

Adaptation and evolution in *Gallotia* lizards from the Canary Islands: age, growth, maturity and longevity

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Abstract. Qualitative and quantitative comparisons of histological data recorded from growing bone from seven extant and extinct taxa of *Gallotia* show that these lizards do not have the same longevity, reach sexual maturity at various ages and probably have different growth rates which are in reverse proportion to the specific size of individuals in each taxon. In term of relative growth, the highest rate is seen in the smallest taxon (*G. atlantica*) and the lowest in the largest taxon (*G. goliath*). It appears that differences between the maximum size reached, irrespective of the size of hatchlings, are only the consequence of changes in longevity allowing a more or less protracted growth; they are not due to differences in growth rates. On the basis of these data we discuss some points relating to adaptive strategies and evolutionary features of these lizards.

Introduction

From many points of view, the situation of the Lacertidae living in the Canary Islands is very unusual—if not unique—and makes this group a very interesting model for the study of several interrelated biological problems.

The lizards all belong to the same genus *Gallotia*, and are endemic to an archipelago of seven main islands and many islets (fig. 1). All the living taxa are allopatric, with one exception on Hierro and what may be a very recent introduction on Gran Canaria. The high chromosome number ($2n = 40$) of *Gallotia* (Cano et al., 1984) against $36 < 2n < 38$ for the other Lacertidae, probably indicates the antiquity of this genus and its affinities with ancestral forms (King, 1981; Baez, 1987a). The genus is polyspecific with four currently extant species (some with fossil material) divided into many subspecies and at least one extinct species, *G. goliath*, the largest lacertid known so far. The diversity of intra- as well as inter-specific body sizes is a major aspect of variation in these lizards. Although some relationships between specific size and island size (Boettger and Muller, 1914; Baez, 1982) and between body sizes and variation

in scalation (Thorpe, 1985a) have been suggested, no convincing explanation for these size variations is available. The evolution of these lizards appears to remain a currently active process, perhaps linked to their insularity, with extension and speciation for both *G. galloti* and *G. atlantica*, an apparently stable situation for *G. stehlini*, a near extinction and a complete extinction for *G. symonyi* and *G. goliath* respectively.

In view of this interesting geographical, biological and evolutionary situation, several studies and hypotheses relating to the distribution, systematics, phylogeny and microevolution of these lizards have been already published (Böhme and Bings, 1975, 1977; Böhme and Bischoff, 1976; Böhme et al., 1981; Molina-Borja, 1981; Bischoff, 1982; Castroviejo et al., 1985; Baez and Thorpe, 1985; Thorpe, 1985a,b,c,d, Thorpe et al., 1985) but many problems remain to be solved (e.g. Baez, 1987a). Paradoxically, with the exception of some behavioural features of *G. galloti* (Böhme and Bischoff, 1976; Molina-Borja, 1985; Molina-Borja et al., 1986; Garcia-Diaz et al., 1989), general data dealing with the biology and ecology of these lizards (as individuals and populations) still remain scarce today.

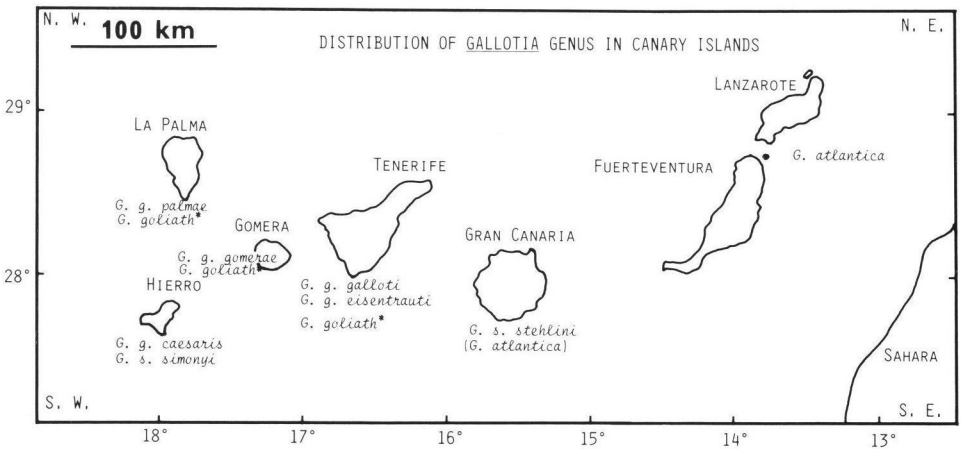


Figure 1. Distribution of taxa within the genus *Gallotia* in the Canary Islands. *: extinct.

Following a preliminary study (Castanet and Baez, 1988) on the age structure, age at maturity, growth and longevity of *G. galloti*, we have now assessed these data for all the different extant and extinct taxa of *Gallotia*, with the exception of *G. symonyi*. This paper provides a synthesis of the results and discusses how comparison between the various taxa involved can foster a better understanding of some adaptive and microevolutionary features of the lizards. Our goal is also to show how the methodology used—bone histology and skeletochronology—can be a powerful tool to obtain such results, especially for the fossil material.

Material and methods

Material

Samples from different populations and different subspecies belonging to the three main extant species of the genus *Gallotia* Boulenger 1916, were studied. All the lizards were of unknown age.

To date we had no possibilities for investigation of the endangered but fortunately well protected species, *G. symonyi* (Steindachner 1889) which only survives on a cliff in the north-east area of Hierro island. However the present study also deals with a large sample of bones of the sub-fossil *G. goliath*, and some other sub-fossil bones supposed to belong to *G. simonyi* and to *G. g. caesaris* (Böhme et al., 1981; Castanet and Baez., in press)

G. galloti (Duméril et Bibron, 1839)

a- *G. g. galloti* (Duméril et Bibron, 1839) and *G. g. eisentrauti* Bischoff, 1982. Island: Tenerife. Measurements were taken from photographs of the bones used in a previous paper (Castanet and Baez, 1988). The sample consists of 36 *G. g. eisentrauti* and 40 *G. g. galloti*. Since no qualitative and quantitative differences could be observed between the growth marks of the two subspecies, these lizards will be considered collectively for the present study as a rather homogenous sample of 76 *G. galloti* (39 males, 23 females and 14 juveniles).

b- *G. g. palmae* (Boettger and Müller, 1914). Island: La Palma. Sample: 30 specimens (12 males, 19 females, 3 juveniles) caught in the same area.

c- *G. g. gomerae* (Boettger and Müller, 1914). Island: La Gomera. Sample: 36 specimens (15 males, 19 females, 2 juveniles) caught in the same area.

d- *G. g. caesaris* (Lehrs 1914). Island: Hierro. Sample: 34 specimens (15 males, 15 females, 4 juveniles) caught in the same area.

G. atlantica (Peters & Doria 1882)

Sample from Lanzarote: 42 specimens (26 males, 9 females, 7 juveniles).
Sample from Gran Canaria: 33 lizards. This species is supposedly of recent introduction in this island (Barquin and Martin, 1982). The specimens were only used for qualitative comparisons of their growth marks with those of Lanzarote.

G. stehlini (Schenkel 1901). Island: Gran Canaria

Sample: 80 specimens (32 males, 47 females, 1 juvenile) from four populations living at different altitudes (fig. 2).

G. goliath (Mertens 1942). Island: Tenerife

Many femurs and humerus were collected from the floor of natural volcanic caves. For this study, 61 left femurs were selected, thus making sure that one bone = one individual.

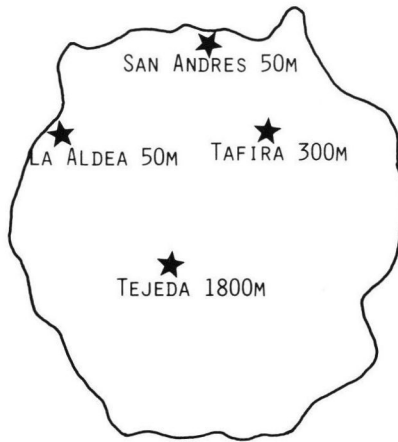


Figure 2. *Gallotia stehlini* in Gran Canaria: location of the four populations studied.

