

Marine iguanas shrink to survive El Niño

Changes in bone metabolism enable these adult lizards to reversibly alter their length.

Change in body length is considered to be unidirectional in vertebrates¹, but we have repeatedly observed shrinkage in the snout-to-vent length of individual adult iguanid lizards. In two studies, one lasting 18 years and one 8 years, of two island populations of Galápagos marine iguanas (*Amblyrhynchus cristatus*), we found that individuals became shorter by as much as 20% (6.8 cm) within two years. This shrinking coincided with low availability of food, resulting from El Niño events. Body length increased again during subsequent La Niña conditions, when algal food was abundant². We found that lizards that shrank more survived longer than larger iguanas during harsh periods because their foraging efficiency increased and their energy expenditure decreased^{3,4}.

Marine iguanas (Fig. 1) are herbivorous reptiles that feed on submerged intertidal and subtidal algae along the rocky island shores of the Galápagos archipelago, Ecuador³. Environmental conditions can change dramatically within an individual's lifetime, as they can live for more than 28 years². El Niño events usually recur at intervals of 3–7 years, but were more prevalent between 1990 and 1999: the El Niño Southern Oscillation Index, a composite measure of the severity of El Niño, was positive throughout 1990–95 and 1997–98 (ref. 5). During El Niño years in the Galápagos, sea surface temperatures increase from an average of 18 °C to a maximum of 32 °C as cold ocean currents and cold nutrient-rich upwellings are disrupted⁶.

The increased rainfall that accompanies El Niño results in greater food availability for most terrestrial organisms in the Galápagos⁷, but marine life generally suffers⁸. Green and red algal species, which are the marine iguanas' preferred food, disappear and are replaced in intertidal areas by brown algae⁸ which iguanas find hard to digest. Up to 90% of marine iguana populations on islands can die of starvation as a result of these environmental changes⁹. The largest iguanas have the highest mortality because, as is often the case with grazers¹⁰, they feed less efficiently than smaller individuals.

During the most recent El Niño event (1997–98), larger individuals of the two island populations shrank more than smaller individuals (even if calculated as a percentage), and females shrank more than males of the same size (Fig. 2a). This sex-specific shrinkage is presumably related to females exporting energy into clutches of eggs during the year before an El Niño³. The scale of the shrinkage — up to 20% of body length —



Figure 1 The marine iguana *Amblyrhynchus cristatus*.

means that it cannot simply be explained by decreases in cartilage and connective tissue, which together make up only 10% of total body length¹¹. We believe that bone absorption accounts for much of the reduction.

Shrinking in marine iguanas may be an adaptive response to low food availability and energetic stress. Measurements of a cohort of adults more than 300 mm long during the strong 1992–93 El Niño event^{2,3,5} show that individuals that shrank more survived significantly longer (Fig. 2b). The mechanisms that determine whether and to what extent an individual shrinks during El Niño events remain unclear.

Reduction in body length has been observed previously, and growth rates set to zero by definition¹, but to our knowledge this is the first report of shrinkage in adult vertebrates. In humans, the long bones of astronauts become reduced both in density and length during prolonged space trips¹². Astronauts experience long periods of microgravity, resulting in limited exercise and high cortisol ('stress') levels^{13,14}, and confining healthy volunteers to months of bed rest has much the same effect¹². Similarly, marine iguanas get very little exercise from feeding during El Niños⁴ and their corticosterone levels are very high (L. M. Romero and M. W., manuscript in preparation). There may be a causal relationship between limited exercise, high corticosterone levels and decreases in body length¹⁴. Similar relationships have been suggested for the regulation of human osteoporosis¹⁵.

Adult marine iguanas can switch repeatedly between growth and shrinkage during their lifetime, depending on environmental conditions². In humans, bone regrowth after osteoporosis is largely impossible, causing major health problems (for example, in postmenopausal women¹⁵). It is not clear whether other vertebrates can shrink and regrow. We propose that growth rates should no longer be set to zero, as shrinkage can confer a biologically important advantage.

