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Body size, island size and variability in the Canary Island lizards of the genus *Gallotia*

by

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Introduction

The positive relationship between island size and body size in *Gallotia galloti* (Fig. 1a) is well known (Boettger & Müller 1914, Baez 1982) but only holds true for the main islands. The relationship does not extend to the lizards on the small islets of Tenerife or Hierro as they are not proportionally smaller. In fact a recent investigation of the lizards of the Tenerife islets (i.e. Garachico, Roque de Dentro de Anaga and Roque de Fuera de Anaga) by Martín (1985) indicates that males from the first and last of these small islets reach a greater size than on the main island of Tenerife.

Moreover, the relationship is not to be found in the other congeners. *G. atlantica* lives on islands that vary greatly in size but there is no relationship to body size (Fig. 1b). Similarly, there is no obvious positive relationship between island size and body size in *G. simonyi* insofar as lizards of extinct islet population of the Salmor rocks were not proportionally smaller than those from the extant population of Hierro (Klemmer 1976; Salvador 1971; Böhme & Bings 1977; Baez & Bravo 1983).

Consequently, there is not a consistent relationship between body size and island size within or between species of *Gallotia*.

Another phenomena that is often quoted (but less frequently observed) is the positive relationship between island size and within-population variation (Soule 1972). However, *Gallotia atlantica* and *G. galloti*, like *Phelsuma* (Gardner 1984) and *Podarcis* (Clover 1979), show no link between morphological variation (see below) and island size (Fig. 2) within the species.

Variability and body size

Using the local population samples described in Thorpe et al. (1985) the maximum snout-vent length (SVL) was recorded for each sex in each population. These estimates of maximum SVL have a rank correspondence to the estimates of other authors except for the small female La Palma sample. Consequently, for this population Baez's (1982) estimate of 98 mm SVL was used.

The within-population variation was estimated using a multivariate statistic, i.e. the mean D^2 between each individual in the population and the population centroid. The

results were supported by the coefficient of variation averaged across the character set. The character sets used were 25 quantitative scalation characters and 24 adjusted body proportions (Thorpe et al. 1985).

One can see from Fig. 3 that, when all available *Gallotia* populations are considered there is an extremely close positive linear relationship between variation in scalation and maximum body size ($r = 0.94$). The extent of the correlation (r) as well as the intercept (a) and gradient (b) of the regression line are all remarkably constant between the sexes even though males and females differ in max SVL. Consequently, for nine out of eleven islands the males have greater max SVL and greater variation than the females. This cannot be explained away as a statistical artefact of males having greater numbers of scales than females because in half of the scalation characters used the grand mean scale number was greater in females than males.

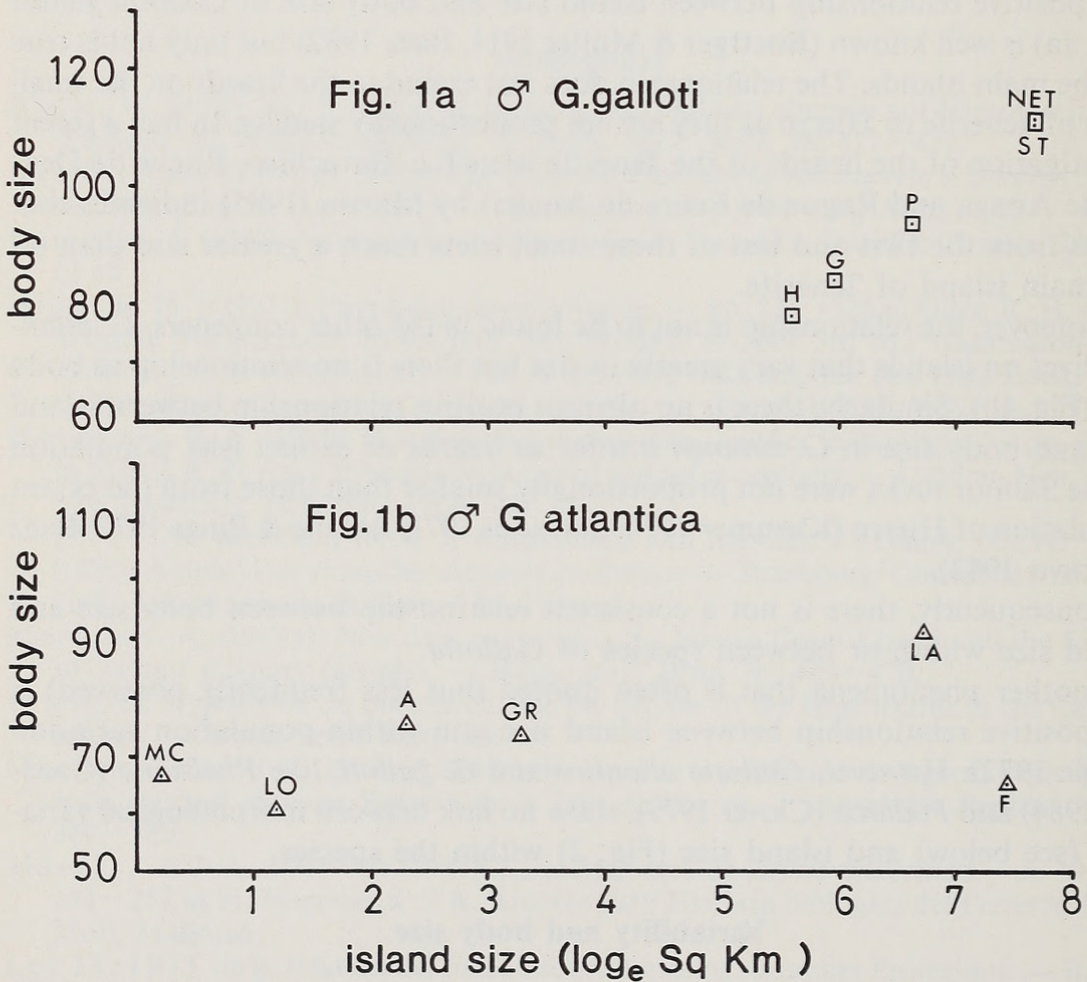


Fig. 1. Body size and island size. Vertical axis is body size (max SVL of males in mm) and horizontal axis is island size (\log_e sq km). Fig. 1a, populations of *G. galloti* (squares), H = Hierro, G = Gomera, P = La Palma, ST = south Tenerife, NET = north-east Tenerife. See text on the small islets of Tenerife and Hierro. Fig. 1b, populations of *G. atlantica* (triangles), MC = Montana Clara, LO = Lobos, A = Alegranza, GR = Graciosa, LA = Lanzarote, F = Fuerteventura.

The same relationship can be seen when adjusted body proportions are considered (Fig. 4). There is an extremely close positive, linear relationship between within-population variability in adjusted body proportions ($r = 0.96$ ♂, 0.94 ♀) and max. SVL. Once again the extent of the correlation, and the intercept and gradient of the slope are extremely consistent between sexes even though the max SVL of females can be considerably less than that of males.

These correlations are obviously across inter- and intra-specific populations. The range of variation and max SVL within species is very much more limited than across species. Nevertheless there is a positive pooled within-species correlation (pooled within the species *galloti* and *atlantica*; across populations and sexes) for both body proportions ($r = 0.52$, 99 % confidence) and scalation ($r = 0.45$, 94 % confidence).

