

Why are there so many giants, including giant squirrels, in the Old World tropics?

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Patterns of body size evolution have long intrigued biologists. One striking pattern is that the Palaeotropics have larger-sized vertebrate herbivores, especially frugivores, compared to the Neotropics. Various explanations have been offered for this pattern, among which are historical and ecological processes. However, it is insufficient to investigate body size evolution in single phyla alone; guilds or communities of interacting taxa have to be considered, even extinct ones, in order to understand present-day patterns. Therefore, the spatio-temporal availability of resources, the physiognomy, chemistry and productivity of forests, trophic competitors and predators, as well as available time and space on evolutionary scales, are determinants of extant patterns. Palaeo-community ecology must become an important research focus in body size evolution. Palaeoecology must be brought to bear on present ecology, to explain why vertebrates, including squirrels, are giants in the Old World compared to the New.

Keywords: Body size evolution, community ecology, ecological clock, frugivory, palaeoecology, *Ratufa*.

Introduction

THE earth has witnessed the evolution of giants and dwarfs across a wide range of taxa. Is there regularity to these patterns? Are the processes determining these patterns definable? Can a research agenda be outlined so that measurable progress can be made in the field of historical ecology? One striking pattern that has intrigued researchers is the small size of extant New World tropical herbivorous vertebrates relative to their Old World counterparts¹. What causes this pattern? To address this, I present a selective review of body size and its interaction with ecology. I restrict myself to patterns and processes relevant to one predominantly herbivorous group of mammals, i.e. the squirrel family Sciuridae, since sciurids also exhibit this continental size dichotomy². Body size scales with diet in squirrels as in most animals with the larger taxa being more herbivorous and the smaller ones more insectivorous². I argue, however, that extant diet and size are consequences of historical processes that must be viewed inte-

gratively across interacting phyla, including plants, in order to understand the evolution of gigantism.

Spatio-temporal patchiness of resources and its effect on body size

A landmark comparison of diversity patterns of tropical vertebrate herbivores (birds, primates and bats) between geographical realms¹ focussed on frugivores because they contribute greatly to biomass and thus to community-level processes within tropical forests. