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EVOLUTIONARY STRATEGIES IN INSULAR ENVIRONMENTS

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> »*The concept of pattern or regularity is central to science.*«
> ROBERT H. MACARTHUR, 1972

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This paper is divided into two parts: classic knowledge on theory of island biogeography (I) and the evolution of behaviour and morphology under insular constraints (II).

The main subjects dealt with are: the problem of small populations (1); the biological definition of an island and the importance of biological studies on islands (2); the species-area effect and its consequences for a nature conservation strategy (3); the equilibrium theory and the weaknesses of this model (4); the founder principle (5); some features of insular populations, such as clutch size, niche enlargement and changes in body size (6); the natural history of colonisation and the success and failure of colonisation (7); the morphological paradigm of island faunas (8) and the evolution of social behaviour under insular constraints – territoriality, altruism, social structure and its relationships with body shape (9).

Key words: evolution, islands, morphology, ecology, behaviour, Berlenga.

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Ovaj rad je podijeljen u dva dijela: klasično znanje o teoriji biogeografije otoka (I) te evolucija ponašanja i morfologija u ograničenim otočnim uvjetima (II).

Glavne teme bile su: problem malih populacija (1); biološka definicija otoka i važnosti bioloških studija na otocima (2); efekt veličine otoka na broj vrsta i njegove posljedice po strategiju zaštite prirode (3); teorija ravnoteže i slabosti tog modela (4); načelo osnivača (5); neke osobine otočnih populacija, npr. veličina potomstva, proširenje niša i promjene u veličini tijela (6); povijest naseljavanja i uspjesi te pogreške naseljavanja (7); morfološka paradigma otočnih fauna (8) i evolucija socijalnog ponašanja pod ograničenjima otočnih uvjeta – teritorijalnost, altruizam, socijalna struktura i njena veza s oblikom tijela (9).

Ključne riječi: evolucija, otoci, morfologija, ekologija, ponašanje, otočje Berlenga

Note: This paper is a review paper, but not an exhaustive one. The idea of writing it, originally in Portuguese, came from the lack of an up-to-date revision on Island Biogeography for graduate students of Ecology at the University of Lisbon. Some ideas of it are based on an anonymous Internet text (http://erasmus.biol.csufresno.edu/Islands/isbio.txt) constructed for the students of the Department of Biology of the California State University at Fresno. Most of the examples provided come mainly from the Berlenga Islands, a small archipelago near the Portuguese central west coast, a European Community natural biogenetic reserve where I work and give field courses on ecology. The main actors are lizard species that inhabit there: *Timon lepidus* (eyed-lizard), the stoutest European continental lizard, and *Podarcis bocagei* (wall-lizard), one of the smaller ones.

1. A QUESTION OF NATURE CONSERVATION (THE PROBLEM OF SMALL POPULATIONS)

Recognition of the importance of island groups dates back at least to 1835 with Charles Darwin. The first paper on Berlenga Archipelago flora and fauna dates back to 1883 (Daveau & Girard, 1883) though early studies had little impact on inculcating greater care of islands and their ecology. Islands became more significant with the advent of modern ecology and particularly after the 1967 publication MacArthur & Wilson's *The Theory of Island Biogeography.*

In terms of nature conservation, it is important to mention that 484 animal and 654 plant species (mostly vertebrates and flowering plants) are recorded as having gone extinct since 1600 (Barbault & Sastrapradja, 1995). One fifth of the species of birds worldwide have been eliminated in the past two millennia, principally following human occupation of islands (Wilson, 1992). About 93% of the birds that have gone extinct since 1600 have been island forms, and destructive pressures continue to the present day. According to Chiras (1991), the rate of vertebrate extinction during the early nineties is about one species every nine months and, by the end of the century, we may be losing one species per hour. These figures are very impressive if we consider that the natural expected rate is about one vertebrate species every 1000 years. One of the main causes for this is the artificial insularisation of Earth (Weiner, 1990). Since the end of the last glacial period, due to the melting of polar ice, the sea levels have risen. All over the world, lands have submerged, mountains and peninsulas have become islands, millions of animals and plants have become isolated on those new islands.

Nowadays, the number of islands on the planet is increasing much faster than at the end of the glacial period, not because of natural changes in the sea level. Rather, it is an anthropogenic phenomenon: we have arrived at a situation in which the landscape is gravely fragmented, being formed of many pieces of biosphere surrounded by people.

To understand these processes requires a profound knowledge of metapopulation dynamics, which deals with situations in which the source population has been reduced to a set of small semi-isolated populations a *metapopulation* is a set of local populations connected by migrating individuals; local populations usually inhabit isolated patches of resources, and the degree of isolation may vary depending on the distance among patches; most metapopulation models are based on colonisation-extinction equilibrium. A metapopulation is most simply described as a population of populations (HANSKI & GILPIN, 1991) .

We have the idea that species extinction due to anthropogenic actions at the turn of the 20th century is at least as important as the great Permian extinction.

Thus, the fantastic loss of biodiversity should be the major problem of mankind at the present and during the coming years and, as pointed by MACARTHUR & WILSON (1967), it is becoming very clear that, in the next century, the shaping of our biosphere will depend on insular effects.

2. BASIC KNOWLEDGE ON INSULARITY

Is it possible to define the biological concept of an island?

For the geographer an island is a piece of land surrounded by water, therefore isolated land formally smaller then Greenland: 2.2 millions square kilometres (GORMAN, 1979) .

For the geologist islands can be roughly divided into two kinds: »land bridge islands« and »oceanic islands«. Land bridge (or continental) islands are those that were recently connected to the mainland and oceanic islands are those that have never been connected to the mainland. As far as oceanic islands are concerned, we can still consider »volcanic islands« (tops of volcanoes from sea floor) and »carbonate islands« (coral reef islands and atolls, formed by corals on top of old volcanoes).

For the meteorologist an island has special climatic features. Being surrounded by sea results in a general reduction of thermal oscillations and in an important increase of atmospheric humidity.

And for the biologist? In biological terms we can consider as »islands« all small biotopes, far enough from continents or isolated to such an extent that migratory movements or genetic exchanges with continental populations became difficult or even impossible. Thus, an island, in a biogeographical sense, can be described as »(...) *a self-contained region whose species originate entirely by immigration from outside the region*.« (ROSENZWEIG, 1995).

This means that we can define a third kind of island, usually called a habitat island (MACARTHUR, 1972). Habitat islands are suitable habitats for an organism that are surrounded by unsuitable areas (e.g., mountaintops, lakes, host plants, or caves). As far as nature conservation is concerned, we must realise that protected areas usually become surrounded by converted habitats.

2.1. Biological interest

Less than six years after the publication of the »*On the Origin of Species*«, Joseph Hooker lectured on insular floras at a British Association meeting, describing four common characteristics in them: endemicity, impoverishment, dispersal, and disharmony (reviewed by BERRY, 1998). Hooker added the problem of the interactions between life form, taxonomic status, and abundance. It was the first comprehensive account of island biology in an evolutionary context. In the peroration of his lecture, Hooker points out that island floras can only be understood within an evolutionary framework.

Islands are commonly regarded, from the biological point of view, as paradigmatic laboratories of evolution, ecology, nature conservation and so on. This results from the possibility of passive variable control. In fact, insular non-flying populations are isolated genetic pools under selective pressures that are different from those that influence their mainland relatives. Furthermore, on islands one can isolate the two parameters that determine life distribution on earth – surface and degree of isolation of an area.

The practical advantages of biological studies of insular populations are:

- easier delimitation;
- quantification not dependent on migration movements;
- simplicity of calculation of mortality and birth rates;
- easy recognition of individuals by the observer.

Thus, from a biological point of view, the definition of an island involves two fundamental traits, each of them being sufficient *per se* to define the model:

- breaking of the genetic flux between populations – genetic isolation;
- breaking of the spatial continuity – demographic isolation.

Species diversity in insular is lower that in continental communities. This is surely due to three kinds of reasons:

- the sort of filter that the sea represents to many of the mainland species;
- the lack of resources (space, food, and so on) for many mainland species;
- the incapacity of many species to adapt to the new conditions.

In 1967, with the publication of *The Theory of Island Biogeography* by ROBERT MACARTHUR & EDWARD WILSON, this field became a predictive science, which turned out to be a great stimulus for a whole generation of ecologists and evolutionists. Islands have become more significant with the advent of modern ecology. Justifications for island studies include (WILLIAMSON, 1981):

- unifying theories relating species number to area had both their origin and applications on islands. This is of importance to »island« situations such as the destruction of continental forests and the production of forest patches;
- techniques for manipulating small populations and habitats are developed and applied on islands. The reduced complexity present on islands helps in such studies and others;
- fragmentation of tropical forests will leave only habitat islands which will be below the minimum level for autochthonous speciation (division *in situ* into subspecies along clines). Island speciation by radiation or multiple invasions will be the only source of novelty after approximately the year 2000.

In addition, it is always important to remember that Charles Darwin and Alfred Russell Wallace based their thinking of evolutionary process on insular studies.

2.2. The species-area effect

The surface of a given region allows us to predict, with a high level of certitude, the number of species present (ANDREWARTHA & BIRCH, 1954; BROWNING, 1963). PRESTON (1962a, b) suggests that the number of species on a given island is usually approximately related to the area of the island by the equation $S=CA^z$, where S is the number of species, A is the area, C and z are, respectively, the intercept and the slope of species-area curve; C varies widely among taxa and according to the unit of area measurement, and z falls in most cases between 0.20 and 0.35. This is the so-called *species-area effect*.

Nevertheless, other authors, having analysed the influence of constraints other than area, have found other variables that enabled the regional prediction of S for particular taxonomic groups (SIMBERLOFF, 1974, 1976; DIAMOND & MAYR, 1976). For example, in the Galapagos, the number of vascular plant species is a good predictor of the number of breeding birds (HARRIS, 1973). CASE (1975) shows that in the islands of the Gulf of California plant diversity is correlated with lizard species diversity. In the case of the rodents of the Virginia barrier islands, specific diversity increases with the area and the elevation of the island, with the vegetation height, the number of vegetal associations and the number of soil types (DUESER & BROWN, 1980).

2.2.1. Consequences for a nature conservation strategy

RAUP (1991) illustrates the consequences of the Preston model for the loss of biodiversity in a fragmented landscape in a very clear way. Suppose we have an island with N species, and we divide it into equal halves by erecting a tall fence across the middle. Suppose further, that at the time of the fence building, all N species lived over the entire island. Then we wait. If the species-area effect is working, neither half of the island will be able to support all N species. Extinction will occur in both halves, reducing each to the number of species sustainable by the smaller area. Total biodiversity will have been reduced if some of the same species happened to die out in both halves.

In conservation biology, the species-area effect is widely used to predict species loss with removal of habitat area.

2.3. The equilibrium theory

MACARTHUR & WILSON (1967), based on the work of the British lepidopterist MUNROE (1948) in his doctoral thesis, which dealt specifically with the distribution of butterflies in the West Indies, searched for general patterns among organisms regardless of phylogenetic affinities. The *Theory of Island Biogeography* describes the relationship between the number of species found on an island, the area of the island and the distance of the island from the mainland.

Three general patterns were observed:

a. there is a relationship between the **size** of individual islands in an archipelago and the number of species that comprise the biota;

b. the more isolated the island, the less species **diversity**.

Distant islands have fewer species, which usually have features that allow them to disperse readily (flight for example).

c. The third pattern is **turnover**. Turnover on islands should be constant, i.e. replacement equals extinction if an island is at equilibrium.

The immigration rates of species into new areas and their emigration rates from them have great influence on succession and species diversity in a given plot. If immigration exceeds emigration, then the net result is an increase in the number of species; if the reverse is true, then the area will lose species over time. Usually, emigration is equated with extinction. For any potential colonist it will probably be easier to colonise islands or areas with an impoverished fauna, because few competitors or natural enemies exist. Consequently, immigration rates are often thought of as being higher on islands. As far as extinction is concerned, the loss of species from an area (through competitive extinction) is likely to be higher in smaller areas, where competition is severe, than in larger areas, which can support more species.

These ideas were expressed by MACARTHUR & WILSON (1967), as *The Equilibrium Theory*. The equilibrium species number in the island is reached at the intersection point between the curve of rate of immigration of new species and the curve of extinction of species. The effects of island size and island distance from a source pool on the expected number of species on an island can be superimposed on this graph.

So, summarising:

a. the number of species increases with island size;

b. the number of species decreases with distance to source area;

c. there must be a continuous turnover of species. Recurrent colonisations and extinctions, but number of species present stays the same.

2.3.1. A critical view on the equilibrium theory of island biogeography – weaknesses of the model

According to BLONDEL (1986), the main problem of this model is in thinking that all species have the same probability of extinction. This may be true in a geologic time scale, but in a biogeographic time scale, the existence of endemic species contradicts the presupposition. In this context, RICKLEFS (1973) pointed out to the importance of speciation rate as a determinant variable.

ANONYMOUS (no date), on a text available on Internet, constructed for the students of insular biogeography of Department of Biology of the California State University at Fresno, summarises in a very clear way the weaknesses of the MACARTHUR & WILSON model:

a. insular biotas may not be at equilibrium. The number of species may increase or decrease over evolutionary time;

b. the model assumes that the identities and characteristics of species can be ignored;

c. colonisation rates and extinction rates are considered random events;

d. colonisation and extinction are considered independent processes;

e. species are all assumed to have identical colonisation potential;

f. larger islands present larger targets. Island size may affect colonisation rates as well as extinction rates;

g. not all the species have the same probability of extinction;

h. interspecific interactions are ignored;

i. the importance of speciation rate must be an important variable, but is neglected in the model;

j. if species are produced within the island or archipelago the basic assumptions of the model do not apply;

k. habitat variability is not included and the diversity of habitats on islands is not constant;

l. Lack (1969, 1971, 1976) emphasises that colonisation can fail only by the absence of favourable biotopes.

m. *stratified dispersal* (Hengeveld, 1989) – another limitation of MacArthur & Wilson model is the assumption of continuous spread. In nature, many organisms can move or can be transferred over large distances. If spread were continuous, then islands would never be colonised by any species. Discontinuous dispersal may result in the establishment of isolated colonies far away from the source population for models on stratified dispersal see Alexei Sharov homepage (http://www.gypsymoth.ento.vt.edu/ sharov/PopEcol/lec12/stratdsp.html) ;

There are so many examples that contradict the model, based on intrinsic features that determine fitness differences between species, and on ecological differences between islands, that its main drawback is in not being a generic model.

Nevertheless, the *Theory of Island Biogeography* as formulated by MacArthur & Wilson (1967) is still a very useful starting point. The fact that it does not have universal application does not diminish its importance. And the fact of continuing to be the only basis for generation of hypothesis confers operationality on it. Thus, it is very important to understand that almost everything we know about insularity is based on criticisms of this model, the model being still there. Almost everything everyone does about insularity is based on the negation of the model. In this context, the model fulfils totally its operational function: it can be used to generate a hypothesis that scientists build experimental designs to refute. For some thirty years, almost all papers on insularity have begun like this: »*according to MacArthur & Wilson (1967)… but…*«

2.4. The founder principle

Usually, we expect a propagule to be formed by a very small number of effectives. Ernst Mayr (1942, 1954, 1963) has explored the possibility of random genetic effects in colonising populations under the idea of the *founder principle*.

The basic idea is the assumption that a propagule carries fewer genes than its ancestral population. If the alleles of the founder population are relatively few, they should operate in a restricted and altered genetic environment and thus, the success of each allele will depend on this genetic environment. Accordingly, gene frequencies different from those of the mother population should be selected.

Although a genetic variability equivalent to that of the mother population will be gradually restored, the equilibrium should correspond to a different point. This way, genetic composition should greatly differ. Therefore, genetic differences between insular populations should result from both random sample effects and selective pressures – environmental differences on islands should act as selective pressures promoting genetic differences.

2.5. Features of island life

According to ANONYMOUS (no date), most features of islands are related to difficulties in dispersal – getting there. After arrival, a number of additional changes can occur. The most important features of island life are summarised above.

A. IMPOVERISHMENT. There are fewer species of organisms on an island than on an equal area of continent. Impoverishment depends on many factors including winds, distance, size of island, individual species characteristics, etc. This is surely due to two factors affecting the colonisation of islands by the mainland species:

- the sort of filter that the sea represents;
- the lack of resources (space, food, and so on).

B. DISHARMONY. This is difficult to define. Most authors consider this to be the presence of a mixture of species different from the mainland, probably largely influenced by impoverishment. The number of species on an island is a consequence of area, impoverishment and in some cases competition with species that have been established earlier.

C. DISPERSAL. Mechanisms of dispersal include:

a. ISLAND HOPPING. Islands are within the normal range of travel for the species. This applies particularly to birds, but can also apply to other large organisms and insects. Chance is less involved.

b. SWEEPSTAKES DISPERSAL. Much more chance is involved. Species arrive due to exceptional or improbable events, e.g., storms, etc.

c. SEAWATER FLOTATION.

d. RAFTING. Drifting pieces of vegetation or other materials may carry an assortment of plants and animals. This is probably the best method of dispersal for reptiles and mammals.

e. AIR FLOTATION. Ferns, winged seeds, fungi, small insects, spiders, all may be spread by this mechanism.

f. TRANSPORT BY OTHER ORGANISMS. Transport by birds on feathers, on feet, or in digestive tract. Snails, fruits, aquatic plants, etc. may be carried this way.

However, after arrival a number of additional changes can occur.

D. ESTABLISHMENT. Arrival in a location is not enough. Establishment depends on a number of factors:

a. first, we must consider the small size of insular populations.

In fact, insular populations typically are small populations. The most important problems of small populations are the following four:

- demographic stochasticity;
- genetic deterioration; the problem of extinction due to genetic rupture;

- social dysfunction;
- extrinsic forces.

a. organism may be in poor condition;

b. mates are necessary at least for vertebrate forms;

c. pollinating agents for some plants must be present;

d. vectors for parasites must also be present;

e. the type of organism makes a difference: generalist species do well while specialists are poor candidates;

f. competition may be severe depending on earlier arrivals;

g. food availability may be low or non existent;

h. niche enlargement.

When a species invades a new island, it encounters in almost every case an environment that is different to some degree. Most frequently, the change is biotic: the island contains new combinations, if not new kinds, of predators, preys and competitors. There is a tendency, by no means universal, for a colonising species to respond by either contracting or expanding its niche, according to the competition circumstances. As a rule, it contracts on meeting more competitors and expands on meeting fewer of them. Niche enlargement may be a cause of some behavioural changes, e. g., the reduction of stereotyped behaviour.

E. INCREMENT IN DENSITY. Islands usually undergo a remarkable increment in population density (CODY, 1971), which must be important in insular community structure. This is usually explained by *density compensation* (MACARTHUR *et al.*, 1972) or by the so-called *Krebs effect* (MACARTHUR, 1972).

F. LOSS OF DISPERSAL ABILITY. It is surprising to many people that island forms lose their ability to disperse further after arrival. For example:

a. insects – Flightless grasshoppers and drosophilids;

b. plants: *Fitchia*, a composite, loses its spikes for adhering to passing animals;

c. birds are notorious for flightlessness. Many are now extinct or endangered.

G. POLLINATION MECHANISMS CHANGE with availability of pollinators and their ecology.

H. REPRODUCTIVE CHANGES. Females of island birds and reptiles tend to lay fewer and larger eggs than their close relatives (FITCH, 1985). One of the most interesting features allowing us to understand survival strategies in insular environments is difference in clutch size. The rule is that on islands animals reduce clutch size. On Berlenga Island, for example, wall-lizards (*Podarcis bocagei*) lay two eggs per reproduction moment, instead of the six eggs laid by their continental conspecifics (VICENTE, 1989a). Two principal causal explanations were proposed:

a. CODY (1966, 1971), based on LACK (1950), defends the idea that reproductive effort is optimised in relation to lifespan. In stable environments, there is a reduction in mortality rate and therefore the energy allocated to reproduction can be used in other success factors.

b. ASHMOLE (*in* RICKLEFS, 1980) bases his explanation on the hypothesis that clutch size is determined by differences in trophic resources between reproductive and non-reproductive seasons.

The two models differ in the causality of the reduction of clutch size. For ASHMOLE (*in* RICKLEFS, 1980), there are not more young because there is no increment of resources during spring. For CODY (1966, 1971), insular animals could have greater clutch size but by means of natural selection they allocate energy to other life traits.

I. BODY SIZE AND OTHER PHENOTYPIC CHANGES. New growth forms arise; gigantism, dwarfism, arborescence, and weird colour variants are common, compared with continental relatives; e.g., tree forms in sunflowers (Compositae) on St. Helena Island (COX & MOORE, 1985). Most insular animals are giant or dwarf when compared with their continental correlates. Those somatic alterations consist, in general, of a tendency towards gigantism in smaller species and dwarfism in the bigger ones (CASE, 1978; HEANEY, 1978). This general phenomenon is known as the *Van Valen rule* (VAN VALEN, 1965, 1973).

Small species tend to be giants and bigger ones to dwarfism. For example, on Berlenga Island, eyed-lizards (*Timon lepidus*) tended to dwarfism and wall-lizards to gigantism (Figs. 2–3).

However, not all size changes are easily explained.

In the California Gulf islands, SOULÉ (1966) has found a negative correlation between the number of competitors and the body size of lizards of the genus *Uta*. His results showed that the body size in *Uta stansburiana* is correlated with the number of competitors – as the number of other sympatric iguanids grows the body size of *Uta stansburiana* decreases. MACARTHUR & WILSON (1967), CASE (1975) and SCHOENER (1977) refer to the work of SOULÉ as a good example of the effect of competition on an important biological trait.

BLONDEL (1986) considers that a reduction of predation pressure is a determining feature of body size in insular animals – those who respond to predation by an increase in body size can reduce it on islands, which is an advantage in a limited space with limited resources. Those who escape predators by hiding (usually smaller species) may find it advantageous to become bigger, useful in niche enlargement and intra-specific competition.

BLONDEL (1986) also argues that another advantage of small body size should be in the favouring of populations that are numerically more abundant, less vulnerable to stochastic extinction.

SCHOENER (1969a, b) suggests the existence of an optimum body size in relation to the availability of resources.

Other authors, like DUNHAM *et al.* (1978), view the phylogenetic history as an important cause of differences in body size. They also stress the importance of mating systems in the determination of body size differences.

J. COMPETITIVE ABILITY DECREASES. Few islands have natural large predators or herbivores, therefore selection relaxes.

K. MUTATIONS that would be potentially deleterious in continental populations can be tolerated to a greater degree under »relaxed« selection.

L. SPECIATION. Rapid speciation is frequent, and morphological and physiological change is inevitable in nearly all groups. Adaptive radiation will proceed to the extent that new niches are available.

M. EXTINCTION is common on islands. General mechanisms include natural causes such as catastrophes and slow capacity of change (overspecialisation) and anthropogenic causes, such as habitat destruction or ecological change, direct or indirect killing, introduced competitors, introduced predators and introduced diseases.

Thus, concerning the main features of island life, under the expression »*insular syndrome*«, BLONDEL (1986) includes a set of ecological adjustments and evolutive modifications acquired by the organisms in insular communities. For this author the most characteristic traits are:

a. reduction of species diversity
b. over-representation of small generalists of large niches
c. enlargement of the niche
d. sedentarisation
e. reduction of predator species
f. increment of reproductive rate
g. increment of life expectancy
h. increment in density

2.6. The natural history of colonisation

In »*The Theory of Island Biogeography*«, MACARTHUR & WILSON (1967) search for answers for the following questions:

a. what is the process of colonisation of an island?
b. is the number of species a function of the area of the island?
c. and a function of the distance from the mainland?
d. are species on an island a random sample of those that live on mainland?
e. or is there a kind of selection, where some species have more chances of colonising than others?
f. is life on islands accompanied by morphological, demographic, ecological and genetic changes?
g. are there special adaptations that favour survival on isolated and exiguous areas?

2.6.1. The success and the failure of colonisation

At this point, it is pertinent to introduce the *r and K strategies* concept, in a very strict sense. It is very important to separate the basis of the r-K model from all the associated considerations, which can be doubtful. So, r and K are simply the parameters of the logistic growth equation – r is the rate of increase, or the *propulsory* effect of reproduction, and K is the carrying capacity of the biotope, or the environmental *depressor* effect.

Thus, in the most pure context of the model, an r-strategist is merely an animal that maximises the number of the offspring, consequently to the detriment of the quality (survivorship) of each young. The detriment of the quality is a consequence of the fact that the budget of energy allocated to reproduction is limited. Therefore, in the basis of the model, to be an r-strategist does not imply living in a certain kind of environment under particular constraints. Those are considerations around the model but not the model itself.

In the same way, again in the most pure context of the model, to be a K-strategist means to be an animal that maximises the budget of energy allocated to each member of the offspring. Obviously to the detriment of the quantity, due to the same reason: the energy budget that can be assigned to reproduction cannot be infinite.

Therefore, in this paper these concepts are only considered as far as the allocation of energy to the reproduction is concerned, without reference to their causality.

In fact, it is not always clear if environmental variability or stability, heterogeneity and unpredictability have a causal relationship with the kind of strategy adopted. But these are considerations around the model that do not contradict the model itself. The existence of an r-K *continuum* regarding the allocation of energy in reproduction is a fact in nature that cannot be questioned in function of the falsity or veracity of acessory considerations. Also, it is not fundamental, in the context of island biogeography, to discuss if it is only for the so-called K-strategists that mortality is density-dependent, or if the competitive capacity of the so-called r-strategists is always tiny, or if for K-strategists selection is always normalising, and so on. Again, these are only some of the hypothesis that the model may generate, but not the model itself. Thus, they cannot formally deny it.

The validity of a model lies on its operationality, that is to say, its capacity to generate a testable hypothesis.

From the so-called r-K model, in the context of the discussion of insular phenomena, only those features related to the allocation of energy to reproduction and their direct consequences are taken into account in this discussion – the quality (survivorship) of the offspring and its relationship with the colonising success and the viability of the colonising population:

- an r-strategist is an animal that invests the available energy for reproduction in numerically abundant offspring to the detriment of quality of each juvenile;
- a K-strategist is an animal that invests the available energy for reproduction in numerically reduced offspring, maximising the quality of each juvenile.

Marginal considerations about environmental stability, predictability, etc. will be left out.

According to MACARTHUR & WILSON (1963, 1967) the evolution of a new population must go through three overlapping phases, as follows:

- firstly, the population must respond to the effects of its small size. The response must be fast, limited to a small number of generations;
- the second phase, that can begin immediately and that can be extended indefinitely, consists in the acquisition of mechanisms of adjustment to the new conditions of the environment that has been invaded;
- the last phase, an occasional outgrowth of the first two, consists of speciation, secondary emigration, and radiation.

In general, when a species invades a new island, it encounters in almost every case an environment that is different from its original one. This should be a strong evolutive force. First, the propagule should minimise the probability of extinction by adaptive, behavioural and demographical mechanisms that have as result to optimise the abundance of the population and assure its stability through time and space – an r-strategy (LEWONTIN, 1965). Later, because of resource constraints, this strategy should tend to K. In theory, it will optimise the competitive abilities of the individuals in a spatial limited and trophically underprivileged biotope.

Therefore, potential colonising species are those r-strategists that exhibit plasticity in what concerns their reproductive strategies. In approaching high-density levels, K-strategists, which were not significant in the population, should be selected.

Additionally, we can consider four possible reasons for the absence of colonisation success:

a. the species is so localised, specialised and sedentary, that its dispersion rate is too feeble to produce a sufficiently strong flux of emigration;

b. its capacity to cross the marine barrier is mediocre;

c. on the island there is a lack of favourable biotopes;

d. the species is not able to compete with the already existing ones.

Common features in a group of organisms in the same environment may be due to shared inheritance and/or shared environmental pressures. In contrast, similar trends among different organisms occupying disparate islands are more revealing about general evolutionary forces. Then the reason for there being repeated evolutionary patterns on islands is that the same shifts in the compromise occur as a result of repeated and similar alterations of the factors that give rise to the selection pressures.

What are these factors?

a. mild equable climate of many islands;

b. year-round availability of food;

c. availability of ecological niches;

d. relative scarcity of predators and ecological competitors.

Secondary factors, dependent upon the primary ones, include:

a. high population densities;

b. intraspecific competitive pressures.

These factors, or a subset of them, occur in other environments that are not traditionally thought of as islands: caves, bogs, lakes, and mountaintops, for example. Like islands, such environments are isolated and generally small. Not surprisingly, therefore, evolutionary trends that are observed on islands are also seen in island-like settings.

