Giant and long-lived? Age structure in *Macroscincus coctei*, an extinct skink from Cape Verde

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Abstract. The age structure of the extinct giant Cape Verde skink *Macroscincus coctei* was studied using skeletochronology applied to 11 preserved males, 15 females, and one juvenile, collected at the end of the 19th century. Counts of lines of arrested growth (LAGs) indicated that in this species — which lived on islets with extreme natural conditions (e.g., hard aridity, lack of rainfall) — the maximum life span was estimated as 16 years for males and 12 years for females; the single juvenile was 4 years old. Although the sexes had similar mean ages, mean body length of males was significantly higher than that of females (283 versus 255 mm). There was no clear relationship between body length and estimated age, although the largest males were also the oldest. The analysis of LAGs revealed a sexual difference in growth rates, males reaching greater size earlier than females.

Introduction

Organisms living in isolated environments, such as oceanic islands, often exhibit extreme ecological adaptations. For instance, many reptiles are characterised by peculiar and independently derived adaptations — such as gigantism or dwarfism, and lack of relevant defensive behaviours — which sometimes differentiate them conspicuously from their closest mainland relatives (Zunino and Zullini, 1995). It is likely that the geographic and ecological isolation, combined with the absence (or scarcity) of original predators and competitors, make them extremely vulnerable to a wide range of disturbances, such as hunting, habitat alteration, competition and predation by introduced animals (Balouet and Alibert, 1989; Hasegawa, 1999). In this sense it is symptomatic that many giant insular species have gone extinct recently or are on the verge of extinction (Pregil, 1986; Case et al., 1991). Typical examples include several giant turtles from islands of the Indian Ocean (Pritchard, 1996), and some lizards (Balouet and Alibert, 1989). One of these cases is represented by the giant Cape Verde skink, *Macroscincus coctei*, which was last reported from the wild in the beginning of 20th century (Andreone, 2000). According to available information, this skink lived on some islets of Cape Verde, an archipelago about 600 km off Senegalese coast. Although attributed to a distinct genus, it was considered in some ways a sort of "specialised form" of *Mabuya* by Carranza et al. (2001). It reached a conspicuous body size (at least 350 mm in snout-vent length), was mainly herbivorous, and exhibited several morphological and natural history peculiarities, such as oviparity, partially prehensile tail, and development of elongated hind-legs in males (Andreone and Gavetti, 1998). Due to the lack of any confirmed observation of this species from the past 90 years, it is most likely that it is nowadays extinct. As for many other insular animals, its extinction was likely due to a combination of human-induced and natural factors, such as active hunting, predation and disturbance caused by introduced animals, as well as the occurrence of extraordinary dry periods (Andreone, 2000). Moreover, due to its large size and peculiar morphology, *M. coctei* was also actively collected by natural history dealers during the 19th and beginning of 20th centuries, and sent to several naturalists and natural history museums. But, as most natural history collections host only single specimens, until recently the scientific information obtainable from these specimens was quite limited (e.g., Greer, 1976).

A remarkable exception to the scarcity of comparative samples is represented by a large series housed at Turin, and which was recently described (Andreone and Gavetti, 1998). This collection is due to the importation made at the end of 19th century by the Italian herpetologist M.G. Peracca, who collected and imported more than forty specimens of *M. coctei* (Peracca, 1891a, b), 26 of which are still preserved in Turin Museum (Andreone and Gavetti, 1998). Due to the lack of detailed information, we assume that these specimens were all captured at the same period and at the same site. For this reason, they represent a valuable data set which may help to clarify aspects of the species' life history (Andreone, 2000).

In this paper we investigated the age structure and eventual intersexual differences in this little known species, by skeletochronology. In particular, (1) we tested whether age estimation of museum samples is possible, in order to use this information to characterise the life span, age structure and longevity of *M. coctei;* and (2) we compared the data from *M. coctei* with those from other insular lizard species, focusing on the parallelism occurring in phylogenetically distant species under comparable environmental and ecological pressures.

