Figure 1 Trade-off in selecting protected areas. Choosing areas without taking between-site complementarity into account results in less efficient reserve networks that need to be larger by *a* to achieve any given conservation goal (*B**).

where *x* and *y* are very low, *z* is also very low[8], so that, even locally, detailed surveys are still highly cost-effective.

These conclusions are conservative in ignoring extra costs of inefficient conservation networks (such as opportunity costs and initial expenditure on reserve infrastructure), in using a low figure for *a*/*A*, and in neglecting the additional benefits of biodiversity surveys for subsequent reserve management and for a broader understanding of biodiversity.

We are not advocating the widespread adoption of immensely detailed and expensive surveys (such as Costa Rica's All-Taxa Biodiversity Inventory): for the purposes of reserve selection, surveys are worthwhile only if $z < [(a/A)(x + y/r)]$ and if they can be conducted before land acquisition opportunities are lost. Indeed, our model can be modified to establish when short-cut survey techniques that reduce inventory time and costs (but yield species accumulation curves lying between the two lines in Fig. 1) provide savings over fuller inventories.

Similarly, we are not arguing that countries should use a complementarity-based approach simply to identify the smallest area capable of representing each species once: this will often fail to conserve important elements of biodiversity over even the medium term[9,10]. Instead, selection algorithms should seek several representations of species, and favour clustered reserves over small or scattered ones. Having more ambitious conservation targets such as these is likely to increase the savings achieved by coupling systematic site selection with detailed surveys.

Our results show that, where possible, government agencies and non-governmental organizations should invest in high quality biodiversity inventories before picking protected areas. If they do not, representative reserve systems will be larger than necessary, available resources will be spread more thinly, and conservation objectives will be substantially less likely to be met[11].

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How the 'terror crocodile' grew so big

Deinosuchus is a giant crocodylian from the Late Cretaceous period of North America. It was 8 to 10 metres long and weighed between 2,500 and 5,000 kg, three to five times more than the largest crocodiles alive today. How *Deinosuchus* attained sizes to rival its dinosaurian contemporaries, on which it undoubtedly preyed, has remained a mystery. Did it exhibit accelerated growth rates, like its dinosaurian cousins[1], or did it simply maintain primitive reptilian rates for decades (as was once proposed to explain gigantism in dinosaurs[2])? We find that growth indices from *Deinosuchus* skeletons reveal rates comparable to those of smaller crocodylian taxa, indicating that the gigantic proportions were attained by prolonging development.

We reconstructed growth patterns in *Deinosuchus* by coupling age and size estimates throughout development, and determined longevity by counting growth rings in dorsal osteoderms from several individuals from the Campanian Judith River Formation of Montana and the Aguja Formation of Texas[3]. Such rings form annually throughout the skeleton in extant members of Crocodylia and in proximate outgroup clades (such as Lepidosauria and Chelonia[3,4]). We based estimates of total length for adult *Deinosuchus* on a large mandibular ramus from Texas and regression curves for the American alligator (*Alligator mississippiensis*) and saltwater crocodile (*Crocodylus porosus*)[5,6]. We used proportions of linear increase per growth ring as standardized measures to estimate annual increases in total body length throughout ontogeny, and conducted comparable analyses on the osteoderms of large individuals from clades closely related to *Deinosuchus*[7] (Fig. 1). In Fig. 2a, length is plotted against age for the extinct taxa; growth curves for large extant crocodylians are also shown. We have made osteohistological characterizations of the jaws, ribs, vertebrae and long bones of *Deinosuchus*, and assessed relative somatic growth rates[1].