Supposed a- *G. g. caesaris* and b- *G. simonyi*. Island: Hierro.

Locality: Playa de La Arena.

a- 5 femurs and 3 humerus.

b- 1 femur and 1 humerus.

Methods

All the samples of extant lizards include specimens from the different size groups encountered in the field, but the number of individual in each group is probably not proportional to their actual number in the population, perhaps with the exception of *G. g. galloti*. Generally, the number of young individual is underestimated by our samples.

Snout-vent length and total length were recorded for all the living specimens. The femurs, where skeletal growth marks are the most reliable and obvious, were selected for skeletochronological analysis.

Extant species: after removal, the bones were demineralized for 4 to 8 hours according to their size, in 5% diluted nitric acid. Frozen sections, taken from the middle of the diaphysis, were stained with Ehrlich's hematoxylin. For each bone, 10 to 20 sections embedded in aquamounting medium were observed. The best slide used for counting the Lines of Arrested Growth (LAG), e.g. those with well marked LAGs, poor endosteal bone resorption and thickest bone crown, was photographed.

Extinct species: whole bones were embedded in a polyester resin (stratyl). Two or three sections were made with a thin bladed diamond saw at the level of the diaphysis, ground to a thickness of about 40 μm and polished. The sections were observed and

photographed under polarized light, where LAGs appear as bright lines because of their higher refringency relative to the contiguous bone tissue.

For reliable comparisons, all the photographs were enlarged to the same magnification. A curvimeter was used to measure the length (perimeter) of the LAGs on the photographs to a precision of one millimeter. The actual lengths (L) were obtained by dividing the measured lengths by the ratio of magnification. The differences in bone radius (r) was calculated ($r = L/2\pi$) between successive LAGs which are supposed to correspond to yearly growth increments.

For the *G. galloti* ssp. these measurements were performed on 10 males and 10 females selected for demonstrating most obvious and well marked LAGs. For *G. atlantica* (from Lanzarote) only 5 males and 6 females were suitable for selection. For *G. stehlini* data were obtained for 30 males and 39 females from the 4 populations studied. For *G. goliath* only 18 bones judged to be reliable were used for measurements, owing to endosteal resorption and to removal of bone tissue as a consequence of mycelial invasion of bone after the death of the lizards (Ricqlès, pers. comm.).

Rates of cortical bone growth are expressed in $\mu\text{m}/\text{day}$. As the duration of the annual growing period is unknown, we have chosen two arbitrary times for this calculation: 365 days or 244 days (8 months—See table 3).

Statistical calculations (correlations, t test, F test) were done using the statistical library of the 41 cx Hewlett-Packard calculator and growth curves were calculated using an Apple II GS computer. The bone growth curves, approximately related to a power function ($y = bx^a$) were compared by a covariance analysis after log transformation, using the procedure GLM of the SAS statistical package.

Results

Bone histology and features of growth marks

The bone structure of all extant *Gallotia* is similar to that of many other Lacertidae (fig. 3). In general the bone cortex at the diaphysis level is avascular and is made of a compact parallel fibered bone tissue. In some old individuals, with the decreasing bone growth rate, the outer part of the cortex progressively changes into a sub-lamellar and lamellar bone tissue. In this last histological type of bone, the LAGs do not appear as distinct as in the inner parallel fibered bone.

The optical recording of the LAGs varies according to the taxa studied. For the *G. galloti* group. LAGs appears very obvious in *G. g. galloti* and although from time to time some LAGs appear as twin or double LAGs in a few specimens (fig. 3d), no major difficulties in counting were encountered. LAG recording is also good for *G. g. palmae* and *G. g. caesaris*, but, without any clear explanation, much weaker for *G. g. gomerae*. Thus, LAGs counting is somewhat more difficult, and consequently age estimation is not as precise, in this sub-species as in the three others. *G. stehlini* show very clear LAGs, even better than those of *G. g. galloti*. However it appears that the

most obvious LAG recording in this species occurs among the population living at 1800 m, probably according to greater seasonality at high altitude (see fig. 2). In contrast to all the previous taxa, LAGs are very poorly expressed in *G. atlantica* (fig. 3a). This holds for the sample from Lanzarote as well as for the sample living in Gran Canaria.

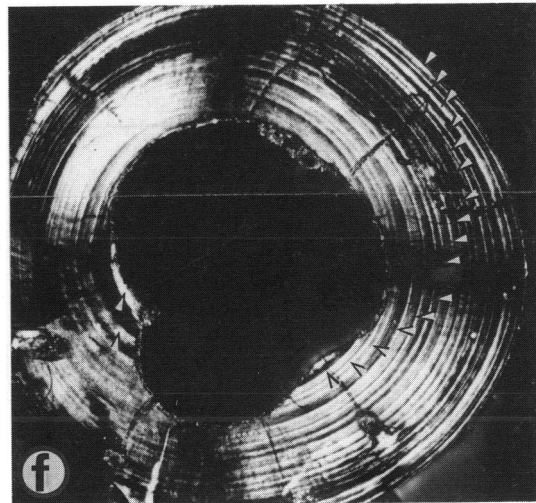
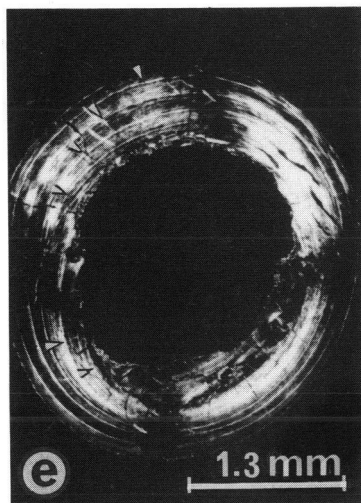
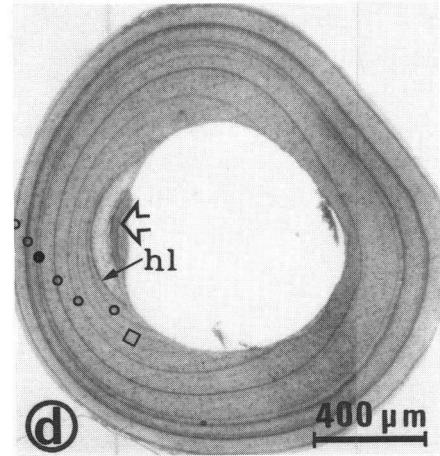
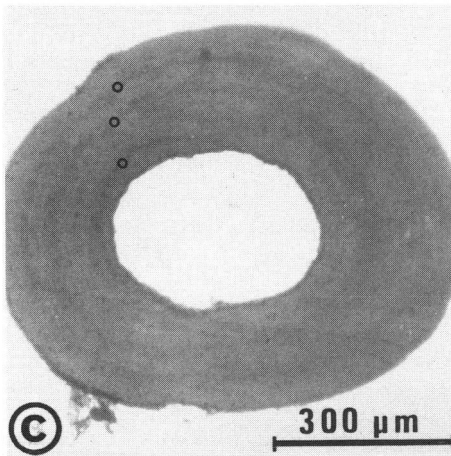
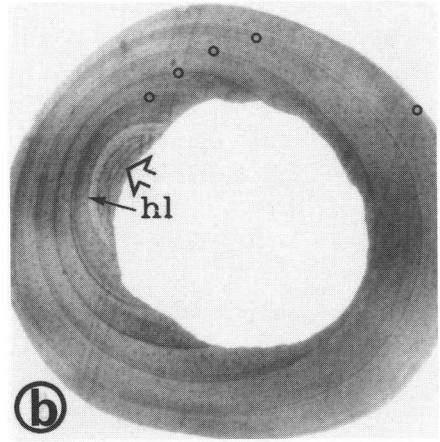
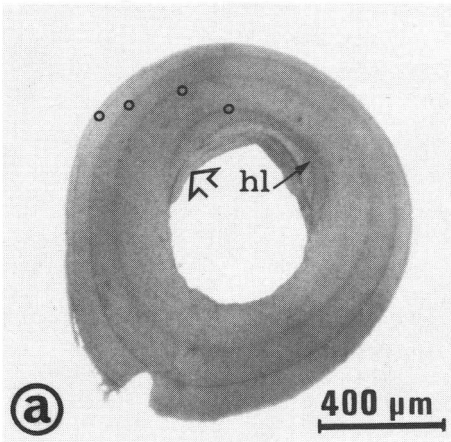
Another important feature is that, with the exception of *G. stehlini*, for more than 90 percent of all the specimens, whatever their age, endosteal bone resorption is never very intense and thus some embryonic bone located below the first LAGs always remains locally present (fig. 3). This makes LAG counting easier and more reliable, without the necessity for a back calculation that would otherwise have been necessary in order to take into account the LAGs removed by endosteal erosion. For *G. stehlini*, endosteal resorption is more extensive than in other taxa. Among old specimens, the LAGs of the first and second year can sometimes be completely removed and lamellar endosteal bone can be centripetally deposited around the medullar cavity (fig. 3).