Material and methods

Eleven adult males and 15 adult females of *Macroscincus coctei* housed in the Zoological Museum of Turin were analysed in this study (MZUT R1981.1-26). The status of sexual maturity was assessed by detection of secondary sexual characters. All animals (maintained in 70% ethanol) came from Ilheu Branco, and belong to the series imported by Peracca (Andreone and Gavetti, 1998). Furthermore, as a complement and to calibrate the age estimation, we analysed a young specimen (MNHN 1984-237) from Paris Museum. This individual was collected on 9 May 1884 during the Talisman Mission (Vaillant, 1888) at Ilheu Branco. This islet (16°40′N, 24°40′W) is approximately midway between the São Vicente and São Nicolau islands, and constitutes, together with Santa Luzia and Ilheu Raso, the "Ilhas Desertas" (Schleich and Schleich, 1995; Mateo et al., 1997).

Each specimen was measured by the senior author from the tip of the snout to the cloaca (snout-vent length, SVL) with a plastic rule (with precision of 1.0 mm). The total length is not provided, because in most specimens the tail was regenerated and shorter than in intact animals (Andreone and Gavetti, 1998). Sex was determined by external analysis (males are much more robust than females, have a bigger head and longer hindlimbs), and, when the belly had been previously opened (for fixation purposes), by analysing gonads.

For age assessment we delicately removed a portion of the second phalanx from the third toe (right hindleg) through a longitudinal skin incision. This careful operation allowed preserving the external appearance of the fingers. The phalanges were then stored in 70% ethanol for one day, decalcified by immersion in 5% nitric acid (3 hours), and rinsed in tape water. Multiple 15 μm thick cross sections were obtained from the diaphysis using a cryostat, and stained with Ehrlich's hematoxylin for 25 minutes. A minimum number of 20 serial cross sections from each phalanx were mounted in aqueous resin and analysed under transmitted light microscope equipped with an image analyser. We identified the hematoxylinophilic growth rings in the bone tissue corresponding to the lines of arrested growth (named LAGs from here onwards). The LAG counting was performed by FMG, and confirmed by FA. In case of discordance, the bone section was analysed by a third person, or reanalysed until consensus was reached. When two sets of counts were different, the lower count was usually considered.

Results

Bone histology and growth mark interpretation

The diaphysis of the phalanx cross sections appeared as formed by an outer cortex enclosing a central marrow cavity (fig. 1a-f). The cortex mainly consisted of parallel fibered bone, although in some individuals it was also formed of lamellar bone (fig. 1a). In most phalanges we distinguished the periosteal from the endosteal bone by identifying the cementing resorption line (fig. 1c, d). In general, the periosteal bone was thicker than the endosteal one, but in some cases the diaphyseal cortex was composed of endosteal bone owing to remodelling changes (fig. 1c). In a few phalanges, some isolated vascular canals were also observed at the diaphyseal level; in some of the vascularised phalanges, canals were enlarged into resorption spaces (fig. 1f).

All the phalanges exhibited concentric LAGs, except that of one female (MZUT R1981.25). The expression of LAGs under transmitted light microscope varied according to the examined phalanx (fig. 1a-f). In fact, most phalanges showed thin lines (fig. 1a-b), while some others were characterized by marked LAGs (fig. 1c), or by lines very close to one other (fig. 1f). Double LAGs were rare and observed without a regular and periodic pattern. Furthermore, they had different spatial pattern in different specimens, and did not indicate a constant double annual growth cycle.

