size is the variable considered. In the remaining cases, although it is not significative, its sign leads us to assume that smaller isles tend to shelter bigger and darker individuals than larger isles.

Multiple regression analysis has permitted isolation of the relative contribution of each variable to overall regression (Table 2). The age of separation of the islands significantly influences in male and female size (>99.9 per cent), as well as in male dorsal luminosity (99.2 per cent). And for female dorsal luminosity, correlation borders on the critical level (93 per cent). The area shows no significative relationship in any case. The overall result confirms those obtained through simple regression: older isles tend to have bigger and darker animals. And the same is true in smaller isles, although the relationship is not significative in this case.

DISCUSSION

Sexual dimorphism. Only a single lacertid species inhabits the Pityusic archipelago: *Podarcis pityusensis*. Therefore, no interspecific competition with other closely-related species exists, although it is logical to assume some occasional competition with geckonid lizards, and the existence of certain intrapopulation competition for food, reproduction and space. Species occupying similar niches often react by accentuating their morphological differences in sympatric areas, to differentiate themselves from one another, thus

avoiding all possible competition, and making optimal use of the resources offered by the ecosystem. This trend is observed both in mainland species: *Podarcis muralis* and *P. hispanica* (Vives-Balmaná, 1982), and in insular ones: *P. melisellensis* and *P. sicula* (Clover, 1975).

The morphological differentiation between both sexes seems to respond to the same need to mitigate the intrapopulation competition, and exploit optimally the resources of the insular ecosystem. Males and females act as two sympatric closely-related species. Clover (1975) points out that this must be the cause of the growing sexual dimorphism in insular Adriatic Sea populations, where this species does not share a habitat with other species of the same genus. Accordingly, the strong sexual dimorphism of *P. pityusensis* seems to respond to this need to make the most of the scarcity of food and space offered by small islets.

The differences observed in the variables defining size and shape (BL, HW, PL, PW, LH and W) show that males are always bigger, fatter, and have a more robust head and extremities. Smaller and less robust females can be predicted to be relegated to more generalised feeding sources requiring no fighting (the smallest preys and plant buds and flowers). Since body size and robustness are positively related to prey size (Hespénhede, 1973; Seva, 1982), both sexes can carry out more efficient predation against a wider range of prey sizes.

Dorsal scaling, as well as scale morphology appears to be related to thermoregulation. Martínez-Rica (1977) observes that more thermophile species have a greater number of dorsal scales and that those scales are smaller. Soule (1966) has observed in *Uta stansburiana* that populations with problems of

| Continental | | | Insular | | |
|--------------------------|-------|---------|-------------------------|-------|---------|
| Species and Locality | Males | Females | Species and Locality | Males | Females |
| <i>P. muralis</i> | | | <i>P. muralis</i> | | |
| France | 58.8 | 60.3 | France (Atlant.) | 64.5 | 60.9 |
| France (mountain) | 59.7 | 62.5 | France (Medit.) | 61 | — |
| Belgium | 56.6 | 55 | Spain | 70 | — |
| Germany | 58 | 57.7 | Italy | 65.5 | 60.2 |
| Switzerland | 59.3 | 65 | All populations | 65.5 | 60.3 |
| Austria | 53.8 | 56 | | | |
| Spain | 58.4 | 58 | <i>P. tiliguerta</i> | 69.8 | 62.4 |
| Spain (mountain) | 57.7 | 60.2 | | | |
| All populations | 58.2 | 59.1 | <i>P. erhardi</i> | 62.5 | 59.5 |
| | | | | | |
| <i>P. hispanica</i> | | | <i>P. lilfordi</i> | 64.8 | 61 |
| Spain | 55 | 53.1 | | | |
| Spain (mountain) | 54.4 | 52.1 | <i>P. pityusensis</i> | 69.4 | 61.2 |
| North Africa (mountain) | 50 | 49 | | | |
| North Africa | 51.2 | 52.4 | | | |
| Portugal | 53 | 49.1 | | | |
| All populations | 53 | 52.1 | | | |
| | | | | | |
| <i>P. bocagei</i> | | | <i>P. bocagei</i> | 61 | 59 |
| Spain | 57.6 | 56.3 | | | |
| Spain (mountain) | 49.4 | 50.2 | | | |
| All populations | 57.7 | 56.4 | | | |
| | | | | | |
| <i>P. melisellensis</i> | 56.4 | 54.8 | <i>P. melisellensis</i> | 62.2 | 53.9 |
| | | | | | |
| <i>P. peloponnesiaca</i> | 73.3 | 65.6 | | | |
| | | | | | |
| <i>P. sicula</i> | 69.5 | 61.7 | <i>P. sicula</i> | 68.3 | 63.1 |
| | | | | | |
| <i>P. taurica</i> | 59.4 | 56.4 | <i>P. taurica</i> | 66 | 60.9 |
| | | | | | |
| All continental forms | 57.7 | 56.4 | All insular forms | 65.5 | 60.9 |

TABLE 3: Body Size (mm) in different European populations of Genus *Podarcis* (Data from Boulenger, 1920 and from Perez Mellado and Galindo, 1986).

overheating tend to show a decrease in their number of dorsal scales, which become bigger and more overlapping. The fact that males have bigger dorsal scales seems to indicate that they have different thermoregulatory requirements from females, with more pronounced overheating problems, possibly due to their greater robustness, or to their different reproductive role.

Trend towards giantism. Median body length in different European lizard populations of *Podarcis* genus, both continental and insular, is shown in Table 3. It is evident that insular species or populations have a greater average size than continental ones, and also that, in the same species, insular populations contain bigger individuals than their continental homologues. This difference shows a trend towards an increase in body size, not easily accounted for by such evolutive models as the one outlined by Thaler (1973) which involves a stable and balanced biocenosis. The Heaney (1978) model appears to be more plausible, even though it assumes an isochronal colonisation which seems not to have existed in the Pityusic Islands.

Anyway, the factors believed to guide size evolution in insular populations are island area and time of isolation of the specific population, and these would act mainly through predative pressure, shortage of resources and competitiveness. These three factors change when island area decreases, in which circumstance we can expect some sort of relationship between the average population size and the average area of the isle inhabited or the time of isolation.

This relationship has in fact been found in the above-mentioned evolutive models and, in some cases (Heaney, 1978), the type of relationship has even been specified. It would be a parabolic one: body size would grow with the logarithm of the isle's area, attaining a maximal value and then decreasing in larger islands, where biocenosis would already be of continental type.

Consequently, the following conclusions can be drawn:

(a) Models linking the trend to giantism in insular environments with isle area are not totally applicable to the case of *P. pityusensis* or at least the differentiation between populations has not existed long enough to make those models seem appropriate.

(b) The fact that the age of insular separation has an effect on the average size of both males and females suggests that this type of evolution is accumulative and is more dependent on a systematic trend than on an arbitrary cause; the role of genetic drift seems then, to be secondary in relation to this feature.

This general trend towards giantism does not seem to be present in the populations inhabiting Punta de Trucadors (the most northerly point in Formentera) and the Isle of Caragoler, which show a certain trend towards a decrease in size. To a lesser extent this trend is also observed in the Isle of Alga and in Punta de Tramuntana (the most northerly point in the Isle of Espardell). These areas have a light brown-yellow coloured sand rock, which is flat and devoid of vegetation. Lizards are small and slender, with highly luminous, ochre dorsal colouring, nearly free of reticular patches and thus cryptic in relation to their environment. It seems evident, in these cases, that the dominant selective pressure is predation and, accordingly, cryptic (light ochre) forms, which must have less thermoregulating capacity, have been selected so that this colouring goes together with lesser sizes, as thermoregulation would be more difficult in larger but not dark lizards.

Trend towards melanism. If, as seems to be the case, the degree of pigmentation changes under the influence of the population size and of the time of its separation, it is necessary to recall evolutive patterns in which these factors work. Genetic drift is one of these evolutive mechanisms, which would adequately explain a quicker evolutive process in smaller populations. But what is the reason for this general trend towards darkening? If genetic drift acts arbitrarily there should not be any preferential evolutive trends. Why then, does this trend towards melanism exist not only in this species, but also in most insular species of Mediterranean lacertids?

The relationship to population age suggests that a weak, but permanent, selective pressure exists, overlapping genetic drift and favouring an increase in pigmentation. Thus, an accentuated melanism must carry with it some sort of ecological advantage for lizards which, some time later, will allow a uniformation of populations after an initial heterogeneity caused by genetic drift.

What advantages might melanism hold for insular mediterranean lacertids? These advantages can obviously only affect the animal's relationship with its environment, with its congeners or with animals belonging to other species.

In relation to the environment, a darker colour can be an advantage to a lizard, only if it affects some exchange process in which the skin plays a role. The only plausible one is the energetic exchange between the animal and its environment. It would not be surprising that a greater or less pigmentation would influence the lizards' ability to absorb heat. Other small saurians, also abundant in the Mediterranean isles, are capable of darkening or lightening their skin according to thermoregulating processes (Martínez-Rica, 1974). Lizards can adapt themselves permanently (and not only physiologically) to a situation of thermal

deficit. It is difficult to imagine a thermal deficit existing in the Mediterranean isles, but lizards' activity patterns suggest the existence of such a deficit at least during the early hours of day. Rapid heating can mean an important ecological advantage for the animal because it allows it to initiate activity sooner, swallow its quarry, take advantage of the dew drops which have not yet evaporated and move swiftly to escape predators.

While studying other lacertids, Crisp *et al.* (1979) established a relationship between average size and degree of melanism, considering both traits as cause and effect, when, probably, they were both dependent on a common cause. The interpretation given by these authors is that size increase favours melanism, because melanism would make up for reduced heating speed of big animals, owing to a smaller area/volume ratio. According to these authors, the trend towards a darker pigmentation would not be selected of itself, but would occur as a consequence of a previous selection, favouring great size. This explanation cannot be considered totally accurate in regard to *P. pityusensis* (there are melanic populations of small lizards and non-melanic, large size populations) since it is excessively simplified, even though a certain relationship between average size and degree of melanism is registered. The explanation that both characteristics depend on common factors seems more plausible.

The second group of factors bound to play a role in favour of an increase in the degree of melanism is related to intraspecific social interactions. Even though a lot is unknown about behaviour patterns and the visual perception of lacertids, it can be stated that design and colouring features affecting social interactions are not located on their backs (the visibility of this part being very problematic in lizards) but on their neck and sides. Apart from that, judging from what happens in other lacertids and other saurians, the designs intervening in intraspecific interactions show a bright colouring and not only melanism. Consequently, hypotheses trying to explain the trend towards melanism by causes linked to intraspecific interactions are not very credible. Giving arguments which are different from the ones here stated, Stamps (1983) also discards the possibility that in most territorial saurians females choose males for mating on the basis of the males' colour or aspect.

The third group of hypotheses related to this topic includes interspecific relationships as agents causing melanism. Among these relationships, there are, logically, the trophic ones, and especially the most often mentioned interactions of lizards with their predators.

Melanism could be favoured by selection if this were to help lizards to be undetected by their predators, which are mainly birds who identify lizards primarily by looking at them from above. If a melanic back can be cryptic in its specific environment, predation will decrease while a trend to melanism grows. In the species studied, this trend is only observed in stony and strongly-fissured isles. The Pityusic Archipelago has a very mild climate, free of mist and with long periods of sunshine during most of the year; especially during the spring, summer and autumn, the period of lacertids

maximum activity (Perez Mellado and Salvador, 1981). Since a very bright sunlight strikes on stone edges and cracks, long and very clear-cut shadows are projected, with little blurring of their profiles. Such an environment makes it easy for birds to confuse a lizard's long black profile with the predominating shadows, especially if we take into account that many birds preying on *P. pityusensis* do not have binocular vision (*Larus*, *Lanius*, *Turdus* and *Upupa*). Subsequently, it seems that melanism would cause a decrease in predation in stony, fissured environments. However, this selective pressure is not completely eliminated since some species of *Falco* (with stereometric vision) also play a role in this predation (Araujo, *et al.*, 1977); accordingly, selective pressure owing to predation would be noticeably reduced with melanism but not completely eliminated.

Summarizing, melanism is a consequence of a balance among the different pressures undergone by the population: there is a trend towards an increase in size and the subsequent need of a more effective thermoregulation, allowing the possibility of being active in the early hours of the morning, suffering less predation. This balance is broken in populations living in sandy and clear areas since dorsal darkening would cause an increase in visibility and, subsequently, in predation. In the last mentioned areas light brown cryptic forms are selected which, in these species, seem to go together with small size.

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