In most specimens, including young of the year, a hatching LAG is present, more or less close to the LAG of the first winter. Thus, the amount of time elapsed between hatching and the first period of arrested growth appears to change from one individual to another. This probably indicates that the breeding period for all taxa is rather widely spread over the yearly cycle (Castanet and Baez, 1988).

The same pattern of spatial distribution of the LAGs is also observed in the 8 subfossil long bones supposed to belong to *G. g. caesaris*.

In *G. goliath* (fig. 3e,f) cortical diaphysis are also avascular and built of parallel fibered or lamellar bone tissue, according to the individual recording variations in growth rate with age. The LAGs appear as very distinct bright lines—or thin layers—even in a local context of finely lamellar bone tissue and are very numerous in the largest bones (see below). Moreover, in contrast with extant lizards, the LAGs of *G. goliath*, even the first ones deposited, appear very close to each other. Double or supplementary LAGs seem scarce. In many bones, especially the largest ones, internal

Figure 3. Growth marks at the femoral diaphysis in different species of extant (a, b, c, d) and extinct (e, f) *Gallotia*. Pictures of LAGs in bones of *G. g. galloti* are shown in Castanet and Baez, 1988. a. *G. g. gomerae* N° 70. Male. Ehrlich's hematoxylin. 4 annual LAGs are present (circles). The hatching line (hl) surrounds the embryonic and less stained bone. Open arrow: endosteal bone centripetally deposited on the previously resorbed periosteal bone surface. b. *G. g. palmae* N° 1. Male. Similar aspect than *G. g. gomerae* N° 70. Same magnification. 5 LAGs can be counted: This specimen is 5 years old. c. *G. atlantica* N° 25. Male. 3 LAGs poorly expressed are present. On this specimen, embryonic bone and hatching line have been removed. No endosteal bone. d. *G. stehlini* N° 408. Female from Tejada population (see fig. 2). At least 6 clear annual LAGs can be recognized. The 4th (solid circle), double, is only counted for one year. One or two (?) thin lines (open square) can be expected to be supplementary LAGs. The age of this specimen can be 6 or 7 years old. Hatching line, embryonic and endosteal bone are similar to species of fig. a and b. e. *G. goliath* N° 136. Polarized light. 6 refringent LAGs can be recognized (arrows). Perhaps one or two internal ones have been completely removed by endosteal resorption. f. *G. goliath* N° 112. Same magnification than fig. 'e'. 18 clear LAGs are present. Perhaps some more have been removed. Thus this specimen was at least 18 to 20 years old. It is obvious that in these fossil species, LAGs are much more closed together than in the extant species.



endosteal resorption has completely removed up to at the least the 4th or 5th LAG deposited during early life (fig. 3). In other bones, the first—or second?—LAG is locally preserved. Endosteal bone deposition can be locally present, forming centripetal deposits around the marrow cavity.

In the few femurs and humerus supposedly belonging to sub fossil specimens of *G. simonyi*, the LAGs are also very close to each other, as in *G. goliath*.

Age groups and longevity

We have no firm experimental or observational assessment of the periodicity of LAG deposition in lizards of the genus *Gallotia* but as their bone growth pattern is quite similar to that of other Lacertidae, where LAGs have been demonstrated to be annually deposited (e.g. Castanet, 1985), we can hypothesize here that it is the same for the *Gallotia* group.

For *G. atlantica* an age estimation was impossible for about 15 to 20 percent of the individuals and is of a low degree of precision (more or less one year) for about half of the others.

For all the other taxa accurate counting of LAGs and consequently accurate age estimation, was possible for more than 90 to 95 percent of the individuals, with only one LAG of uncertainty for 60 percent. Table 1 reports the longevity *in natura* of the different taxa of *Gallotia* according to their maximal number of LAGs. As the samples

Table 1. Estimated longevity (years), average and maximum body size (mm) for lizards of *Gallotia* genus. m = males. f = females. 1: Castroviejo et al. 1985. 2: Salvador 1385. 3: Salvador 1971. 4: Gasc 1971.

Taxa	Longevity this sample	Average SVL		Maximum SVL	
		this sample m + f	literature	this sample m	literature
<i>G. atlantica</i> N = 45	5	60	m:67 f:55 ¹	88	90 ²
<i>G. g. caesaris</i> N = 33	6	69	—	90	m:82 f:78 ²
<i>G. g. gomerae</i> N = 33	6	76	—	95	—
<i>G. g. palmae</i> N = 31	7	85	—	111	m:112 f:98 ²
<i>G. g. galloti</i> N = 77	8-9	90	—	132	m:135 f:126 ²
<i>G. stehlini</i> N = 80	10-11	121	—	206	240 ²
<i>G. simonyi</i> -----	—	—	—	—	f:255 ³
<i>G. goliath</i> N = 48	20 at least	358	—	478	400 to 450 ⁴
<i>Lacerta lepida</i>	—	—	—	—	m:235 f:210 ²

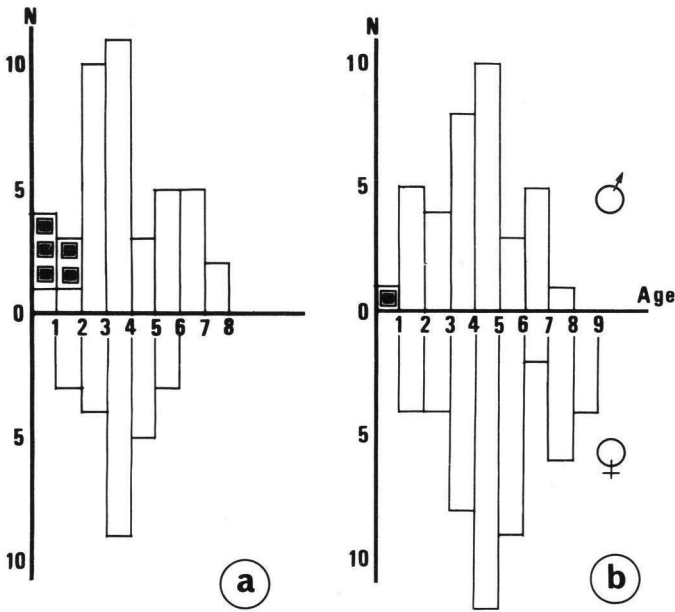


Figure 4. Example of rough age groups distribution for the samples of two species of the *Gallotia* studied.

N = number of specimens.

a. *G. g. galloti*. 39 M; 25 F.

b. *G. g. stehlini*. 32 M; 47 F.

The juveniles (solid squares) are voluntarily under-represented.

are not exactly representative of the actual populations (young individuals being largely under represented), we will only give the age group distribution for *G. g. galloti* and *G. g. stehlini* as examples (figs. 4a,b; 5a,b).