One male (MZUT R1981.13) and two females (MZUT R1981.16 and R1981.26) showed poorly distinguished or incomplete LAGs, and thus count data was dubious. We cannot find a reason for such a phenomenon: these specimens were not considered in the following analyses. Of the remaining individuals (10 males and 12 females) with well-defined LAGs, we did not converge on a single LAG number for 6 males and 5 females. In all cases, the

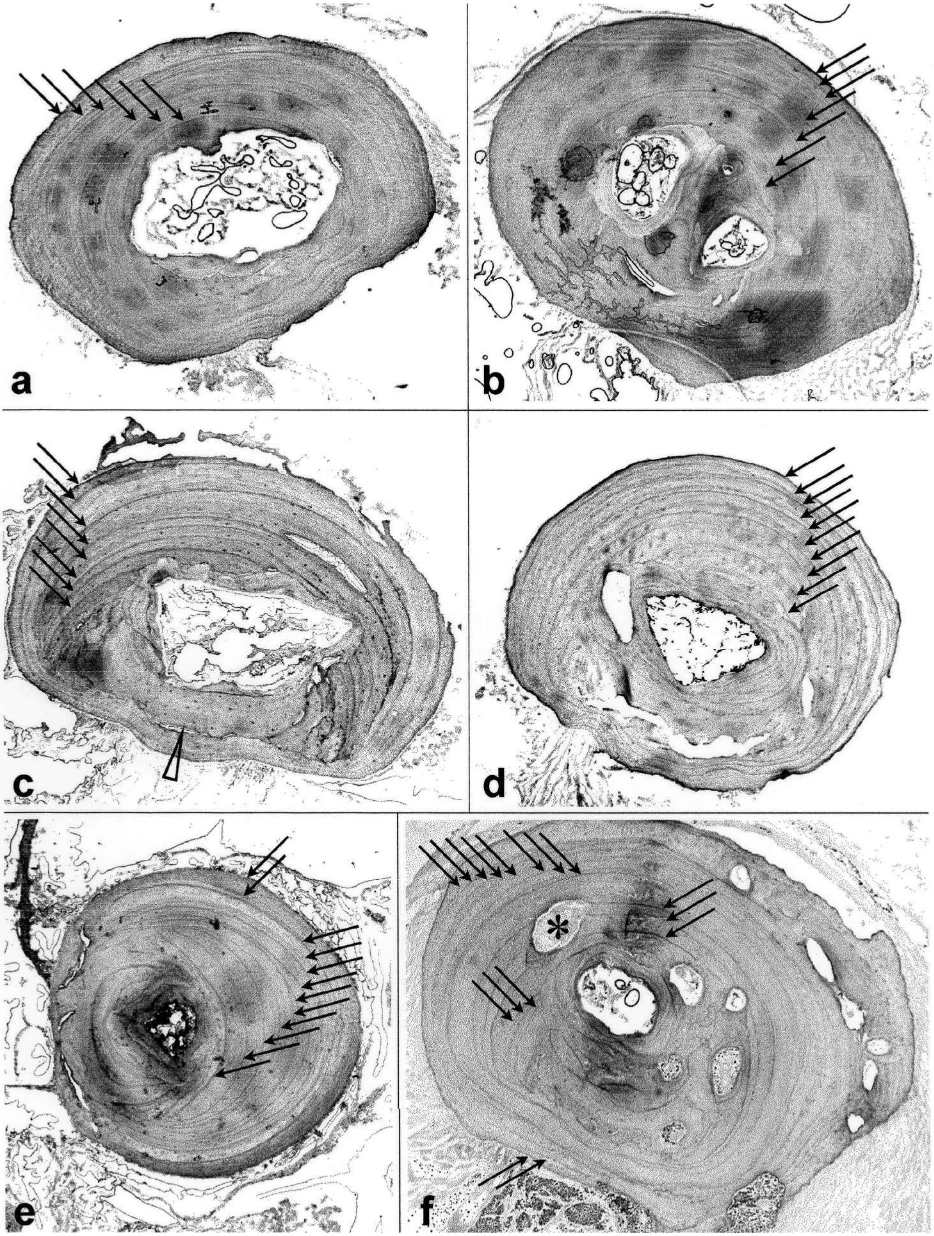

Figure 1. Representative phalanx cross sections of *Macroscincus coctei*. Black arrows indicate the lines of arrested of growth (LAGs). All the figures are given at the same magnification (×45). (a) female (MZUT R1981.10), SVL = 243 mm, 6 LAGS; (b) male (MZUT R1981.7), SVL = 282 mm, 7 LAGs; (c) female (MZUT R1981.4), SVL = 274 mm, 8 LAGs (note the marked bone remodelling indicated with a white arrow); (d) female (MZUT R1981.15), SVL = 282 mm, 10 LAGs; (e) female (MZUT R1981.20), SVL = 225 mm, 11 LAGs; (f) male, (MZUT R1981.6), SVL = 320 mm, 16 LAGs (the asterisk indicates the presence of one among many resorption spaces in the cortex).

differences between the counts made by a single observer in different times or between the counts of two observers were never higher than 2. The identification of the lamellar periosteal matrix represented one of the main difficulties, because it could in some cases be confused with LAGs (fig. 1a, e). In these cases it was sometime necessary to replicate the observations on the