3. MORPHOLOGICAL AND BEHAVIOURAL PATTERNS

3.1. The morphological paradigm

It is a fact that, in most cases, morphological diversity between insular populations and their continental correlates differs. Studies on the morphology of insular vertebrate populations point frequently to opposite directions: sometimes we find an increment of diversity, other times a decrease.

Populations of lizards can vary quite substantially in morphology across the terrain of a single island, even on small islands (THORPE & MALHOTRA, 1998). Understanding such variation can provide insights into factors responsible for the evolution of differences between populations on different islands, or between island and mainland populations (GRANT, 1998).

Ecotypic variation is conspicuous in relatively sedentary lizards, as in plants, and absent or minor in the more mobile small and large mammals (BARRET, 1998; BERRY, 1998; PEMBERTON *et al.*, 1998).

According to GRANT (1998), from the work of THORPE & MALHOTRA (1998), three lines of evidence support the hypothesis of adaptation to local conditions:

a. there are strong associations between morphological variables such as colour, body size and scalation patterns and environmental variables such as habitat structure and climate.

b. there is little residual influence of phylogenetic history on morphology, as indicated by a lack of association between morphological and DNA-based phylogenetic reconstructions.

c. related species on different islands show similar, parallel, geographical variation in morphology in relation to the same environmental gradients.

We can then point out that ecology is shared but history is not. In other situations, ecology and history may be shared and difficult to disentangle when different taxa display parallel patterns on the same island, as in the case of butterflies on Celebes described by Wallace (GRANT, 1998).

The main conclusion is that natural selection arising from current ecological conditions is a primary force influencing morphological population differentiation, irrespective of phylogenetic history.

Climatic and biotic factors (predation, etc.) are implicated as agents of natural selection. It would be interesting to know to what extent dietary factors, sexual selection and random genetic drift have contributed to the patterns of ecotypic variation that have been so well documented. Some colour variation may be influenced by sexual selection.

However, a rule is not easy to establish. The most parsimonious explanation is to admit that insular intrapopulation diversity is the expression of equilibrium between diversifying and normalising factors. MARC CHEYLAN (1988), who studies lizard populations on Mediterranean islands, presents a list of those factors (Tab. 1).

Therefore, the degree of diversity of an island population cannot be explained only by the intensity of genetic flux. Diversity and intensity of environmental constraints also have to be taken into account.

To these factors we can add genetic drift and the development of r-strategies as diversifying factors, and endogamy and selective pressures of low resource diversity as normalising factors.

We can always put forward the question: »*is it possible to define a morphological paradigm for insular animal populations?*« and, if possible, »*will it be operational?*« or, »*from a morphological analysis of an insular population, can we deduce if we are in pres-*

Tab. 1. Normalising and diversifying factors implied in the biological diversity of insular populations (CHEYLAN, 1988).

NORMALISING FACTORS	DIVERSIFYING FACTORS
Reduced population size	High population size
Old and total isolation	Absence of isolation
Homogeneous environment	Heterogeneous environment
Predictable environment	Unpredictable environment
High degree of competition	Low degree of competition
Absence of spatial structure	Spatial structure
Low renovation rate	High renovation rate
Small number of founders	Large number of founders

ence of an island from a biological point of view?« or, still in other words, »*should the dispersion of a morphological measure of insular populations be a measure of its degree of isolation?*«.

It is surely possible and, at least for some non-flying vertebrates, there is some evidence to support this.

Generally, when we carry out a phenotypic study of a population, we assume that the dispersion of the measurements around the mean obeys to the normal law. Usually we test kurtosis, skewness, and the coefficient of variation.

The coefficient of variation is independent of the unit of measurement and is expressed as a percentage. Discernment of the meaning of a value of CV is largely a matter of experience. Its interpretation on functional zoological grounds depends on non-numerical biological knowledge (SOKAL & ROLPH, 1995).

From of observation, we know that the great majority of them lie between 4 and 10, and that 5 and 6 are good average values. Much lower values usually indicate that the sample was not adequate to show the variability. Much higher values usually indicate that the sample was not pure, for instance, that it included animals of clearly different ages or of different minor taxonomic divisions (SIMPSON, ROE & LEWONTIN, 1960).

The taxonomist becomes happy if »*everything is according to the rules*« (or »*by the book!*«). As they usually say: »*if everything is normal, then I'm probably dealing with a »good« or representative sample*«.

And this is just because non-normal distributions or very high or very low dispersion measures are not usually »natural« things, at least in a »pure« population. A *pure population* can be defined as an archetypal panmictic dynamically stable population.

In addition, it is legitimate to ask »*why are natural populations usually normally distributed?*« or »*why does the Central Limit Theorem work in nature?*«.

Firstly, we can say that there are critical levels of dispersion. *Critical levels of dispersion* are those levels that, if exceeded, cause the distribution not to return to its point of equilibrium. That is to say, the population will evolve to something new or to extinction. This can be viewed as an analogy with the Lagrange idea of a stable system.

As said before, close to those critical levels, we expect that biological phenomena will occur, promoting a return to normality. It is the so-called stabilising tendency. Very high dispersions, exceeding the critical level, seem possible to lead to sympatric speciation phenomena, and we can call it a *critical level of speciation*. Very low dispersions, exceeding the critical level, seem to lead to a process of extinction and, likewise, we can call it a *critical level of extinction*.

This may be just because morphologic variability and heterozygosity are closely related in natural populations (EANES, 1978). For example, in lacertid lizards, a good correlation between heterozygosity and morphologic variation is confirmed in the populations of *Uta stansburiana* of the California Gulf islands (SOULÉ & YANG, 1973) as well as in the *Anolis* species of the Greater Antilles (SOULÉ *et al*., 1973). For GORMAN *et al*. (1975), in the genus *Lacerta*, genetic variability is bigger in continental populations that in insular ones and on bigger than on smaller islands.