Sexual maturity

For the extant lizards, the first 3, 4 or 5 LAGs, according to taxa, generally appear further apart from each other than the following ones (fig. 3). Such a feature clearly records a decrease in the diametric growth rate, which probably occurs at, or sometimes after the attainment of sexual maturity (as in some snakes, for instance—Saint Girons pers. comm.) as has already been suggested (e.g. Castanet, 1986-87).

For *G. g. galloti* we have already suggested that sexual maturity was reached during the 3rd or the 4th year of life (Castanet and Baez, 1988). For *G. g. palmae*, *G. g. gomerae* and *G. g. caesaris* the “break” in the spatial sequence of the LAGs appears between the 2nd or the 3rd LAG. This suggests that maturity is reached during the 2nd or the 3rd year of life in these taxa. For *G. g. stehlini* sexual maturity would be reached during the 4th or the 5th year of life, according to the same data. The poor quality of LAGs

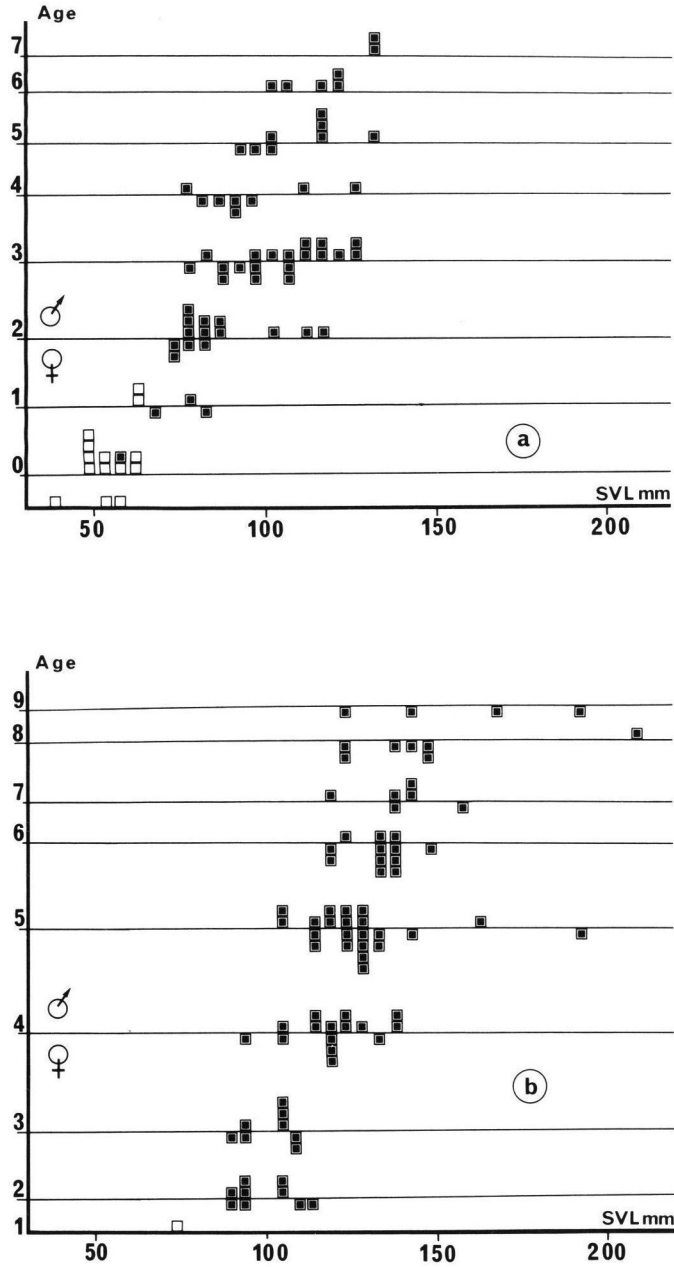


Figure 5. Age-size relationships: this diagram clearly shows the individual variability of body sizes for the same age group in these lizards.
 a. *G. g. galloti* 39 M; 25 F; 14 juveniles (open squares).
 b. *G. stehlini* 32 M; 47 f; 1 juvenile (open squares).

recorded in *G. atlantica* does not allow us to indicate the age of maturity precisely. Nevertheless, this phenomenon probably appears not later than the 2nd year of life, taking into account the short individual longevity in this species.

For *G. goliath* it is very difficult to notice any break in the spatial distribution of the LAGs even until the 15th or 16th LAG (figs. 3, 7). Consequently, the age of sexual maturity cannot be reliably estimated. We can only suggest that sexual maturity was delayed in this species in comparison with the living ones.

Relationship between bone diameter and snout-vent-length (SVL or body size)

For all the extant taxa studied, correlations between diameter of the femur at the diaphysis level and the SVL are generally higher than $r = 0.80$ and better for males than for females (table 2). These results are significant ($P > 0.01$). Consequently all the following results dealing with the growth rate in thickness of the femoral diaphysis give a good idea of the body growth rate, especially for the males (such a good correlation between increments of long bones diameter and overall body length has also been observed in the amphibian *Rana temporaria*, (see Ryser, 1988).

Table 2. Correlations between SVL and femoral diaphysis perimeter.

	<i>G. g. gal.</i>	<i>G. g. gom.</i>	<i>G. g. caes.</i>	<i>G. g. palm.</i>	<i>G. atl.</i>	<i>G. stehli.</i>
Males	0.94 <i>N</i> = 40	0.84 <i>N</i> = 14	0.92 <i>N</i> = 15	0.95 <i>N</i> = 13	0.94 <i>N</i> = 21	0.96 <i>N</i> = 33
Females	0.79 <i>N</i> = 22	0.82 <i>N</i> = 20	0.78 <i>N</i> = 15	0.88 <i>N</i> = 15	0.69 <i>N</i> = 10	0.96 <i>N</i> = 47
M + F	0.93	0.84	0.90	0.92	0.86	0.95

Size of lizards

For the *G. galloti* taxa and *G. atlantica*, a size dimorphism can be observed between males and females after the reaching of sexual maturity: in each age group, males always become larger than females (figs. 5a, 6), a result consistent with all other previous data on these lizards (Thorpe, 1985a; Castroviejo et al., 1985). For *G. stehlini* there is no apparent dimorphism (fig. 5b). Data dealing with the average body size and the maximal body size in this species, are consistent with those of previous authors (table 1).

Taking into account the positive correlation between the diameter of the femoral diaphysis and body size among living *Gallotia*, it is easy to estimate body sizes for *G. goliath* in our sample. Such calculations show that the SVL average was 358 mm for the *G. goliath* studied and reached 478 mm for the largest specimen (*N*. 100) corresponding to a maximal length of about 1300 mm. These calculations suppose that the relative body proportions and the body/tail ratio are similar between extant and extinct species of *Gallotia*. We must note that the two last size figures are consistent with those already estimated by Gasc (1971).

Table 3. Absolute growth rate in thickness of femoral diaphysis. μ /day.

Males + females. A = calculated for 365 growing days.

B = calculated for 244 growing days.

(L2-L1 = LAC2-LAC1)

	L2-L1	L3-L2	L4-L3	L5-L4	L6-L5	L7-L6	L8-L7	L9-L8	L10-L9
<i>G. g. gal.</i>	A 0.33	0.26	0.20						
	B 0.50	0.30	0.30						
	N = 19	N = 20	N = 1						
<i>G. g. pal.</i>	A 0.31	0.24	0.22						
	B 0.46	0.36	0.32						
	N = 18	N = 18	N = 9						
<i>G. g. gom.</i>	A 0.36	0.16	0.10						
	B 0.54	0.25	0.15						
	N = 12	N = 12	N = 6						
<i>G. g. cae.</i>	A 0.28	0.15	0.09						
	B 0.42	0.22	0.11						
	N = 19	N = 13	N = 6						
<i>G. atl.</i>	A 0.30								
	B 0.45								
	N = 11								
<i>G. stehl.</i>	A 0.35	0.30	0.24	0.20					
	B 0.53	0.46	0.36	0.31					
	N = 53	N = 66	N = 61						
<i>G. gol.</i>	A 0.27	0.31	0.49	0.17	0.19	0.27	0.26	0.25	0.18
	B 0.41	0.47	0.74	0.26	0.29	0.41	0.40	0.38	0.27
	N = 12	N = 15	N = 15	N = 15	N = 16	N = 16	N = 16	N = 14	N = 14
.....									
<i>G. gol.</i> (continue)	L11-L10	L12-L11							
	A 0.32	0.20							
	B 0.49	0.30							
	N = 11	N = 10							

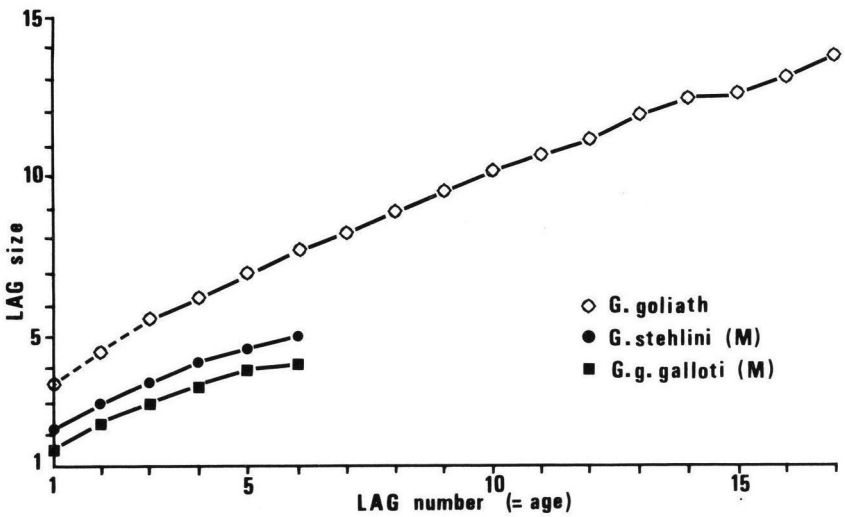
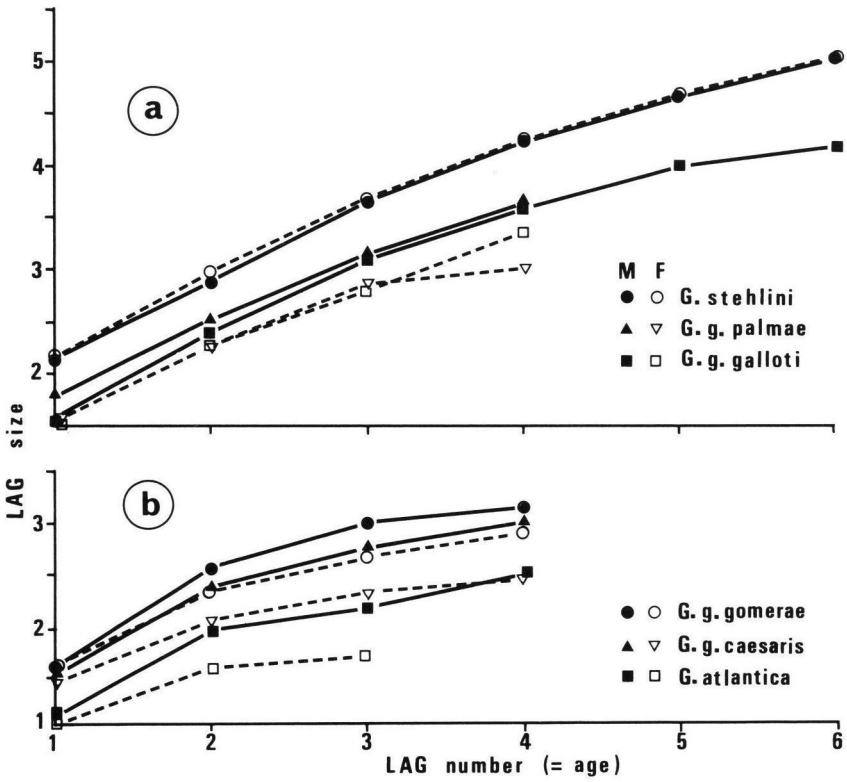
Sphenodon punctatus: 0.28-0.36 μ m/day for 365 days, up to 15 years at least (Castanet et al. 1988).

Growth rate comparison

The growth rates of the femoral diaphysis are never significantly different between males and females, at least until the fourth year of life for all the *G. galloti* studied and the fifth year for *G. stehlini* (*t* test: $P < 0.01$). Covariance analysis confirms that the slopes of the growth curves between series of *G. g. galloti*, *G. g. palmae* and *G. stehlini* (fig. 6a), do not significantly differ ($F_{1,459} = 0.91$ $P = 0.01$). Thus both sexes were pooled for the following results.

The comparison of absolute annual growth rates between the extant taxa shows that:

- a- no significant differences are observed between the samples from the four populations of *G. stehlini* which are therefore pooled.
- b- There are no significant differences between *G. g. galloti*, *G. g. palmae*, *G. g. gomerae*,



the absolute growth rate of *g. goliath*, until at least its 12th or 14th year of life, was rather similar to that of the extant species (table 3, fig. 7) during their 4 or 5 first years of life.

In terms of relative growth rate, it is obvious (table 4) that the relative bone growth rate of *G. goliath*, even during its first year of life, is very low in comparison to those of all the living species at an equivalent physiological age. Nevertheless, the bone growth—and probably the body growth—of *G. goliath* is still quite noticeable up to 15 or 16 years old.

Discussion

Bone histology and skeletochronological features

We will not take into account either inter-individual differences dealing with the spatial sequences of the LAGs, or the random presence of double LAGs. Such phenomena are of minor significance for our present study and have already been discussed for *G. galloti* (Castanet and Baez, 1988) and they appear less pronounced in the other taxa.

— *Endosteal resorption of femoral diaphyses.* This process rarely completely destroys the first LAGs deposited in the *G. galloti* group. This feature contrasts with observations of *Lacerta lepida*, and has been previously discussed (Castanet and Baez, 1988). For *G. stehlini*, the complete endosteal removal of the first and sometimes second LAG in older specimens does not preclude an exact age estimation. These first LAGs, when present, are far from each other and their measurement in juveniles clearly allows the assessment of the number of LAGs ultimately lost among adults. For *G. goliath* the problem is more difficult because: 1) for this study, very few supposedly young specimens were available, 2) the first LAGs already appear close to each other. Thus, the value of their successive lengths can overlap which does not allow their discrimination. This explains the inaccuracy of age estimation which spreads over 1 or 2 years. Nevertheless, taking into account the high longevity of this species, such an error becomes relatively small. Moreover, because of the constancy of the bone growth rate from the first LAG observed to at least the tenth, we may assume that this growth rate was rather similar (and relatively low, see above) for the first and second or second and third years. Com-

Figure 6. Bone growth curves in thickness of the extant *Gallotia* (cumulative data). 10 males (M) and 10 females (F)—those with the best LAGs—of each species where used here. Each means corresponds to 3 individuals at least. The slopes of these curves are very closed to each other, especially for the species of fig. 6a. The first year of life, this slope is even higher for the smallest species (6b) than for the largest ones (6a).

Figure 7. Growth in bone thickness of the extinct *G. goliath* (18 individuals) compared to *G. stehlini*, *G. g. galloti* and the other species of fig. 6. For *G. goliath* the slope is very close to those of the extant *Gallotia* at similar physiological ages. The dotted line corresponds to a back calculated part of the curve because of the possible removing of the two first LAG deposited in most of the *G. goliath* studied.

parison of growth rates between *G. goliath* and the other taxa therefore appears reliable indeed at least until the sexual maturity.