same histological section to get a final consensus on the LAG estimation. Moreover, in some individuals, the extensive remodelling partly masked the LAG identification. However, when the endosteal bone deposition occurred only at a certain cortical area, resulting in a "shift" of the marrow cavity, counting LAGs (and/or identifiable LAG fragments) was usually possible in the opposite periosteal side (fig. 1c).

Body size, longevity and growth

Among the adults, males were significantly larger than females (mean SVL ± s, Males: 282.82 ± 26.27 mm, females: 255.13 ± 17.83 mm, $t = 3.21$, $P = 0.0037$). The largest examined male was 320 mm long (MZUT R1981.6), while the longest female (MZUT R1981.15) measured 282 mm. The smallest specimen (MNHN 1984-237) was 140 mm in body size, and its age, assessed on the basis of the LAG number, was estimated as 4 years. Adult ages ranged 5-16 years for males ($n = 10$; mean number of LAGs = 8.80 ± 3.42), and 6-12 for females ($n = 12$; 8.77 ± 2.17). Contrary to SVL, the mean age was not significant different between sexes (Mann-Whitney U-test = 59.50, $P = 0.733$). The age class distribution had two peaks in males (6 and 8 years), and was unimodal in females (8 years) (fig. 2). This distribution was not significantly different between sexes (Kolmogorov-Smirnov χ^2-test, $P = 0.962$).

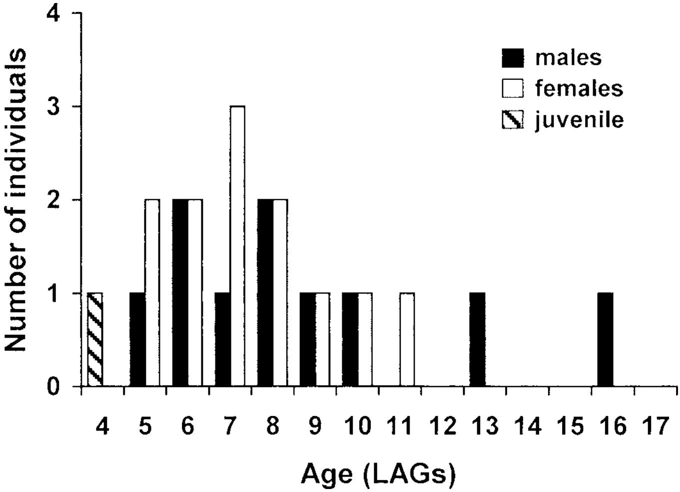

Figure 2. Age distribution of *Macroscincus coctei* as assessed from counts of LAGs. Doubtful cases were excluded.