We estimate longevity in the *Deinosuchus* specimens to be 50 and 51 ($\pm$ 2) years (Fig. 2b). Extant crocodylians rarely live this long in the wild[8], and none of the fossil specimens from related lineages attained such ages (Fig. 2a). We estimated
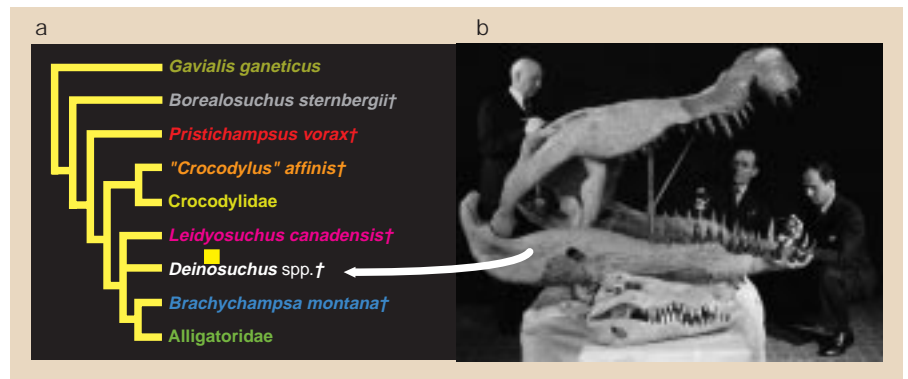

Figure 1 *Deinosuchus* and its phylogenetic position. **a,** Phylogenetic hypothesis for the Crocodylia showing the relationship of *Deinosuchus* to other clades. The cladogram is based on maximum-parsimony analysis of 164 morphological characters from both fossil (†) and living taxa. **b,** The size of an adult *Deinosuchus* skull relative to a specimen of a large extant crocodile. Pictured from left to right are B. Brown, R. T. Bird and E. M. Schlaikjer (negative no. 318651, courtesy of the Department of Library Services, American Museum of Natural History). Although the overall size of the *Deinosuchus* reconstruction is generally correct, recent finds show the skull to have had a broader snout, giving it a more alligator-like appearance. Growth rings in precaudal dorsal osteoderms were studied from extinct non-gavialoid crocodylians in the phylogenetic bracket.
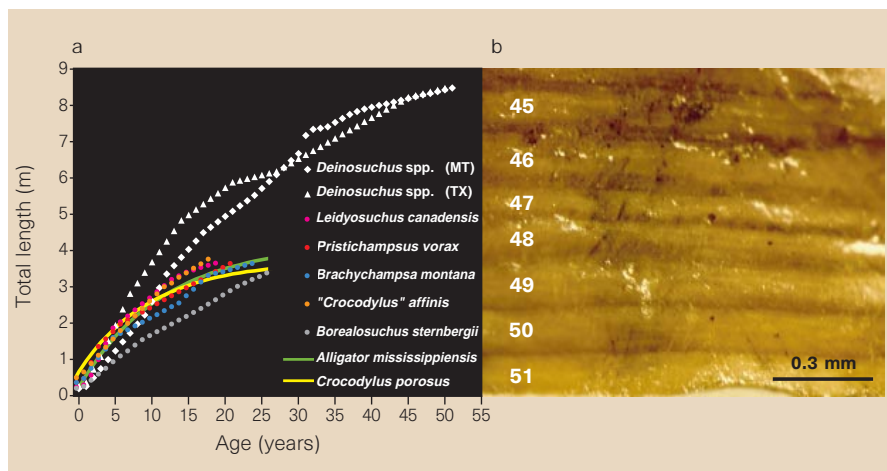
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Figure 2 Growth rates of crocodylians and osteoderm growth rings. **a,** Total length against age in non-gavialoid crocodylians. The data for individuals from extinct clades (symbols; specimen numbers are available from the authors on request) are based on growth line counts in dorsal osteoderms extrapolated to total body length. The idealized growth curves for large extant crocodylians (lines) are from capture–recapture analyses from hundreds of individuals[10,11]. The similar patterns between the two data sets for specimens of comparable sizes indicate that the methods used provide reasonable estimates of crocodylian growth. The *Deinosuchus* growth curves show a continuation of ancestral juvenile growth rates past 10 years of age and presumably greater longevity. **b,** Lamellar bone growth rings from the ventral surface of an osteoderm representing the final seven years of growth (years 45 to 51) in a specimen of *Deinosuchus* from the Aguja Formation of Texas.

the total length for the *Deinosuchus* specimens to be 8.43 to 9.10 metres. Plots of length against age for *Deinosuchus* outgroups show that the primitive character state for growth in non-gavialoid crocodylians was characterized by rapid linear increases early in development, with rates typically declining by the first decade after hatching (Fig. 2). *Deinosuchus* showed similar rates (about 0.3 metres per year) to other crocodylians from the phylogenetic bracket during the first five to ten years of life, but maintained these juvenile growth rates for several decades (Fig. 2).