There are various explanatory hypotheses that one can consider but they must not only take into account differences between populations they must also take into account the sexual differences in this size-correlated variability. At this stage it is pertinent to discuss sex determination in *Gallotia*. One could assume that in *Gallotia* sex is determined by the temperature at a critical stage of embryonic

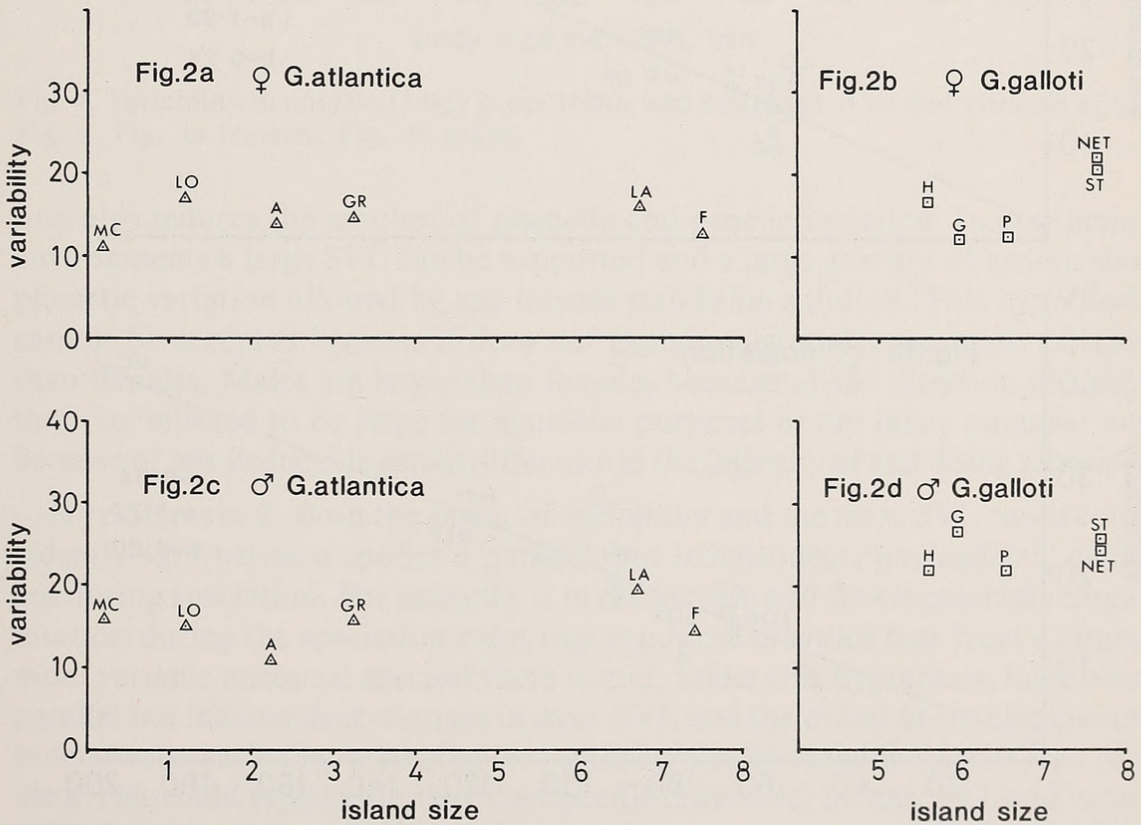


Fig. 2. Variability and island size. Vertical axis in within-population variability measured in units of D^2 (see text) and horizontal axis is island size measured as \log_e sq km. Symbols as for Fig. 1. Fig. 2a female *G. atlantica* populations, Fig. 2b female *G. galloti* populations, Fig. 2c male *G. atlantica* populations, and Fig. 2d male *G. galloti* populations.

development because karyotypic studies (Cano et al. 1984) reveal no differences in gross chromosome morphology between the sexes. Under this assumption sexual dimorphism in the mean and variance of a character is not determined by a series of genes on a section of chromosome peculiar to only one of the sexes but is presumably due to genes being switched 'on' or 'off' by the internal biochemical environment once the sex is determined. Hypotheses 1 to 3 below are considered in light of this assumption. However, recent karyotypic studies of *G. galloti* by Olmo (pers. comm.) show that a ZZ (σ), ZW (ϕ) system operates with the appropriate part of the W chromosomes being largely heterochromatic.