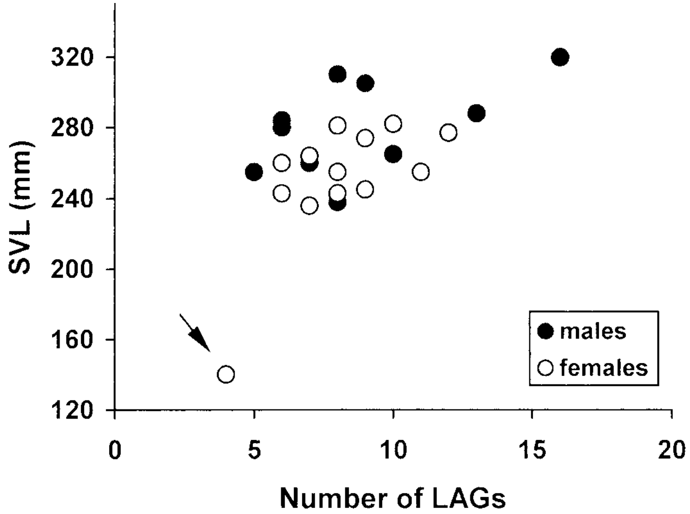

Figure 3. Relationships between age and SVL in the analysed phalanges of *Macroscincus coctei.* Doubtful cases were excluded. The juvenile is indicated with an arrow.

There was no apparent and significant relationship between SVL and number of LAGs (males, $r = 0.54$, df = 8, $P = 0.11$; females, $r = 0.41$, df = 10, $P = 0.20$; fig. 3), although the largest males tended to be also the oldest ones. Furthermore, single factor analysis of covariance (with sex as the factor and age as the covariate) showed that at the same age, male and female *M. coctei* did not differ for body length (ANCOVA on slopes, $F = 0.098$, df = 1, 18, $P = 0.758$). The analysis carried out upon three LAG groups (1 = 5-8; 2 = 9-12; 3 = 13-16) was also non-significant ($F_{2,18} = 2.69$; $P = 0.09$), but tne Tukey-HSD *post-hoc* test gave lack of significant difference between groups 1 and 2 ($P = 0.66$) and between groups 2 and 3 ($P = 0.11$), while it was different between groups 1 and 3 ($P = 0.03$).

Discussion

Reliability of the skeletochronologicalmethod

When longitudinal studies of marked animals are not possible, skeletochronology is the most reliable method for assessing age in ectothermal terrestrial vertebrates (Castanet et al., 1993; Castanet, 1994). In amphibians and reptiles living in the temperate regions, each LAG corresponds to an arrested osteogenesis during the autumn-winter cessation of growth. Alternatively, in tropical species the presence of bone growth marks may depend more on factors other than temperature, such as rain-dryness alternations, or food availability (e.g., Zug and Rand, 1987; Guarino et al., 1998; Andreone et al., 2002).

Many skeletochronological studies performed on amphibian or reptilian remains from archaeological or paleontological sites show that age estimation by LAG counting is possible in subfossil and fossil specimens (Peabody, 1961; Buffrenil and Buffetaut, 1981; Reid, 1981; Esteban, 1990; Sander, 1989, 1991; Sanchiz and Alcobendas, 1994; Horner et al., 2000). Although the wide use of toe-clipping methods (e.g., Saint Girons et al., 1989; Andreone et al., 2002) does not require sacrificing the sample, the use of preserved specimens for age determination is still scarcely considered. We stress therefore the importance of the present study in demonstrating the efficacy of skeletochronology on preserved specimens. In agreement with McCarter et al. (2001), the possibility of assessing age of museum specimens is a process that increases the scientific value of zoological collections. The analysis of preserved samples goes beyond the classical taxonomic assessment, and allows to gather further biological data that can be correlated with general ecology. The case study of *M. coctei* is important for two reasons: (1) skeletochronology allows detailed speculations and inferences about the life history of an extinct species, and (2) provides support for using this method on animals preserved for approximately a century.