The primary histological structure of *Deinosuchus* skeletal elements supports the interpretation that primitive developmental growth rates were retained. Bones from the giant crocodylian showed slowly deposited lamellar–zonal bone tissue typical of non-gigantine crocodylians (the ancestral pattern in reptiles). Because patterns of bone fibre packing correlate with osseous deposition rates[1], it seems that bone formation was not accelerated appreciably. This is in contrast to the skeletons of dinosaurs, which show evidence of derived, accelerated rates in the form of rapidly deposited fibro-lamellar bone[1].

The evolution of increased metabolic rates in dinosaurs is believed to have facilitated the evolution of gigantism by enabling them to build their skeletons swiftly using fibro-lamellar bone[1]. *Deinosuchus* achieved the same outcome, but it took much longer. Dinosaurs of similar size to *Deinosuchus*, such as hadrosaurs ('duck-billed dinosaurs'), reached adult size in only seven to eight years[9], whereas the giant crocodylian

required more than 35 years. We believe that the retention of an ectothermal physiology constrained *Deinosuchus* to the deposition of slow-forming somatic tissues (such as lamellar bone) throughout development, necessitating a greater developmental time to reach dinosaurian proportions.

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Localization or classical diffusion of light?

Wiersma *et al.*[1] have reported near-infrared optical transmission and coherent backscattering data from strongly scattering slabs of micrometre-sized semiconductor particles. Their optical transmission was much weaker, and the angular shape of their coherent backscattering more rounded, than would be expected for classical diffusive light propagation without absorption. The authors interpret this as evidence for the onset of strong localization of light, but we find that their data can be explained by classical diffusion combined with reasonable amounts of absorption. Moreover, the turbidities of their samples are much lower than those given in ref. 1 and are comparable to samples with classical transport properties. We therefore question whether their samples are in fact close to the proposed localization transition.

In diffusive transport through disordered non-absorbing media in which $\lambda \ll l^* \ll L$, we have $T \propto l^*/L$, where $\lambda = 2\pi/k$ is the wavelength, l^* is the transport mean free path, T is the optical transmission, and L is the slab thickness. For $kl^* \to 1$, the scaling theory of localization predicts that $T \propto L^{-2}$, whereas inside the regime of strong localization ($kl^* \leq 1$), $T \propto \exp[-L/l_{\rm loc}]$, where $l_{\rm loc}$ is the localization length. In classical diffusion ($kl^* \gg 1$) with absorption, T crosses over from $T \propto L^{-1}$ at small L to $T \propto \exp[-L/L_{\rm a}]$, where $L_{\rm a}$ is the absorption length, at large L. Thus, it is difficult to distinguish localized light from absorbed light solely on the basis of measured average light intensities.

Wiersma *et al.*[1] used powders of gallium arsenide produced by grinding. No significant distortion of the bandgap was seen, but this does not exclude absorption for wavelengths inside the gap, because contributions from surface states, dangling bonds, defects, internal stress or impurities, for example, are likely to increase upon grinding. For the 1-μm particles, the coherent-backscattering cones were found to be substantially flatter close to backscattering than for non-absorbing samples, but were not much wider at larger angles (Fig. 1a). Figure 1a compares data from ref. 1 with data from a dense powder of non-absorbing TiO_2 particles[2]. Because the cone width scales with kl^* and the TiO_2 sample has $kl^* \approx 5.8$ (ref. 2), the comparable widths suggest that $kl^* \approx 5.0 \pm 1$ ($l^* \approx 0.8$ μm) for this GaAs sample, in contrast to $kl^* \approx 1.5$, as given in ref. 1. The latter value was obtained by fitting the low-angle (≤ 10 mrad) slope in the region of strong rounding. This provides unphysically