A hypothetico-deductive analysis of the environmental factors involved in the current reptile distribution pattern in the Canary Islands

José C. Guerrero*, J. Mario Vargas and Raimundo Real

ABSTRACT

Aim We analyse the influence of different factors on the inter-insular colonization processes that yielded the current distribution pattern of endemic reptile species in the Canary Islands.

Location The seven main islands of the Canary Islands.

Methods We tested 11 hypotheses about factors that might have affected the colonization processes. We used Mantel and partial Mantel tests to establish the statistical significance of the relationship between the islands predicted by each hypothesis, and a parsimony analysis to detect the most parsimonious hypothesis.

Results The only significant relationships were those predicted by inter-island distance, also taking area into account, and habitat similarity, considering current vegetation in the islands. The latter was the best hypothesis according to the parsimony criterion.

Main conclusions Our results support the hypothesis that habitat similarity between islands is the main factor affecting the colonization processes of the whole group, although inter-insular distance seems to play a separate role in colonization events.

Keywords Canary Islands, colonization, habitat similarity, inter-insular distance, island biogeography, Mantel test, parsimony, reptiles.

INTRODUCTION

The reptiles that inhabit the Canary Islands comprise a group of 15 living species with well-known insular distributions. Fourteen species are endemic and only have limited capability to disperse across marine barriers. Their distribution was not well understood until recently (Joger & Bischoff, 1983; Bischoff, 1985; Machado et al., 1985; Izquierdo et al., 1989; López-Jurado, 1989; Naranjo et al., 1991; Pleguezuelos, 1997; Nogales et al., 1998a; Hernández et al., 2000; Valido et al., 2000), and the causal processes involved in the islands’ colonization were mainly discussed speculatively (see, for instance, Báez, 1987; López-Jurado, 1991; Nogales et al., 1998b; Pestano & Brown, 1999; Carranza et al., 2000).

Several authors have studied the distribution patterns of different taxonomic groups of animals and plants within the Canary archipelago (Báez, 1982a; Rivas-Martínez, 1987; de Nicolás et al., 1989; Machado, 1992). Many of these studies analysed the number of species on each island, following MacArthur & Wilson’s (1967) model (see, for example, Bacallado, 1976; Oromí, 1982; Becker, 1992; Fernández-Palacios & Andersson, 1993, 2000), or attempted to group the islands according to their faunistic similarity (Báez, 1982b; Bioni, 1990). However, such quantitative analyses are not suitable for the study of Canarian reptiles, as the very low number of species per island (between two and four) precludes these approaches.

Williamson (1989) encouraged searching for explanations concerning species distribution patterns outside the framework of MacArthur and Wilson’s model. Haila (1990) suggested that the construction of a realistic model of island ecology should include the development of distinct models that reflect the various dynamics that might be important in the system studied. That is, the observed biogeographical pattern needs to
be related to different hypotheses that define exclusive alternatives.

The reptiles of the Canary Islands exemplify the diversity and stability paradox defined by Cronk (1997): oceanic islands tend to be poor in species but rich in endemism. This implies the existence of community stability over geological time, and may give the appearance of a static equilibrium condition (Whittaker, 1998, 2000). Such a concept forms part of a new theoretical framework of island biogeography (Lomolino, 2000), involving three basic processes that act hierarchically, namely immigration, extinction and speciation (Lomolino, 1999), and a set of factors which include isolation, area, geological history, climate, habitat features, disturbances and inter-specific interactions that affect these processes both spatially and temporarily (Fox & Fox, 2000). The distribution pattern of the relatively high number of endemic reptile species includes the sharing of several islands by the same species. This must be the result of inter-insular colonization processes as – leaving vicariance due to geological reasons aside (Thorpe et al., 1994) – an endemic species may only inhabit several islands if an interchange of individuals between the islands has occurred. Colonization implies immigration and (lack of) extinction, and these processes might be differentially affected by several environmental factors such as inter-insular distances, habitat similarity, climatic similarity and similarity in human activities.

Testing the hypotheses concerning the factors that affect inter-insular colonization processes requires either the use of new analytical tools or the novel application of established methods. Cladistic biogeography allows the researcher to deduce the sequence of individual colonization events, but provides little information about the environmental factors affecting the success of those events (Nelson & Platnick, 1981).

The aim of the present study was to analyse the possible roles of different factors on the inter-insular colonization processes that have yielded the current distribution pattern of endemic reptile species in the Canary Islands. For this purpose, we proceeded as follows: (1) we formulated operationally several explanatory hypotheses regarding the environmental factors that might have affected the current distribution of the group; (2) we used the Mantel test and partial Mantel test to compare the matrix of faunistic similarity between islands – obtained using the simple matching coefficient – with the matrices of similarity between islands that were obtained for each hypothesis such that the statistical significance of each hypothesis could be calculated; and (3) we simultaneously compared the distribution pattern of reptiles in the islands with the relationships between islands predicted by the hypotheses in order to select the most parsimonious hypothesis. Thus, the most parsimonious hypothesis was selected provided that it showed a statistically significant association with the observed pattern.

**MATERIALS AND METHODS**

The Canary Islands comprise seven main islands and several smaller islands. With an area of about 7500 km², the archipelago is located close to the Moroccan coast, between 27°37′ and 29°23′ N and 13°20′ and 18°16′ W. The distribution of reptiles on each island has been studied by several authors (Báez, 1984, 1987; López-Jurado, 1991; Naranjo et al., 1991; Pleguezuelos, 1997; Barbadillo et al., 1999; Juan et al., 2000; Pleguezuelos et al., 2002). We compiled a presence/absence matrix of the 14 living endemic species on the seven main islands (Table 1). *Hemidactylus turcicus* (Linnaeus, 1758) has been excluded from our analyses because of its non-indigenous character. The presence of *Gallotia stehlini* (Schenckel, 1901) in Fuerteventura and of *Gallotia atlantica* (Peters & Doria, 1882) in Gran Canaria have not been considered, because they appear to be due to recent introductions (see González et al., 1996).

We tested 11 hypotheses referring to four factors that might have affected the colonization processes that yielded the current reptile distribution pattern in the Canary Islands. The variables associated with each hypothesis, and their sources, are presented in Table 2. For each hypothesis, we derived an expected relationship tree between the islands (Fig. 1).

**Hypothesis I (a, b, c, d): inter-insular distance**

The closer two islands are, the more similar their biota will be, as it will be easier for a propagule to cross from one island to the other. As the probability of a propagule reaching an island is also affected by the area and elevation of the island, this hypotheses may be formulated into four variations, which take into account: (a) distance between islands only; (b) distance between islands and area of each island; (c) distance between islands and maximum elevation of each island; and (d) distance between islands, area and maximum elevation of each island.

The relationship between the islands was established by means of the following indices:

\[
I_a = \frac{\text{minimum distance between islands (Fuerteventura and Lanzarote)}}{\text{distance between the two islands under consideration}}
\]

\[
I_b = I_a \times \frac{\text{area of the smallest island}}{\text{area of the biggest island}}
\]

\[
I_c = I_a \times \frac{\text{maximum elevation of the lowest island}}{\text{maximum elevation of the highest island}}
\]

\[
I_d = I_b \times \frac{\text{maximum elevation of the lowest island}}{\text{maximum elevation of the highest island}}
\]

**Hypothesis II (a, b, c, d): habitat similarity**

Islands with greater similarity in habitat would show greater similarity in their biota, because certain habitat requirements need to be met for a propagule to settle on a new island. Four
types of habitat were taken into account: (a) current vegetation; (b) phytoclimatic subregions; (c) geomorphology; and (d) the types of ecological succession of vegetation. We applied Baroni-Urbani and Buser’s index (Baroni-Urbani & Buser, 1976) based on the presence of the categories considered for each type of habitat in each island.

Hypothesis III: climatic similarity

Those islands showing greater similarity in climate would present greater similarity in their biota, as different climatic conditions in the new island may entail too much environmental stress for the propagule to settle. We carried out a principal components analysis using a correlation matrix of 15 climatic variables (Table 2) to identify the principal independent axes of the multidimensional space defined by the environmental variables. The similarity between each pair of islands is then inversely related to the Euclidean distance between them within the space defined by the ecologically interpretable axes. A principal axis is considered to be ecologically interpretable when its eigenvalue is greater than the mean of the lambdas (Legendre & Legendre, 1979).

Hypothesis IV (a, b): human activity

The current biota of the Canary Islands may be affected by recent human influence, regardless of the origin of the archipelago or the biota. As human interchange is higher between islands with similar human activities, those islands with similar human activity might also tend to have similar biota.

The similarity between each pair of islands was defined as in the previous hypothesis, but using the following variables divided by the area of the island: (IVA) Total fuel consumption, total vehicles and population as a measure of the general intensity of human activities. (IVB) Proportion of cultivated land and total livestock as a measure of the influence of human activities through habitat modification.

We obtained the matrix of faunistic similarity between islands using the simple matching coefficient (Sokal & Numerical Table 1 Presence (1)/absence (0) matrix of reptile species in the Canary Islands

<table>
<thead>
<tr>
<th>Species</th>
<th>H</th>
<th>P</th>
<th>G</th>
<th>T</th>
<th>C</th>
<th>F</th>
<th>L</th>
</tr>
</thead>
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<td>0</td>
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<td>0</td>
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<tr>
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<tr>
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<td>1</td>
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<td>1</td>
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</tbody>
</table>

H, El Hierro; P, La Palma; G, La Gomera; T, Tenerife; C, Gran Canaria; F, Fuerteventura; L, Lanzarote.


Table 2 Variables associated with each hypothesis and their sources

<table>
<thead>
<tr>
<th>Hypotheses</th>
<th>Associated variables and sources</th>
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</thead>
<tbody>
<tr>
<td>I</td>
<td>Minimum distance between islands¹</td>
</tr>
<tr>
<td></td>
<td>Area²</td>
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<tr>
<td></td>
<td>Maximum elevation²</td>
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<tr>
<td>II</td>
<td>Current vegetation³</td>
</tr>
<tr>
<td></td>
<td>Phytoclimatic subregions⁴</td>
</tr>
<tr>
<td></td>
<td>Geomorphology³</td>
</tr>
<tr>
<td></td>
<td>Ecological succession of vegetation⁴</td>
</tr>
<tr>
<td>III</td>
<td>Mean annual temperature⁵</td>
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<tr>
<td></td>
<td>Mean annual precipitation⁵</td>
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<tr>
<td></td>
<td>Mean annual number of days with precipitation⁶</td>
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<tr>
<td></td>
<td>Mean annual days with fog²</td>
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<td></td>
<td>Mean annual potential evapotranspiration⁶</td>
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<td></td>
<td>Mean annual hours of sunshine⁶</td>
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<td></td>
<td>Precipitation range⁶</td>
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<td></td>
<td>Mean annual actual evapotranspiration⁷</td>
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<td></td>
<td>Temperature range⁸</td>
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<td></td>
<td>Mean relative air humidity in January⁸</td>
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<td></td>
<td>Mean relative air humidity in July⁸</td>
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<td></td>
<td>Maximum precipitation in 24 h⁸</td>
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<td></td>
<td>Mean temperature in January⁸</td>
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<tr>
<td></td>
<td>Mean temperature in July⁸</td>
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<tr>
<td></td>
<td>Relative maximum precipitation (MP24/MAP)⁹</td>
</tr>
<tr>
<td>IV</td>
<td>Population density⁹</td>
</tr>
<tr>
<td></td>
<td>Total fuel consumption⁹/area³</td>
</tr>
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<td></td>
<td>Total vehicles⁹/area²</td>
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<tr>
<td></td>
<td>Total cultivated area⁹/wasteland²</td>
</tr>
<tr>
<td></td>
<td>Total livestock⁹/area²</td>
</tr>
</tbody>
</table>

Michener, 1958) and the presence/absence of the 14 endemic reptile species in each island. We transformed all the matrices into dissimilarity matrices and, using the Mantel test (Mantel, 1967; Legendre & Legendre, 1998), we compared the matrix of faunistic dissimilarity with the expected dissimilarity matrices according to each hypothesis. Thus, we obtained a significance value for each hypothesis. To eliminate crossed effects due to covariation among significant factors, we performed a partial Mantel test to compare the matrix of faunistic dissimilarity with the expected dissimilarity matrices according to each significant hypothesis after removing the linear effect of the other significant hypotheses (Smouse et al., 1986).

The islands were classified according to each hypothesis by applying the UPGMA algorithm to the corresponding similarity matrix. The resulting dendrograms were transformed into area cladograms by considering the tree topologies – without taking into account the length of the branches – attaching to them the species distributions considered as characters, and using Lundberg rooting (a hypothetical locality that has no species at all) to root the trees. The resulting cladograms were those expected for each hypothesis because they were consistent with the relationships predicted for the islands.

We used PAUP 3.1.1 (Swofford, 1993) software after adding a constraint statement for each cladogram. The length, consistency index (CI) (Kluge & Farris, 1969) and retention index (RI) (Farris, 1989a,b) of each cladogram were compared with those obtained for the other hypotheses (Table 3). We used the parsimony method described by Fitch (1971); the hypothesis with the shortest tree and highest consistency and retention indices was considered to be the best hypothesis according to the parsimony criterion.

**RESULTS**

Six of the 14 species analysed, Gallotia bravoana (Hutterer, 1985), Gallotia intermedia (Hernández et al., 2000), Gallotia simonyi (Steindachner, 1889), Gallotia stehlini, Chalcides sexlineatus (Steindachner, 1891) and Tarentola gomerensis (Joger & Bischoff, 1983), were non-informative for the parsimony analysis, because their distribution is restricted to only one island each. However, they were informative for the Mantel test and were used in the parsimony analysis, contributing one step each in all the trees considered. They also had an effect on the consistency indices, although this does not affect the results.

The strict consensus tree based on the three equally most parsimonious trees is shown in Fig. 2. The length of the most parsimonious trees was 16, their CI was 0.875 and their RI was 0.778.

Two hypotheses were significant according to the Mantel test (Table 4): inter-insular distance, also taking the area into account; and habitat similarity, taking the current vegetation of the islands into account. The partial Mantel test showed that the matrix of faunistic dissimilarity was significantly correlated.
with the current vegetation matrix after removing the effect of distance between islands and area ($r = 0.362; P < 0.05$). Faunistic dissimilarity was also significantly correlated with the distance between islands and area after removing the effect of current vegetation ($r = 0.628; P < 0.05$). This indicates that habitat similarity and inter-insular distance have separate significant relationships with the faunistic similarity between islands.

The hypothesis that best explains the biogeographical pattern for the endemic reptiles on the Canary Islands, according to the parsimony analysis, is the habitat similarity hypothesis, which takes into account the current vegetation of the islands (Fig. 1, hypothesis IIa). This hypothesis requires the fewest steps and yields the highest consistency and retention indices (Table 3).

**DISCUSSION**

**Theoretical basis of the method for comparing hypotheses**

Our approach assumes that the inter-island colonization of the different islands may be affected by common factors, even though individual colonizations and extinctions constitute separate and unrelated events (Connor & Simberloff, 1983). This assumption is sound if one considers that the colonization of an island not only requires the accidental landfall of a propagule, but also that certain conditions allow its subsequent survival and reproduction (Lomolino, 1999; Fox & Fox, 2000). These conditions could be similar for reptiles and affect separate events at different geological times in a similar way, thus yielding a distribution pattern that could be used to identify the affecting conditions. It is appropriate to use variables related to current conditions and relate them to current species composition to test different hypotheses about which environmental characteristics most affect colonization processes. The hierarchical phylogenetic relationships between taxa are less informative in this context, because they provide information about older colonization and speciation processes that occurred when the islands probably had different environmental conditions.

On the other hand, mere statistical analyses might suffer from phylogenetic non-independence. For instance, there could be different degrees of faunistic dissimilarity between two pairs of islands with different species if in one pair the genera are shared but in the other pair the genera are different. However, although this concern is legitimate in most cases, in the Canary Islands all genera are represented in all islands, with the exception of La Palma where the genus *Chalcides* is absent (Table 1). Nearly all the faunistic dissimilarity occurs at the species level, and we consider that our analyses deal with this correctly. The subjectivity of the species designation could also affect our results (Claridge et al., 1997). For example, *Gallotia caesaris* and *G. galloti* were until recently considered to be the same species (see González et al., 1996, for instance). We re-ran the **PAUP** software merging the data for both species.
which entailed that hypothesis IIa would require one more step while hypotheses Ia and Ib would require one less step each, with the other hypotheses unaffected. In this situation hypotheses Ib and IIa would be the most parsimonious hypotheses with 17 steps, which would reinforce our conclusions that these are the most supported hypotheses. Another possibility is to consider *G. bravoana*, *G. intermedia* and *G. simonyi* as the same species, or *Chalcides viridanus* as three different species in El Hierro, La Gomera and Tenerife. This would not affect our conclusions either, as the former option would add one step to all hypotheses and the former would subtract one step from them, so keeping hypotheses Ib and IIa as the most parsimonious hypotheses.

The use of the Mantel test for matrix comparison allowed us to reject the hypotheses that were non-significant; however, this analytical tool was not powerful enough to distinguish between significant hypotheses. To choose between competing hypotheses we used a cladistic approach in which the relationship between islands is directly evaluated by considering their shared species as shared qualitative characters (Rosen, 1984; Morrone, 1994; Garcia-Barros et al., 2002). In fact, the real power of cladistic methods resides in their capacity to compare different hypotheses according to the parsimony criterion (see, for example, Baroni-Urbani, 1993). Similar to previous parsimony analyses of endemics on islands (Trejo-Torres & Ackerman, 2001), our cladistic data consist of island matrices of living species, and the cladograms consist of nested sets of endemic biota as found on the islands. However, terminal dichotomies are here assumed to represent two islands between which the greatest interchange of biota has occurred (Myers, 1991).

We do not attempt to explain the history of colonization of reptiles, but only to determine the environmental factors most likely affecting the colonization events. To perform a historical analysis, different phylogenetic relationships for each reptile group must be taken into account, including the relationships between populations (Thorpe et al. 1994 for the genus *Gallotia*, Nogales et al. 1998b and Carranza et al. 2000 for the genus *Tarentola*, and Brown & Pestano 1998 for the genus *Chalcides*). Conversely, a historical account of the colonization events does not provide a comprehensive explanation of the conditions or environmental factors involved in the colonization, which must be addressed by testing alternative hypotheses.

**The role of habitat similarity between islands**

Inter-insular distance is probably mainly related to immigration whereas habitat similarity probably mainly affects extinction. Although both habitat similarity and inter-insular distance were found to be significant factors, the distribution of current reptile fauna was best explained by the habitat similarity hypothesis, which seems to point to the pre-eminence of extinction over immigration in colonization processes amongst these lizards.

This result contrasts with those of other authors who only mention that there is a correlation between inter-insular biotic similarities and the minimum distance between islands. Oromi (1982) pointed out that for tenebrionid beetles the highest faunistic similarities are found between contiguous islands, and the lowest faunistic similarities occur between the most distant islands, which may be a consequence of the role of inter-insular colonization. Fernández-Palacios & Andersson (1993) studied the distribution of trees and shrubs, ferns, land birds, beetles and butterflies in the Canary Islands, and found that species similarity between the islands decreased with distance. However, no alternative hypothesis was tested in these studies, even though a correlation between biotic similarity and distance between islands does not automatically imply that this is the main factor involved in the colonization process.

Our results show that, for reptiles, faunistic similarity also decreases with the distance between islands, which, according to Terborgh (1973), implies that there is a non-random structure in the species distribution within the archipelago; however, when contrasted with alternative hypotheses, habitat similarity between islands is a better explanatory factor. Despite this, the similarity between the current vegetation of the islands may be related to the distance between them. The inter-island relationship found by de Nicolás et al. (1989) using phanerogamous plants is the same as the one predicted by our inter-insular distance hypothesis Ic, which takes the minimum distance between islands and elevation similarity into account (see Fig. 1). This may be due to the high elevation specificity of many plants, such that those islands that do not reach high elevations are in practice non-existent for them. As Cox & Moore (1999) indicated, the high volcanic peaks seem to be islands within islands, because it is difficult for alpine plants to disperse from one island to another. However, the factor that best explains the current distribution of phanerogamous species in islands with similar elevations is the minimum distance between islands.

The habitat similarity hypothesis yielded one of the three most parsimonious cladograms that can be obtained with our data. This implies that, although an equally parsimonious hypothesis can still be formulated, it is not possible to devise a better one, as it is mathematically impossible to find a relationship between the islands with one step less. However, this does not rule out that several factors might be involved in the colonization of the Canary Islands by reptiles. It only means that this is a major factor affecting the colonization processes of the whole group, not that this is the only factor involved in each individual colonization event. The results of the Mantel test seem to highlight the separate, complementary, and significant effects of distance and area on the colonization of the islands by reptiles.

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REFERENCES


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