Ecology and evolution of dwarfing in insular elephants

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SUMMARY: Elephants approach one extreme in the spectrum of terrestrial mammalian body sizes. In the Pleistocene, on islands, they have also undergone size reduction to an extreme degree. An understanding of the evolutionary origins and ecological roles of dwarfed forms of elephants on Pleistocene islands both benefits from, and may allow us to test, general hypotheses about the relationship between (a) body size and (b) the processes involved in organismal function, ecology, and evolutionary mechanisms.

1. Introduction

Fossils from insular populations of elephants are the most extreme examples of Foster's Island Rule for mammalian body size (Foster 1964, Van Valen 1973, Lomolino 1985): on islands, mammals larger than a rabbit almost invariably evolve smaller body size (whereas mammals of small body size on islands typically enlarge).

Insular elephants are of particular interest because of the magnitude of their reduction in size. The island forms may be half or even one-quarter the shoulder heights of their mainland ancestors, with body mass reduced to just one or a few percent of the original (Roth 1990). This degree of body size reduction is more extreme than that observed for any other insular dwarfs, even allowing for the fact that very large mammals generally undergo proportionately the greatest reduction on islands.

The terms "dwarf" and "pygmy" have both been used, with nearly equal frequency, to denote forms or species of mammals that are smaller in body size than their close relatives (Nowak 1991). I will use the terms synonymously, without intending them to carry any specific implications about the mode or mechanism of size reduction. Dwarfed forms of elephants have been reported from islands off California, Siberia, eastern Asia, and in the Mediterranean–wherever, in fact, elephants have colonized islands free of large predators (Roth 1992; Vartanyan *et al.* 1993).

2. Elephants on Islands as "Natural Experiments"

The frequency with which elephants have colonized islands and undergone size reduction provides paleoecologists and evolutionary biologists with multiple instances of a natural experiment.

The experimental conditions offered by island habitats typically differ from corresponding habitats on the mainland in their smaller geographic area, their reduced accessibility to colonizing or migrating terrestrial species, and their more equable climate which is moderated by the surrounding water. Island communities often comprise fewer species, in combinations differing from the mainland. The island populations themselves may undergo divergence from their mainland ancestors, giving rise to forms that are distinctive or even unique.

The existence of dwarfed elephants on Pleistocene islands raises a number of questions, in two interrelated categories: 1. By what mechanism(s) did insular elephants attain their diminutive sizes? and 2. What ecological role did elephants weighing just a few hundred kilograms play in their respective communities? Suitable answers to these questions must be consistent with what is known about the differences between conditions on mainland and island, as well as what can be inferred about characteristics of the animals from their fossils.

3. Open Questions

3.1 Evolutionary mechanisms

Mechanisms of change in body size include phenotypic plasticity (stunting, for example in this instance) and genetic divergence. Genetic change can arise through drift and natural selection.

The size difference between the smallest of insular dwarfs and their mainland ancestors was too great to be achieved by stunting alone. Among lineages, the net change is too consistent in direction–exclusively toward smaller size–to be explained by genetic drift, so we infer that natural selection must have been involved.

Natural selection among individuals is generally considered the most efficient and well documented mechanism of evolution; however, selection can in principle operate at multiple levels (such as the gene, organism, or deme). Islands may not have been able to sustain large populations of large-bodied forms, in which case it is plausible that differential extinction of low-density populations (and conversely, persistence of high-density, dwarfed populations) could have played a role in the evolution of insular elephants (Wassersug *et al.* 1979). Evidence of such differential extinction would include islands with deposits of fossils of large elephants overlain by no evidence that the population had any direct descendants.

More conventional explanations of dwarfing focus on selection acting on traits of individuals. Marked dimorphism in *Elephas falconeri* from Sicily (Ambrosetti 1968) provides evidence of the action of sexual selection, as well as natural selection, on dwarfed elephants.

The processes affecting extinct animals cannot be observed directly, but the morphology of the animals can reveal the type of variation on which natural selection may have acted. Contrary to some suggestions, achondroplasia, a type of dwarfing that can be produced by mutation at a single genetic locus, was evidently not involved (Roth 1993). The high frequency of certain dental anomalies known to be common in modern populations that are food-stressed hints at similar stresses in insular populations (Roth 1989). The substantial amounts of morphological variability found within dwarfed elephant populations suggests that small body size, rather than a particular paedomorphic morphology, was the target of selection (Roth 1984, 1993). As more is inferred about the ecology, environment, and life-history of the animals, more informed inferences can be made about the action of natural selection within these populations.

3.2 Natural history

An animal's body size reveals much about its way of life (Peters 1983). At the same time, techniques for the functional analysis of fossils continue to be developed and enhanced, and these allow predictions based on estimates of body mass to be tested. Analysis of stable isotopes and of dental striations may give clues to diet; bone histology may reveal patterns of growth; dentine layers may provide a tally of years that facilitate inferences of lifespan. Among the questions raised about tiny elephants are:

How did they subsist, persist, grow and reproduce? What did they eat? How did the morphology of their teeth and jaws reflect or constrain their diets? What morphological evidence is there of their locomotor agility or greater maneuverability (e.g. Sondaar 1977)? What modifications do they show in their patterns of growth? How was their demography and population structure affected by body size? Among modern mammals many life-history variables are known scale with body size. Do the size-related trends in natural history observed for bovids and other large herbivores also apply to the Elephantidae (Jarman 1974)? For example, did the smallest elephants require food with more highly concentrated nutrients?

How do the characteristics of insular elephants vary in relation to the characteristics of the islands and their biotas?

3.3 Many islands; much time

Ultimately, an understanding of the natural history and evolution of dwarfed elephants must be understood in the context of their history, and the history of the islands they inhabited. Paleontological subjects offer the study of biology a unique perspective from the vantage of lengthy periods of time. The replicated experiments of elephants evolving on islands allow us to observe both variation and patterns. Patterns and regularities in turn allow us to infer more general evolutionary and ecological principles.

As more information emerges about fossil elephants from islands, we will know with increasing confidence which islands supported such populations and which did not; what the relationship is between an island's area, its distance from the mainland, and the body size of its inhabitants; how these quantities varied in place and changed through time; and over what time course the events occurred. These facts will enhance our understanding of the more fundamental processes that govern the evolution of communities, the divergent process of speciation, and the origin of evolutionary novelty.

4. References

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