— *Histological sharpness of LAGs*. The variability of the histological expression of LAGs between the different taxa or populations studied still remains difficult to understand. The general assessment is that, at least in reptiles, LAGs originate from an endogenous (genetic) biological rhythm but are synchronized and reinforced by external factors, mainly seasonality (Buffrénil, 1980; Castanet, 1982). In fact, even if growth marks appear in animals living in apparently non-cyclical environmental conditions (Patnaik and Behera, 1981; Castanet, 1982, Castanet and Gasc, 1986), they are better expressed when animals are submitted to contrasting climates during the yearly cycle (e.g. populations in high latitudes or altitudes). The present study reveals such a difference, between lowland and highland populations of *G. stehlini*.

As the intensity of seasonality is indirectly linked to bone growth (Castanet, 1982), the change in local climatic conditions from one island to another may be partly involved to explain some tiny differences of LAG features between *G. g. gomerae* and the three other *G. galloti* sub-species. The same argument could be put forward for *G. atlantica*. In this species however, LAGs always have uniformly poor optical contrast in specimens from Lanzarote as well as from Gran Canaria populations, but since in Gran Canaria the population of *G. atlantica* is sympatric with *G. stehlini*, which shows very clear LAGs, climatic differences cannot be invoqued as a total explanation of variations in the histological expression of LAGs. Consequently, the poor aspect of LAGs in *G. atlantica* could well be considered an autapomorphic character of this taxon, one rooted in its genetic set-up.

— *Total number of LAGs—Individual longevity*. It has already been shown that, especially for reptiles, bone growth in thickness can stop well before the death of the individual (e.g. Castanet, 1986-1987; Castanet et al., 1988), and consequently ceases to record LAGs. Thus, the true age of old individuals can be underestimated. In other words, according to the species, the highest number of LAGs may only indicate a minimum longevity. This raises the possibility that other specimens of the same population record at least the same highest number of LAGs which could mistakenly suggest that the population structure involves a high percentage of old individuals (see discussion in Castanet 1986-87).

For the different extant taxa of *Gallotia* studied, we have no idea of the importance of such a phenomenon, but we expect the possibility that the actual ecological longevity could be one or two years higher than recorded, according to the different taxa studied. Nevertheless, such a tentative conclusion is impossible for *G. goliath* because in this species, even at the maximal ages estimated by skeletochronology, no significant decrease of the bone growth rate appears. Moreover, as already explained, this circumstance hampers any estimate of the age of sexual maturity in this species. Nevertheless in *Sphenodon punctatus*, LAGs have a pattern rather similar to that of *G. goliath*, the maximal number of LAGs recorded being 35 in the femur of this species (Castanet et al., 1988), although the longevity is known to exceed 60 years (Dawbin,

1982). Thus, by comparison, it is possible to suggest that a *G. goliath* exhibiting 20 femoral LAGs (meaning 20 years old) may in fact be several years older.

Growth, size, maturity, longevity: relationships and biological significance

The observation of differences in the mean longevities reached by the various taxa of *Gallotia* is one of the major result of this study. The main other result deals with the demonstration of species specific growth rates. First, the *absolute* bone growth rate in thickness, and probably also the overall body growth rate at equivalent physiological ages, appears similar for all the extant and extinct taxa. Second, the *relative* growth rates, are very significantly different and inversely correlated to the specific adult size of the taxa. This means that in the genus studied, the smallest and most short lived species (e.g. *G. atlantica*) grow faster than the largest and more long-lived species (e.g. *G. goliath*). Such a result is consistent with the general rule of “life duration” (Sacchi and Testard, 1971) validated for many reptiles at the inter or intra specific level (Tinkle, 1967; Saint Girons and Duguy, 1970; Turner, 1977; Strijbosch et al., 1980; Andrews, 1982; Bauwens and Verheyen, 1985; Tinkle and Duhnam, 1986; Castanet and Naulleau, 1985; Bauwens et al., 1987; Barbault and Mou, 1988). However, some external limiting pressures (e.g. available food supply), can disturb the usual relationships between these biological parameters, as has been recently demonstrated for two allopatric populations of *Lacerta viridis* (Saint Girons et al., 1989).

Since body size is accorded importance as an adaptative character (e.g. Barbault and Blandin., 1980; Barbault, 1988) and since the various *Gallotia* species show a large spectrum of sizes, the obvious question is: “how is the specific adult body size reached”? Three factors are currently involved in the attainment of specific body sizes: 1) Initial size at hatching. 2) Post-embryonic growth rate. 3) Duration of growth.

In plethodontid amphibians, for instance, recent studies show that, depending on the species, growth rate differences may (Tilley, 1980) or may not (Bruce, 1989) account for the variations in adult body size. The possibility of protracted juvenile growth due to delayed sexual maturity also must be taken into account (Tilley, 1980; Bruce, 1989). For the genus *Gallotia*, the answer to the previous question appears very clear: the interspecific differences between the maximum body sizes reached, irrespective of the size differences at hatching, are mainly the consequence of differences of longevity and time of sexual maturity, allowing a more or less protracted growth, but not to differences in growth rates. In other words, that clearly argue for the presence of heterochronic mechanisms of growth between the different taxa of *Gallotia*.

Bearing in mind that in the genus *Gallotia*, the maximum body size reached is a direct consequence of longevity, it is interesting to consider the causality of this last character. In line with the great intra- and interspecific phenotypic (ecological) plasticity of reptiles, differences concerning factors such as local population density, competition, predation, food supply and climates could easily account for small

individual variations of longevity. The breeding of the different taxa in various experimental conditions could provide valuable data on this point (e.g. Castanet and Naulleau, 1985). Nevertheless, "as maximum longevities in a species represents genetic and phenotypic maximum which have some reasonable relationship with potential longevities under natural conditions" (Gibbons, 1976) the important longevity differences observed between, for instance, *G. atlantica*, *G. stehlini* and *G. goliath* probably have a genetic basis.

For this hypothesis we suppose that external pressures are able to induce selection of lizards according to their longevity, e.g. to favor adaptive strategies in which longevity is a target for selection as well as any other morphological or physiological adaptive character.

Until now many data dealing with reproductive characteristics, mortality, survivorship, energy supply, competition, predation and other biological features of the different living taxa and populations of *Gallotia* were still unavailable, and they will remain so for *G. goliath*. Nevertheless, according to the present results one can make the hypothesis that the different taxa of extant and extinct *Gallotia* exemplify different adaptive strategies, probably linked to a strong polymorphism. First, according to the r-K classification (MacArthur and Wilson, 1967; Pianka, 1970; see also Barbault and Blandin, 1980; Barbault, 1983; Blondel, 1986), *G. goliath* with a prolonged longevity, a large adult size but a low growth rate and a probably delayed sexual maturity could appear as more of a K strategist, relative to more r strategists such as *G. atlantica* and *G. galloti*, with short longevity, high growth rates and early maturity. However according to preliminary data dealing with reproduction, all the extant *Gallotia* forms could be regarded as K strategists in comparison to any continental lizards of similar size (Baez, 1987b). On the other hand if the sexual maturity of *G. goliath* is really delayed, the big size of this species in comparison with those of living ones, could appear as a post developmental mechanism (e.g. Alberch et al., 1979).

What could be the consequences for the extinction and the evolution of the different taxa of *Gallotia* genus in Canary Islands? It has been already stressed by Andrews (1982) that "the rate at which an individual grows is intimately tied to its fitness" (by way of an enhanced fitness when growth rate increases). Facing drastic changes in selective pressures, which probably appear from time to time in the context of their insular situation (see also Cheylan, 1988), the different taxa of *Gallotia* would not have the same chances for survival, and a clear advantage for the more r strategists would be most likely. In this way, it seems possible to explain, at least partially, the extinction of *G. goliath* as a result of its unfavorable competitive situation relative to *G. galloti*, a situation aggravated by humans and their pets when these predators invaded Tenerife Island.