Hypothesis 1. Intensity of selection influences both max. SVL and variability. That is, in barren hostile environments, with little primary production only a small max. SVL can be supported and the intensity of stabilising selec-

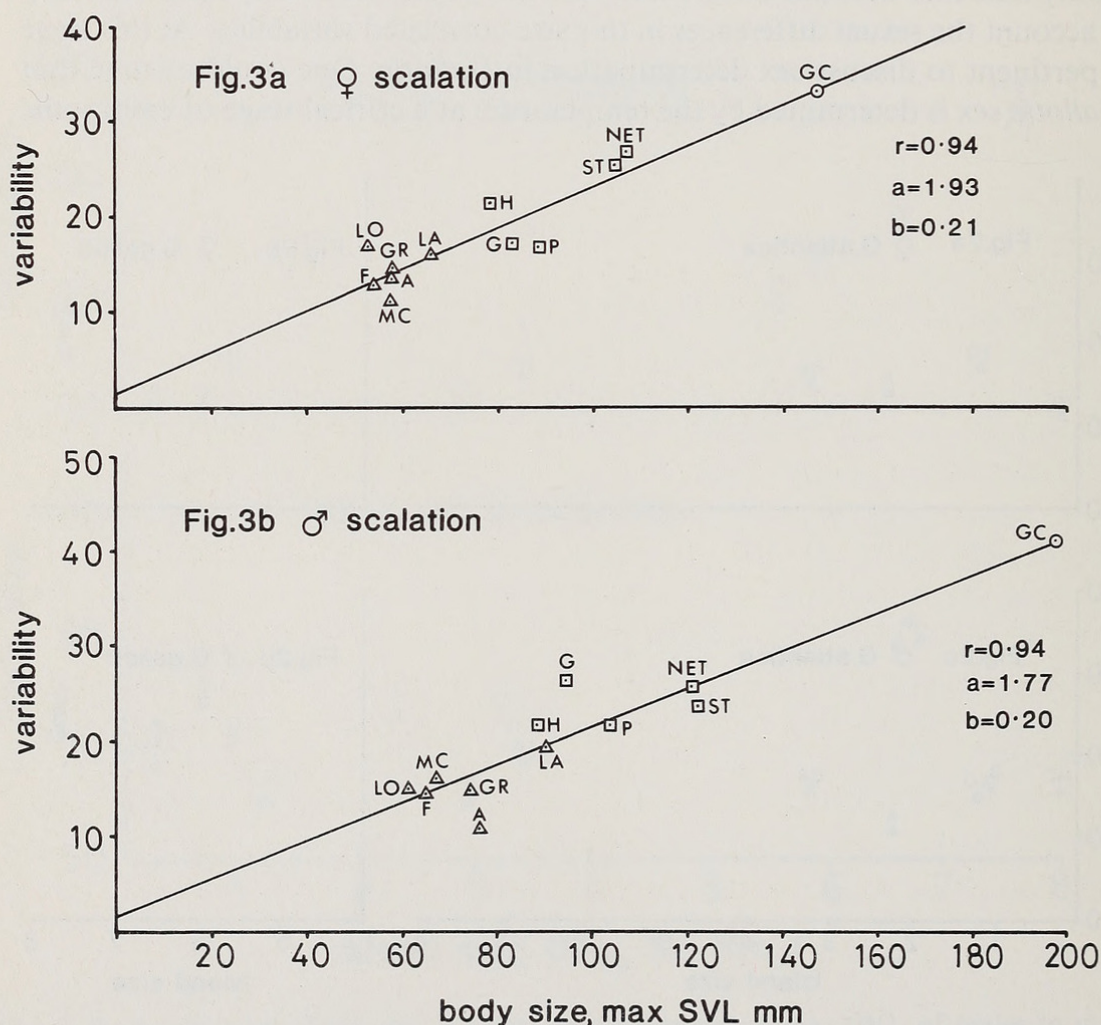


Fig. 3. Variability in scalation and body size. Vertical axis is the within-population variability measured in units of D^2 (see text) and the horizontal axis is the max SVL in mm. Linear regression line indicated with r = correlation, a = intercept and b = gradient. Symbols as for Fig 1 except *stehlini* from Gran Canaria = GC (circle). Fig 3a females, Fig. 3b males.