Thus, we can say that natural populations are self-regulating according to Gauss's Law.

That is precisely the idea of the *Central Limit Theorem*. The central limit theorem is a »limit« that is »central« to statistical practice. For practical purposes, the main idea of the central limit theorem is that the average (centre of data) of a sample of observations drawn from some population is approximately distributed as a normal distribution if certain conditions are met.

In continental non-isolated populations, the maintenance of statistical normality is strongly dependent on an external factor, which is the genetic exchange with other conspecific populations. But not only. The absence of space limits as well as the availability of resources allows, generally, the growth of the population and, consequently, an increment in its diversity.

What happens to a population that starts an isolation process (Fig. 1)?

At a first phase, an r-type selection is expected. Despite the reduction of gene flux, an initial increment in diversity will be possible, resulting from an increment of stochastic processes. We can call this the *insulation process*, or metaphorically, the *peninsula effect*.

And afterwards?

Well, let us suppose that the island is small and biotopically uniform (obviously from the point of view of the species in question). In that case, without genetic flux, with high homozygotic levels, the coefficient of variation will tend to zero. We may say that it tends to the critical level of extinction. However, the possible absence of competitors should, at an initial phase, allow the essay of sub-populations, the essay of exploitation of the so-called *adaptive zones* (*sensu* SIMPSON, 1953). However, in this case, poverty of the biotope conjugated with the lack of space will prevent the development of sympatric speciation processes. The better survival chance will be for a population with plasticity to adopt a K-strategy and be composed of generalist individuals, with normal curves having very low dispersions.

Therefore, in this way, an operational approach to the *biological concept of island* will be the analysis of intrapopulation phenotypic dispersion (for a practical example see Fig. 2).

This is of great importance for the definition of nature conservation strategies.

Moreover, it can be, at the moment, an important low cost approach for the evaluation of the state and the viability of an endangered population. If its phenotypic dispersions are under the values of an insular conspecific, the critical levels of extinction have probably been reached. This should be an important empirical tool for the management of natural reserves, the definition of minimum numbers of individuals for a viable population and of minimum areas for the maintenance of essential biodiversity.

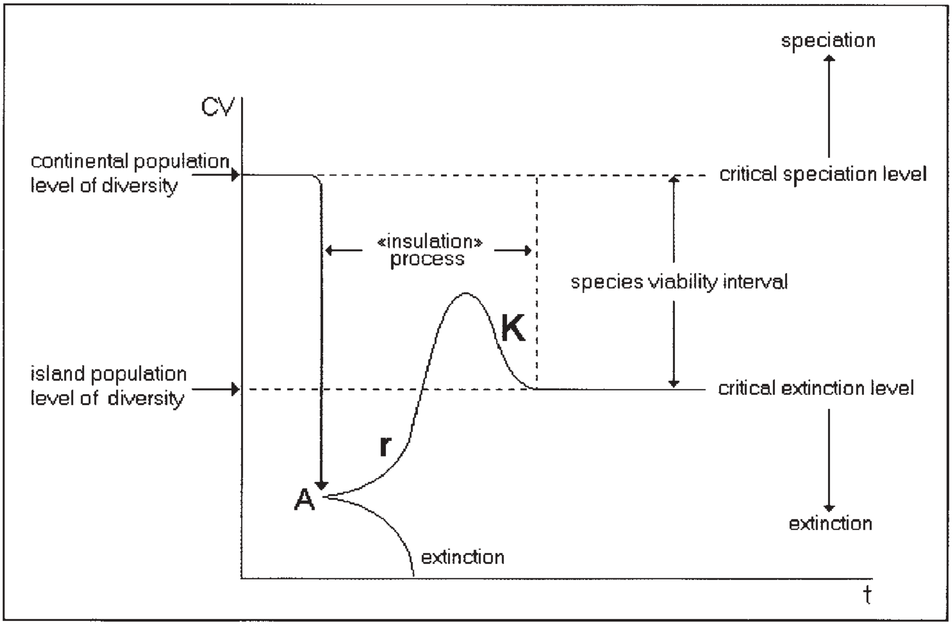

Fig. 1. Variation through time of the coefficient of variation in a process of insularity. The »insulation process« starts at point A with the breakdown of the link of a very small propagule with the mother-population. If the species has the capacity to develop an r-type strategy, there is an initial increment in diversity, until the carrying capacity of the island is achieved. Then a K-type selection acts and, as the carrying capacity of the island is small, the CV will stay near the minimum population viability (critical level of extinction). If the propagule has no capacity to develop an r-type strategy, the colonisation process fails.

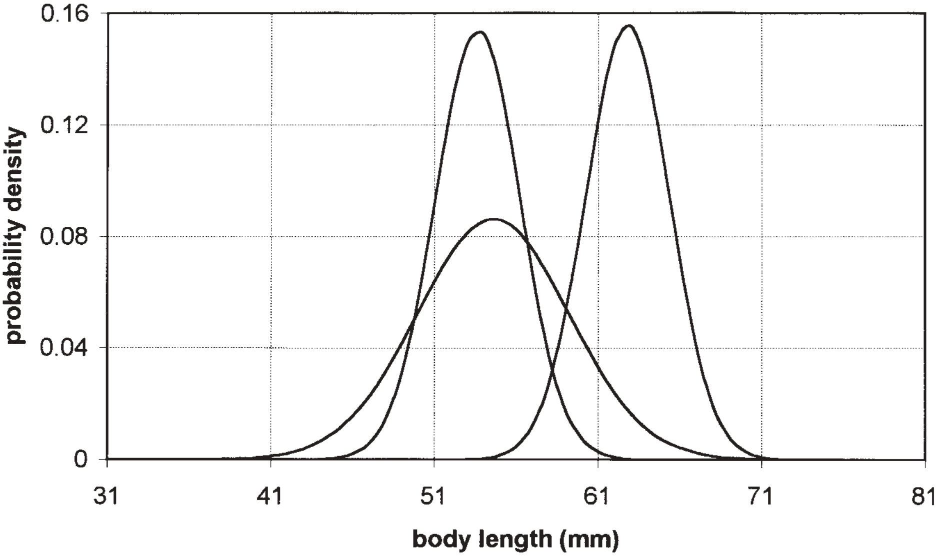

Fig. 2. Probability distribution of body length in the males from three *Podarcis bocagei* populations. The left leptokurtic curve refers to an isolated population of *Podarcis bocagei carbonelli*, the right leptokurtic curve refers to an insular population, *Podarcis bocagei berlengensis*, and the normal curve refers to a north-Portuguese continental population of *Podarcis bocagei bocagei* (for details see VICENTE, 1985)