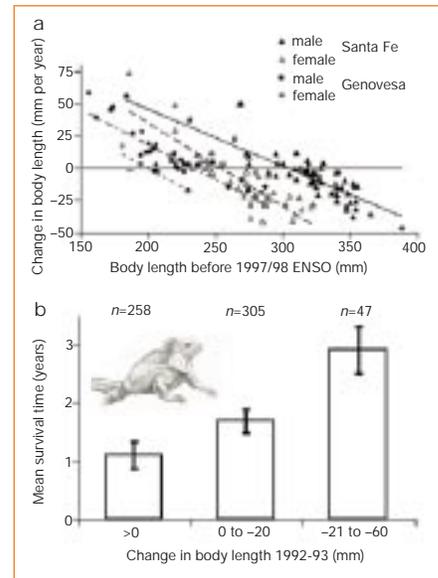


Figure 2 Change in body length as an adaptation to harsh conditions. **a**, Reduction in body length (snout-to-vent length, SVL) of Galápagos marine iguanas on the islands of Santa Fe (90° 02' W, 0° 50' S) and Genovesa (89° 59' W, 0° 19' N), Ecuador. Males (filled symbols) shrink less at a given body length than females (open symbols). Individuals are marked for life⁸ and measurements were taken without knowledge of shrinkage pattern or previous body length. Mean (\pm s.d.) maximum intra- and inter-individual measurement errors were $1.47 \pm 0.6\%$ and $2.1 \pm 0.8\%$ body length ($n=9$ and 12), respectively. Body mass and condition do not influence SVL measurements. Lines show linear regressions for each island and sex. Santa Fe males: shrinkage, $134(\pm 12) - 0.44(\pm 0.03) \times \text{SVL}$, $F_{1,62} = 129$, $P < 0.001$, $r^2 = 0.67$; Santa Fe females: shrinkage, $164(\pm 16) - 0.65(\pm 0.06) \times \text{SVL}$, $F_{1,43} = 123$, $P < 0.001$, $r^2 = 0.74$; Genovesa males: shrinkage, $127(\pm 11) - 0.54(\pm 0.05) \times \text{SVL}$, $F_{1,26} = 119$, $P < 0.001$, $r^2 = 0.82$; Genovesa females: shrinkage, $85(\pm 20) - 0.44(\pm 0.10) \times \text{SVL}$, $F_{1,4} = 18$, $P = 0.01$, $r^2 = 0.82$. **b**, Relation between change in body length and survival time of adult iguanas on Santa Fe. Large adult individuals (SVL > 300 mm) that shrank most during the 1992–93 El Niño event survived longer (analysis of variance, $F = 21$, $P < 0.001$). Using other categories or relative shrinkage data exaggerates the observed trends². Data show mean survival time (\pm 95% confidence intervals) after March 1993 for all individuals ($n = 610$) measured from January to March 1992 and remeasured from January to March 1993.

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Conservation

Biogeography of the Indonesian coelacanths

Living coelacanths (*Latimeria chalumnae*) are normally found only in the western Indian Ocean, where they inhabit submarine caves in the Comores Islands¹. Two specimens have since been caught off the island of Manado Tua, north Sulawesi, Indonesia, some 10,000 kilometres away². We sought to determine the ecological and geographic distribution of Indonesian coelacanth populations with a view to drawing up conservation measures for this extremely rare fish^{2,3}. During our explorations, we discovered two living Indonesian coelacanths 360 km southwest of Manado Tua.

Analysis of mitochondrial DNA from a single Indonesian specimen, described as a distinct species, *L. menadoensis*⁴, revealed significant differences with the published mitochondrial genome of *L. chalumnae*. These differences indicate that the Indonesian and Comoran coelacanths diverged 1.8–11.0 million years ago⁵.

In an attempt to find more fish, we performed a total of 34 dives in the research submersible *JAGO* down to a depth of 400 metres at points along the northern coast of Sulawesi, the Sangihe islands and the Bay of Tomini in central Sulawesi. We failed to find any coelacanths during seven dives off Manado Tua, where the two previously reported coelacanths were caught², but 360 km southwest of Manado Tua we found two coelacanths approximately 120 and 140 cm long in a deep carbonate cave at a depth of 155 m (water temperature, 17.8–20.1 °C).

The substrate and oceanographic conditions in the Indonesian and Comoran dive sites are completely different. The Comores have steep, young volcanic slopes with numerous lava caves, whereas the slopes of the Indonesian dive sites are older, more eroded and less steep, with very few caves, and these are mainly carbonate in origin. The Indonesian sites are exposed to strong currents (with an estimated peak velocity of 3–4 knots) of variable directions and with sudden up- and downwellings. In contrast, the Comoran habitat is frequently devoid of currents, and these are slower than 1 knot.

These differences may be important, as

Comoran coelacanths are sluggish, nocturnal drift hunters that feed on other fish and have a low metabolic rate⁶. During the day, they retreat to the still water of deep lava caves¹. The Indonesian sites would therefore seem to be unsuitable for sustaining a viable population of *L. chalumnae*.

So far, four Indonesian coelacanths have been found in a relatively small area along the north Sulawesi coast. We suggest that the population is very small and requires strict conservation measures. But we cannot exclude the possibility that the coelacanths of north Sulawesi are derived from a different area and drifted there with oceanic currents. The dominant current driving Indonesian throughflow water in the area of north Sulawesi is the southerly Mindanao current⁷, indicating that the potential source population may be in the southern Philippines or remote Pacific islands.

Furthermore, geological evidence and our genetic studies of the Comoran population indicate a young age for this population of less than 100,000 years. The reported older genetic separation of the Indonesian coelacanth of more than 1 million years would suggest that Comoran *L. chalumnae* probably derived from a third, as yet unknown, population.

The biogeography of the new coelacanth population remains enigmatic, although perhaps this is for the best. An undiscovered home is probably the best possible protection for these endangered fish.

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Neuroscience

Extrapolating movement without retinal motion

In contrast to the perception of a stationary object that is briefly flashed in the dark, a continuously visible moving object is seen as being ahead of its actual position at the time of the flash. An explanation for this simple effect, in which a stimulus moving on the retina is seen as being further along its path and not where it was in space when its signal impinged on the retina, is keenly debated^{1–6}. We show here that this illusion is not just limited to retinal motion, and that perceptual mislocalization occurs even when stimulus motion is inferred entirely from extra-retinal information, for example by movement of the observer's head or whole body, without retinal motion. The phenomenon may therefore rely on a much more general mechanism.

Nijhawan^{1,2} originally suggested that the illusion is the product of a brain process that tries to overcome at least some of the visual transmission delay (more than 50 ms) through extrapolation, so that we should be able, for instance, to catch a moving object accurately. Other observations^{3,4} indicated that the apparent stimulus misalignment could be the passive consequence of the difference in the afferent delay between a stimulus that is moving on the retina and a stationary one. The physiological properties of the retina itself may even be sufficient to produce the misalignment⁶. These explanations are all based on retinal motion, however, which is the only condition under which the phenomenon has so far been demonstrated.

We set up two situations in which the movement of the stimulus in space was generated entirely by the movement of the

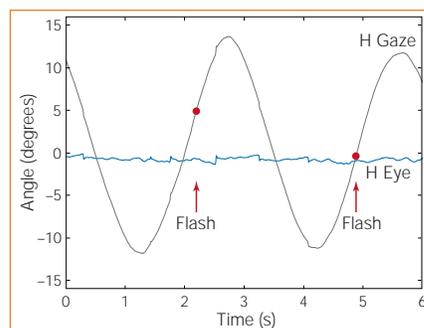


Figure 1 Recording of horizontal eye movement relative to external space, and eye movement relative to the head. The subject rotated his head sinusoidally back and forth while fixating a light-emitting diode array mounted on a recording Eyelink helmet. Flashes occurred at times indicated by arrows and were perceived as lagging behind the continuously lit stimulus. Subjects estimated the perceptual misalignment in this condition by comparing it afterwards, head fixed, with the misalignment of the same stimulus rotating on a turntable at 30 revolutions per minute, as previously^{1,2}.