Because of the lack of data about *G. symonyi* it is difficult to speculate about the reasons for the progressive disappearance of this species from Hierro, although several hypotheses dealing with human activities are suggested (Rica, 1982). However, the fact that the pattern of LAGs in long bones of two sub-fossil specimens of *G. symonyi*

is rather similar to one of *G. goliath* (Castanet et Baez, in press), leads us to think that if extant *G. symonyi* have indeed the same bone growth pattern, the near disappearance of this species could have a similar causality than that suggested for *G. goliath*. In order to test this hypothesis, future histological studies of some bones of *G. symonyi* are especially needed.

In this context it must be stressed that *Sphenodon punctatus*, a rather large reptile which also has a low growth rate, great longevity and a delayed maturity (Crook, 1975; Dawbin, 1982) linked to LAGs patterns rather similar to those of *G. goliath*, (Castanet et al., 1988) is also a very endangered species, only surviving in New Zealand islets where predators (especially rats) are lacking (Crook, 1973; Saint Girons, com. pers.). This situation probably represents an interesting example of an adaptive and evolutionary convergence between two distant taxa of reptiles which today, unfortunately, leads them towards extinction.

To conclude, it must be emphasized that the present results and hypotheses were obtained principally on the basis of bone histology and skeletochronology. Although these methods for the study of the biology of living (and fossil) species are obviously not reliable at a 100% level, when the material permits, they allow qualitative and quantitative comparisons of growth marks between different populations and species which can provide very useful data in a relatively short time. Moreover, as has once again been shown by Esteban (1990) for amphibians and by Sander (1990) for reptiles, it is a unique tool for obtaining such data for fossils.

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References

- Alberch Pere, Gould, S. J., Oster, F., Wake, D. B. (1979): Size and shape in ontogeny and phylogeny. *Paleobiology* 5: 296-317.
- Andrews, R. M. (1982): Patterns of growth in Reptiles. In: *Biology of the Reptilia*, 13, Physiology D, p. 273-320. Gans, C., Pough, F. H., London etc., Academic Press.
- Baez, M. (1982): Consideraciones sobre las características zoogeográficas de la fauna de Canarias. *Inst. de Estudios Canarios 50 Aniversario. Aula de Cultura de Excmo. Cabildo Insular de Tenerife*, 23-70.
- Baez, M. (1987a): Les Reptiles des Iles Canaries. *Bull. Soc. Zool. France* 112: 153-164.
- Baez, M. (1987b): Datos sobre la reproducción de *Gallotia galloti* en Tenerife (Lacertidae). *Revista Española de Herpetología*. 2: 29-32.
- Baez, M., Thorpe, R. S. (1985): Microevolution of the lizard *Gallotia galloti* within the island of Tenerife. *Bonn. zool. Beitr.* 36: 513-515.
- Barbault, R. (1983): *Ecologie générale*. Paris etc., Masson.
- Barbault, R. (1986): Body size, ecological constraints and the evolution of life history strategies. *Evol. Biol.* 22: 261-286.
- Barbault, R., Blandin, P. (1980): La notion de stratégie adaptative: sur quelques aspects énergétiques, démographiques et synécologiques. In: *Recherches d'écologie théorique*, p. 1-27. Paris, Maloine.
- Barbault, R., Mou, Y.-P. (1988): Population dynamics of the common wall lizard, *Podarcis muralis*, in south-western France. *Herpetologica* 44: 38-47.
- Barquin, J., Martin, A. (1982): Sobre la presencia de *Gallotia* (= *Lacerta*) *atlantica* (Peters y Doria, 1982) en Gran Canaria (Rep., Lacertidae). *Don. Acta Vert.* 9: 377-380.

- Bauwens, D., Verheyen, R. F. (1985): The timing of reproduction in the lizard *Lacerta vivipara*: differences between individual females. *J. Herpetol.* **19**: 353-364.
- Bauwens, D., Heulin, B., Pilorge, T. (1987): Variations spatio-temporelles des caractéristiques démographiques dans et entre populations du lézard *Lacerta vivipara*. In: Coll. Nation. du CNRS. Actes du colloque; Biologie des populations, p. 531-536, Lyon, 1986.
- Bischoff, W. (1974): Beobachtungen bei der Pflege von *Lacerta symonyi stehlini*. *Salamandra* **10**: 93-103.
- Bischoff, W. (1982): Die innerartliche Gliederung von *Gallotia galloti* (Duméril & Bibron 1839) (Reptilia: Sauria: Lacertidae) auf Teneriffa, Kanarische Inseln. *Bonn. Zool. Beitr.* **33**: 363-382.
- Blondel, J. (1986): Biogéographie évolutive. Paris etc., Masson.
- Boettger, C. R., Muller, L., (1914): Preliminary notes on the local races of some Canarian lizards. *Ann. Mag. nat. Hist.* **14**: 67-78.
- Böhme, W., Bings, W. (1975): Zur Frage des Überlebens von *Lacerta s. symonyi* Steindachner (Sauria: Lacertidae). *Salamandra* **11**: 39-46.
- Böhme, W., Bings, W. (1977): Nachträge zur Kenntnis der kanarischen Rieseneidechsen (*Lacerta simonyi*-Gruppe) (Reptilia, Sauria, Lacertidae). *Salamandra* **13**: 105-111.
- Böhme, W., Bischoff, W. (1976): Das Paarungsverhalten der Kanarischen Eidechsen (Sauria, Lacertidae) als systematisches Merkmal. *Salamandra* **12**: 109-119.
- Böhme, W., Bischoff, W., Nettmann, H.-K., Rykena, S., Freundlich, J. (1981): Nachweis von *Gallotia simonyi* (Steindachner, 1889) (Reptilia: Lacertidae) aus einer frühmittelalterlichen Fundschicht auf Hierro, Kanarische Inseln. *Bonn. Zool. Beitr.* **32**: 157-166.
- Bruce, R. (1989): Life history of the salamander *Desmognathus monticola*, with a comparison of the larval periods of *D. monticola* and *D. ocofphaeus*. *Herpetologica*, **45**: 144-155.
- Buffrénil, V. de, (1980): L'histologie osseuse comme indicateur de la croissance et de la morphogenèse post-natale du squelette chez les crocodyliens actuels et fossiles. Thèse Dr. 3ème cycle, Université Paris 7.
- Cano, J., Baez, M., Lopez-Jurado, L. F., Ortega, G. (1984): Karyotype and chromosome structure in the lizard, *Gallotia galloti* in Canary Islands. *J. Herpetol.* **18**: 344-346.
- Carr, A., Goodman, D. (1970): Ecological implications of size and growth in *Chelonia*. *Copeia* **1979**: 783-786.
- Castanet, J. (1982): Recherches sur la croissance du tissu osseux des Reptiles. Application: la méthode squelettochronologique. Thèse Doctorat, Paris.
- Castanet, J. (1985): La squelettochronologie chez les reptiles. I. Résultats expérimentaux sur la signification des marques croissance squelettiques chez les Lézards et les Tortues. *Ann. Sci. Nat. Zool. Paris* **7**: 23-40.
- Castanet, J. (1986-1987): La squelettochronologie chez les reptiles. III- Application. *Ann. Sci. Nat. Zool. Paris* **8**: 157-172.
- Castanet, J., Baez, M. (1988): Data on age and longevity in *Gallotia galloti* (Sauria, Lacertidae) assessed by skeletochronology. *Herp. J.* **1**: 218-222.
- Castanet, J., Gasc, J. P. (1986): Age individuel, longévité et cycle d'activité chez *Leposoma guianense*, microteiidé de litière de l'écosystème forestier guyanais. *Mém. Mus. Nation. Hist. Nat. (Paris)* **132**: 281-288.
- Castanet, J., Naulleau, G., (1985): La squelettochronologie chez les reptiles. II. Résultats expérimentaux sur la signification des marques de croissance squelettiques chez les Serpents. Remarques sur la croissance et la longévité de la Vipère aspic. *Ann. Sci. Nat., Zool., Paris* **7**: 41-62.
- Castanet, J., Newman, D. G., Saint Girons, H. (1988): Skeletochronological data on the growth, age, and population structure of the Tuatara, *Sphenodon punctatus*, on Stephens and Lady Alice islands, New Zealand. *Herpetologica* **44**: 25-37.
- Castroviejo, J., Mateo, J. A., Collado, E., (1985): Sobre la sistematica de *Gallotia atlantica* (Peters y Doria, 1882). *Don. Acta Vert. Pub. Ocasional*: 1-85.
- Cheylan, M. (1988): Variabilité phénotypique du lézard des murailles *Podarcis muralis* sur les îles de la côte provençale, France. *Rev. Ecol. (Terre Vie)*. **43**: 287-321.
- Crook, I. G. (1973): The tuatara, *Sphenodon punctatus* Gray, on islands with and without populations of the Polynesian rat, *Rattus exulans* (Peal). *Proc. New Zealand Ecol. Soc.* **20**: 115-120.
- Crook, I. G. (1975): The Tuatara. In: *Biogeography and Ecology in New Zealand*, p. 331-352. Kuschel, G., Ed., The Hague, Junk.
- Dawbin, W. H. (1982): The tuatara *Sphenodon punctatus*; aspects of life history, growth and longevity. *New Zealand Wild. Serv., Dept. Intern. Aff., Occas. Publ.* **2**: 237-250.