In this context, islands are an important research target leading to essential tools for nature conservation.

3.2. The evolution of social behaviour under insular constraints – territoriality, altruism, social structure and its relationships with body shape

The evolution of behaviour on islands should be discussed based on the history of colonisation.

The main question is: »*how do insular constraints interfere with the evolution of behaviour?*« Or, in other words, »*which selective pressures have conditioned the social behaviour of island animals?*«.

Social behaviour is determined by genetic and environmental factors, basically related to the availability of resources, and also to the density of conspecifics.

At low-density levels, it might be an advantage to be territorial and aggressive, while at high-density levels it might be a disadvantage. So, territoriality is a trade-off. In high-density situations, if an animal is territorial, too much time and energy is lost in aggression, as a result of the high frequency of encounters. The most important selective pressures must be spatial exiguity and population high densities, which together determine an increment in the frequency of encounters.

On the other hand, according to EDWARD WILSON (1975), population stability and sedentarisation are two of the causes of genetic flux reduction and consequently, of consanguinity. In the context of sociobiological thought, this fact tends to maximise agonistic ritualisation in spite of open aggressive behaviour. Simultaneously, an increment in altruistic behaviour is expected.

According to STAMPS & BUECHNER (1985), the evolution of behaviour on high density populations (insular environments, for example) can be characterised by:

a. reduction in the size of territory;
b. enlargement in the overlapping of territories;
c. acceptance of subordinates;
d. reduction of aggressiveness;
e. loss of territoriality.

On Berlenga Island, spatial constraints have determined the aggregation of individuals of the species *Timon lepidus*, which ritualise their agonistic behaviour and are non-territorial. On the contrary, in the continent, low-density populations are aggressive and territorial. It seems evident, in this case, that social structure should be related with population density, thus, social structure must be driven by spatial constraints. In summary, a high frequency of encounters favours the establishment of agonistic and submissive ritualised behaviours, while a low frequency may favour aggression, which is effective in the case of spaced individuals (for more details see VICENTE, 1987; VICENTE *et al.*, 1987; VICENTE, 1989b; VICENTE & PAULO, 1989).

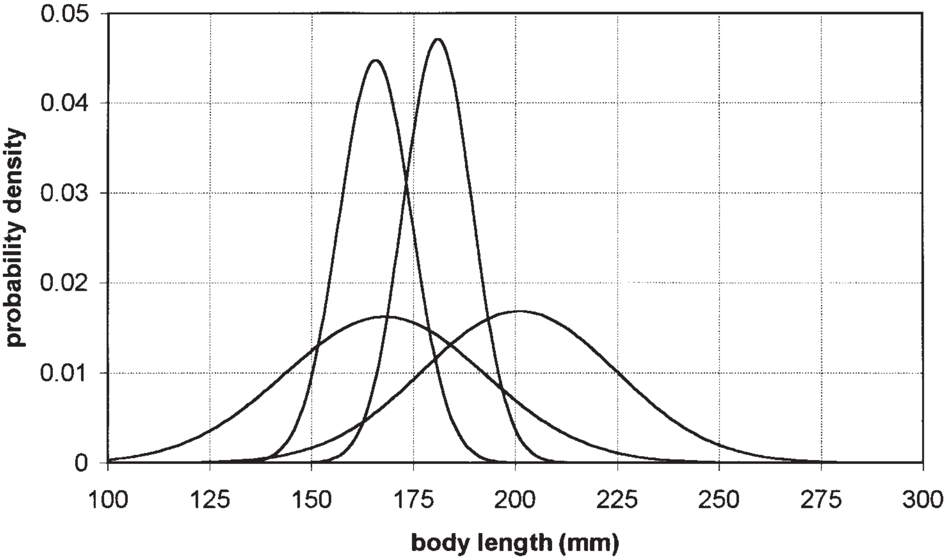

Fig. 3. Comparison of probability distributions of the body length between insular (leptokurtic curves, the left for females and the right for males) and continental (normal curves, the left for females and the right for males) populations of *Timon lepidus* (VICENTE, 1989a).

In addition, the last question in this context should be: »*can behavioural changes be related to body shape changes?*«.

To answer it we can point out that the most conspicuous morphological change in Berlenga eyed-lizards is a strong reduction of sexual dimorphism, with male character displacement towards female (or juvenile) body size and proportions (Fig. 3).

To explain this phenomenon we can put forward two hypotheses:

a. NON-ADAPTIVE: fixation of an allele of a pleiotropic gene regulating body growth, as a result of genetic drift.

b. ADAPTIVE: male acquisition of feminine (or juvenile) phenotype leading to low sexual dimorphism may act as an inhibitor of effective aggressive behaviour. This could be the effect of the so-called »*kindchenschema*« in the Konrad Lorenz sense (LORENZ, 1943, 1950).

By way of concluding remarks, we can say that, the capacity to become established on an island requires adaptive plasticity, in particular regarding:

a. capacity of an r-strategist to become a K-strategist;

b. capacity for niche enlargement;

c. open behavioural program in the Ernst Mayr sense (MAYR, 1974).

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