Age estimate was possible for most examined specimens. LAGs were not different in quality and evidence from those of freshly cut phalanges (or other bones). Then, two questions arose: (1) what is the seasonality in LAG formation, and (2) does the number of visible lines in the bone sections correspond to the actual LAGs number formed during ageing? The answer to the former question relies on the observation that for most amphibian and reptile species living in regions with conspicuous seasonal climatic variations, one LAG is formed yearly (Francillon, 1979; Castanet, 1985; Francillon and Castanet, 1985; Buffrenil and Castanet, 2000). Regarding our *M. coctei* sample, we should take into consideration the peculiar climate of the area where it lived. In fact, Cape Verde is an archipelago with tropical seasonality, and where rainfalls are extremely low and concentrated from August to October (Schleich and Schleich, 1995). Although we cannot assess experimentally if there is a periodicity in the LAG deposition in *M. coctei*, we are led to consider each LAG to be deposited yearly, as it is the rule for species belonging to the genus *Gallotia* (Castanet and Baez, 1991). Indeed, the general consensus is that LAGs originate from endogenous rhythms, and are reinforced and synchronized by external seasonality (Castanet and Baez, 1991; Castanet et al., 1993).

With respect to the validity of LAG count, it must be taken into account that one or more LAGs can be totally destroyed by bone remodelling, mainly in the periosteal cortex toward the marrow cavity (endosteal resorption). This is particularly true for phalanges, since they are more frequently affected by intense remodelling than other long bones (Buffrenil and Castanet, 2000). As a rule, the method used to evaluate the possible resorption of inner periosteal LAGs is the comparison of different osteometric parameters between juveniles and adults (Castanet et al., 1993; Guarino et al., 1999). We could study only a single juvenile of *M. coctei* (distinguished from the adults for a typical brighter colouration). Its analysis was crucial, since it allowed us to make a preliminarily estimation of the number of LAGs resorbed during the growing process. Our comparisons suggest that bone remodelling destroyed at least one LAG. Another possible source of underestimation of individual age is the arrest of periosteal osteogenesis in the oldest individuals of long-lived species, such as *Sphenodon punctatus* (Castanet et al., 1988). Owing to the osteogenetic arrest, LAG formation stops in the phalanx earlier than in other long bones: accuracy of the phalanx to assess the age in *M. coctei* can be evaluated analysing the relationship between LAG number and SVL. The great difference in size between the juvenile with 4 LAGs and the specimens with 6 or 7 LAGs suggests that the age in the adults is possibly underestimated. We therefore believe that the *M. coctei* longevity reported here is underestimated, and the reported LAG number should be interpreted as a minimum longevity.

Considerations about the species' ecology

The age estimation also turned out to be crucial in assessing the ecological traits of *M. coctei*, and possibly uncover some of the causes underlying its extinction. It was thereafter worth, in terms of comprehension of parallel evolutive adaptations, to compare the natural history traits of *M. coctei* with those of two other insular reptiles, *Gallotia simonyi* and *Sphenodon punctatus* (table 1). The former is a lizard from Canary Islands (Barahona et al., 2000), while *Sphenodon punctatus* is a well known relict rhynchocephalian inhabiting remote islands of New Zealand.

Age structure data are available for subfossil and living *G. simonyi* specimens (Castanet et al., 1991; Romero-Bevìa et al., 1999). *Macroscincus coctei* and *G. simonyi* share parallelisms in ecology and habitat adaptation, although belonging to two different families (Scincidae and Lacertidae). They both reach a very large size (about 350 mm SVL in *M. coctei*, and 500 mm in *G. simonyi*), have a remarkable sexual dimorphism, with males being larger then females, and show peculiar longevity (at least 16 years in *M. coctei*, and 20 in *G. simonyi*, see table 1). Another similarity between is in the bone growth pattern:

Table 1. Estimated longevity, average and maximum body size (SVL) for lizards inhabiting two Atlantic archipelagos (*Macroscincus coctei* and *Gallotia simonyi*) and a rhynchocephalian from New Zealand (*Sphenodon punctatus*).