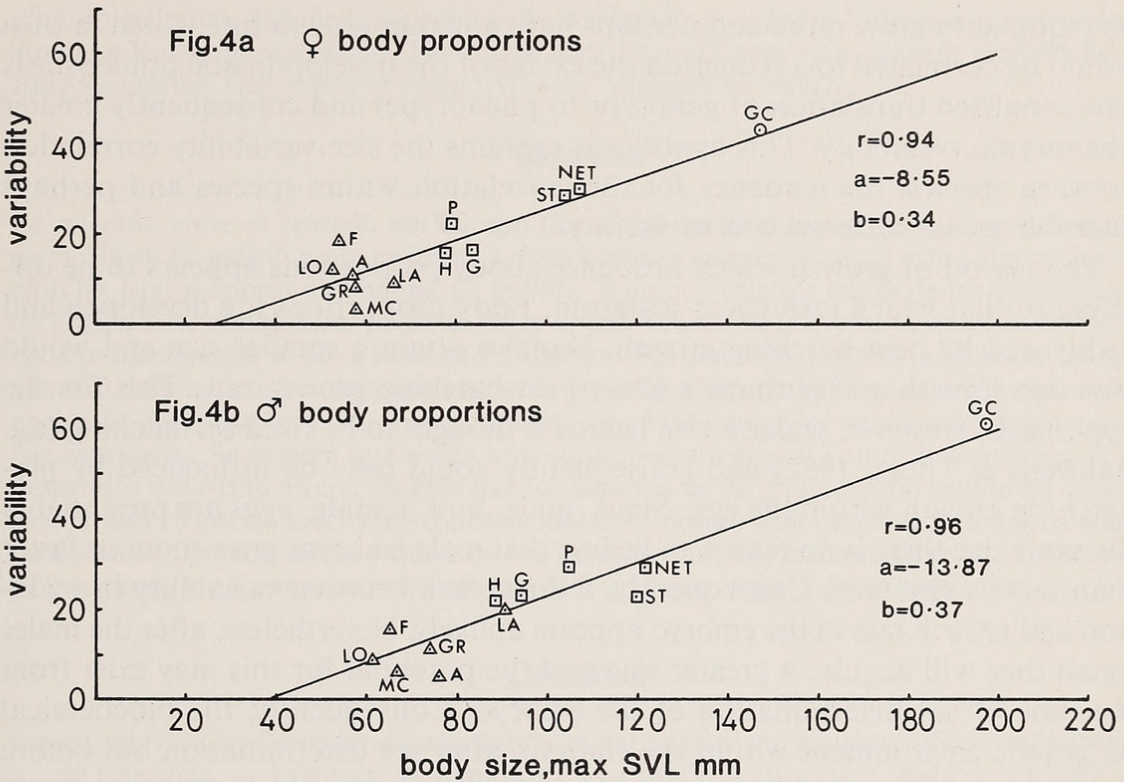


Fig. 4. Variability in adjusted body proportions and body size. Axis and symbols as for Fig. 3. Fig. 4a females, Fig. 4b males.

tion also reduces the amount of phenetic and genetic variation. In productive environments a large SVL can be supported and a large amount of genetic and phenetic variation allowed by less intense stabilising selection. This hypothesis cannot be accepted because it does not explain why males are more variable than females. Males are larger than females because of the direction of selection (i.e. selected to be large for agonistic purposes as are many animals) not because of any deducible sexual difference in the intensity of stabilising selection.

Hypothesis 2. Both the extent of variability and the max. SVL could coincidentally vary between species a parallel, but independent, phylogenetic changes during speciation. For example, if in the genetic and developmental reorganisation during the speciation event that produced *atlantica* (say from a larger, more variable ancestral species) there would, under this hypothesis, have been parallel but independent changes in max. SVL and the extent of developmental homeostasis such that a smaller less phenotypically variable species was formed. This could explain the clear interspecific differences in max. SVL and variability but does not explain the sexual difference in size correlated variability or the tendency for their intra-specific correlation, particularly with adjusted body proportions.

Hypothesis 3. There is a link between growth/growth rate and extent of developmental homeostasis. Under this hypothesis the larger specimen would

be required to grow more and perhaps have a higher growth rate which in turn would be correlated to a reduction the extent of the developmental homeostasis (the canalized translation of genotype to phenotype) and consequently greater phenotypic variability. This hypothesis explains the size-variability correlation between species, the tendency for the correlation within-species and perhaps also the sexual difference is variability.

The period of growth which influences body proportions appears to be different to that which influences scalation. Body proportions are developed and influenced by post-hatching growth. Females attain a smaller size and would have less growth and perhaps a lower post-hatching growth rate. This fits the hypothesis. However, scalation on lizards is thought to be fixed on hatching (e.g. Bauwens & Thoen 1982) and consequently could only be influenced by pre-hatching growth within the egg. Since 'male' and 'female' eggs are presumably the same size there is no reason to believe that male embryos grow more or faster than female embryos. Consequently, a direct link between variability in scalation and growth rate in the embryo appears unlikely. Nevertheless, after the males hatch they will acquire a greater size and the potential for this may exist from the time of sex determination of the embryo. Consequently, the biochemical or genetic environment within the embryo, after sex determination but before the determination of scalation, may be such that the factors that subsequently result in lesser or greater growth also result in lesser or greater developmental homeostasis and consequently phenotypic variability. For this to be feasible sex determination in the embryo must occur before the scalation is fixed which must be the case with chromosomal sex determination but need not be the case with temperature determination.

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Zusammenfassung

Die Beziehung zwischen Körpergröße (maximale Kopf-Rumpflänge) und Inselgröße bei *Gallotia galloti* trifft nicht auf andere Arten der Gattung zu, auch berücksichtigt sie nicht die kleinen Inselchen, die von *G. galloti* bewohnt werden. Auch die bei anderen Eidechsen beobachtete positive Korrelation zwischen Inselgröße und populationsinterner Variabilität existiert nicht bei *Gallotia*. Dagegen besteht eine sehr enge Beziehung ($r \geq 0.94$) zwischen Körpergröße und Variabilität bei allen Populationen von *Gallotia*, die für beide Geschlechter und verschiedene Merkmalstypen bemerkenswert durchgängig ist. Die Variabilität des Phänotyps wird durch ontogenetische Homöostase-Mechanismen in der Weise beeinflusst, daß eine starke Tendenz zur Homöostasis nur eine geringe Variation in der phänotypischen Ausprägung der Gene erlaubt. Umgekehrt

gilt infolgedessen, daß die hohe potentielle Wachstumsrate großer Eidechsen einer weniger strengen Kontrolle unterliegt. Hierdurch dürfte zu erklären sein, warum großwüchsige Eidechsenarten eine stärkere phänotypische Variabilität zeigen.

Resumen

La relación entre el tamaño del cuerpo (longitud máxima hocico-cloaca) y el tamaño de la isla en *G. galloti* no se extiende a otras especies congénéricas ni toma en consideración las islas menores que habita *G. galloti*. Tampoco existe a través de las poblaciones de *Gallotia* la correlación positiva entre el tamaño de la isla y la variabilidad dentro de la población que se observa en otros lagartos. Sin embargo, entre el tamaño del cuerpo y la variabilidad a través de todas las poblaciones de *Gallotia* hay una relación muy estrecha ($r \geq 0.94$) que es extraordinariamente constante entre los sexos y los tipos según sus caracteres. Se sugiere que existe una conexión tal entre el grado de homeostasis de desarrollo y el ritmo de crecimiento que los lagartos de un gran tamaño último de cuerpo tienen un ritmo de crecimiento potencialmente rápido que necesita una homeostasis de desarrollo menos severa y que a su vez permite una más extensa expresión fenotípica de los genes y en consecuencia una mayor variación dentro de la población.

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