- Duméril, A. M. C., Bibron, G. (1839): *Erpétologie générale ou Histoire naturelle complète des Reptiles*. Vol. 5. Paris.
- Esteban, M. (in press): Environments in the skeletochronological record on recent and fossil frogs. *Ann. Sci. Nat.* (in press).
- García-Díaz, C., Molina-Borja, M., Gonzales-Gonzales, J. (1989): Circadian rhythm and ultradian oscillations in the motor activity of the Lacertid lizard *Gallotia galloti* in continuous light. *J. Interdiscipl. Cycle Res.* **20**: 97-105.
- Gasc, J. P., (1971): Les variations colonnaires dans la région présacrée des sauriens. Application à la reconstruction de *Lacerta goliath* Mertens. *Ann. Paléont.* **57**: 133-155.
- Gibbons J. W., (1976): Aging phenomena in Reptiles. Special review of experimental ageing research. M. F. Elias, Eleftheriou, B. E., Elias, P. K., Eds., Bar Harbor, ME, 453-475.
- King, M. (1981): Chromosome change and speciation. In: *Evolution and speciation*, p. 263-285. Atchley, R. C., Woodruff, D. S., Eds., Cambridge Univ. Press.
- Lehrs, P. (1914): Description of a new lizard from the Canary Islands. *Proc. Zool. Soc. London* **1914**: 681-684.
- MacArthur, R. H., Wilson, E. O. (1967): *The theory of island biogeography*. Princeton Univ. Press, N.J.
- Mertens, R. (1942): *Lacerta goliath*, n. sp., eine ausgestorbene Rieseneidechse von der Kanaren. *Senck.*, **25**: 330-339.
- Molina-Borja, M. (1981): Etograma del lagarto de Tenerife *Gallotia galloti galloti* (Sauria-Lacertidae). *Don. Acta Vert.* **8**: 43-78.
- Molina-Borja, M. (1985): Spatial and temporal behaviour of *Gallotia galloti* in a natural population of Tenerife. *Bonn. Zool. Beitr.* **36**: 541-552.
- Molina-Borja, M., Gonzalez, J. G., Soutulo, T. G., Diaz, C. G. (1986): 24-H entrainment and ultradian fluctuations in the activity of the lizard *Gallotia galloti galloti* (Sauria-Lacertidae). *J. Interdiscipl. Cycle Res.* **16**: 295-305.
- Patnaik, B. K., Behera, M. N. (1981): Age determination in the tropical agamid garden lizard, *Calotes versicolor* (Daudin) based on bone histology. *Exp. Geront.* **16**: 295-308.
- Peters, W., Doria, G. (1882): Note erpetologica e descrizione di una nuova specie di *Lacerta* delle isole Canarie. *Ann. Mus. Civ. Stor. Nat. Giacomo Doria* **18**: 431-434.
- Pianka, E. R. (1970): On r- and K- selection. *Amer. Nat.* **104**: 592-597.
- Rica, J. P. M. (1982): Primeros datos sobre la población de lagarto negro (*Gallotia simonyi simonyi* Stein.) de la Isla de Hierro. *Amphibia-Reptilia* **2**: 369-380.
- Ryser, J. (1988): Determination of growth and maturation in the common frog, *Rana temporaria*, by skeletochronology. *J. Zool., Lond.* **216**: 673-685.
- Salvador, A. (1971): Nota sobre el lagarto negro gigante de Canarias, *Lacerta simonyi*. *Bol. R. Soc. Española Hist. Nat. (Biol.)* **69**: 317-320.
- Salvador, A. (1985): *Guía de campo de los anfibios y reptiles de la península Ibérica, islas Baleares y Canarias*. S. García, León.
- Sacchi, C. F., Testard, P. (1971): *Ecologie animale: Organismes et Milieu*. Paris, Doin.
- Saint Girons, H., Duguy, R. (1970): Le cycle sexuel de *Lacerta viridis* en plaine et en montagne. *Bull. Mus. Nat. Hist. Nat., Paris* **42**: 609-625.
- Saint Girons, H., Castanet, J., Bradshaw, S. D., Baron, J. P. (1989): Démographie comparée de deux populations françaises de *Lacerta viridis* (Laurenti, 1768). *Rev. Ecol. (Terre Vie)* **44**: 361-386.
- Sander, M. (in press): Skeletochronology in the small Triassic reptile *Neusticosaurus*. *Ann. Sci. Nat.* (in press).
- Schenkel, E. (1901): Achter Nachtrag zur Katalog der Herpetologischen Sammlung des Basler Museums. *Verh. Naturf. Ges. Basel* **13**: 142-199.
- Steindachner, F. (1889): Über eine von Prof. O. Simonyi auf den Roques del Zalmor bei Hierro (Canarische Inseln) entdeckte neue Eidechsenart von auffallender Grosse, *Lacerta simonyi* (Steind...). *Anz. Akad. Wiss. Wien* **1889**: 259-263.
- Strijbosch, J. J., Bonnemayer, A. M., Dietvorst, P. J. M. (1980): The northernmost population of *Podarcis muralis* (Lacertilia, Lacertidae). *Amphibia-Reptilia* **1**: 161-172.
- Thorpe, R. S., (1985a): Body size, island size and variability in the Canary Island lizards of the genus *Gallotia*. *Bonn. Zool. Beitr.* **36**: 481-487.
- Thorpe, R. S. (1985b): Alternative hypotheses for the causation of geographic variation in the western Canary Island lizard *Gallotia galloti*. *Bonn. Zool. Beitr.* **36**: 533-539.

- Thorpe, R. S. (1985c): Relative similarity between subspecies of the western Canary Island lizard, *Gallotia galloti*. *Bonn. Zool. Beitr.* **36**: 529-532.
- Thorpe, R. S. (1985d): Extend of racial divergence in the eastern Canary Island lizard, *Gallotia atlantica*. *Bonn. Zool. Beitr.* **36**: 507-512.
- Thorpe, R. S., Watt, K., Baez, M. (1985): Some interrelationships of the Canary Island lizards of the genus *Gallotia*. *Bonn. Zool. Beitr.* **36**: 577-583.
- Tilley, S. G. (1980): Life histories and comparative demography of two salamander populations. *Copeia* **1980**: 806-821.
- Tinkle, D. W. (1967): The life and demography of the side-blotched lizard, *Uta stansburiana*. *Misc. Publ. Mus. Zool. Univ. Mich.* **132**: 1-182.
- Tinkle, D. W. Dunham, A. E. (1986): Comparative life history of two syntopic sceloporine lizards. *Copeia* **1986**: 1-18.
- Turner, F. B. (1977): The dynamics of population of squamates, crocodylians and rhynchocephalians. In: *Biology of the Reptilia, Ecology and Behavior A*, 157-264. Gans, C., Tinkle, D. W., Eds, London etc, Academic Press.

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