Species	Provenance	Family	Maximum Longevity (years)	Average SVL (mm)		Maximum SVL (mm)	Reference
				Males	Females	Males	
Macroscincus coctei	Cape Verde (Ilheu Branco)	Scincidae	16	283	255	320	This study
Gallotia simonyi	Canary Islands (Tenerife)	Lacertidae	20	358	–	478	Castanet and Baez, 1991
Sphenodon punctatus	New Zealand (Stephen Island)	Sphenodontidae	35	239	196	264	Castanet et al., 1988

in both species the inner (perimedullar) LAGs showed a regular disposition. This indicates that the growth rate was almost constant in both species, without a higher velocity during the early years of ontogeny, as occurs in most short-lived lizards before reaching sexual maturity (Castilla and Castanet, 1986; Saint Girons et al., 1989; Wapstra et al., 2001). This similarity can be interpreted as evidence of an analogous life style. It is likely that sexual maturity was reached quite late in both the species: during this period a protracted juvenile growth pattern was more or less constant and allowed the animal to attain a conspicuous size, as already stressed by Castanet and Baez (1991), and Shine and Charnov (1992).

Since all the analysed *M. coctei* specimens were mature at the time of capture, we may hypothesise that sexual maturity was reached at 5 years for males and 6 for females, or even later (if age determination is underestimated). Our analysis suggests that sexual maturity was reached late, and growth was probably continuous across all ages for males. As a consequence, *M. coctei* was a long-lived lizard, with a conspicuous inter-sexual difference in body size. In fact, it is typically advantageous for males to be large, the body size being related to defence of territory and mating success (Stamps, 1983; Pough et al., 2001). Our results indicate that such sexual dimorphism is accompanied by a differential growth rate: males are larger as a consequence of an accelerated growth, likely from the 9th year onwards. The growth in the first part of their life (e.g., until the 8th year) does not appear to differ between sexes. The difference is shown starting from this age, when likely females invest more in reproduction (egg-laying), while males in body growth and, consequently, success in territory defence. We can expect that older males probably have a higher reproductive success. In *M. coctei* eggs are relatively large (up to 24 mm in diameter; see Andreone and Gavetti, 1998). Two analysed females still had in their body two eggs: this suggests an invariable clutch size of two eggs per female. These females (MZUT R1981.18 and 20) had respectively 7 and 11 LAGs, thus being in accord with our projection concerning the reproductive mode. Although we do not have information on the number of clutches per reproductive season, we are inclined to consider this number as genetically determined and a realistic estimate of species fecundity. All these reproductive features together with the large body size, late maturity and long life expectancy are typical K-selected traits (Barbault and Blandin, 1980; Shine and Charnov, 1992), as proposed for *G. simonyi* (Castanet et al., 1991).

Macroscincus coctei, therefore, was a specialised insular lizard, adapted to the environment and likely unable to recover in case of habitat disturbance and introduction of alien elements. Finally, we do not know whether the absence of juveniles in the series coming from the Turin Museum reflects the reality of the wild population at the time of capture. In fact, all the analysed specimens were adults, being much larger than the juvenile from the Paris Museum. Together with a second one from Genova Museum this is the only juvenile individual we found in the large collections of *M. coctei* at Turin, Genova, Treviso, and Paris (Andreone and Gavetti, 1998). The collectors at that time likely selected adult and large specimens for the trade. However, it cannot be excluded that *M. coctei* had a demography similar to that of *Sphenodon punctatus*, where adults represented the majority (95%)

of the whole population at Chicken Islands, as a consequence of differential predation by introduced rats (Castanet et al., 1988). Hence, both selective collecting of adult specimens (possibly due to the demands of natural history museums), as well as low juvenile recruitment rate — which might have been reduced by predation of eggs and juveniles by introduced mammals (e.g., cats, dogs and rats) — may have contributed to the extinction of this peculiar species.

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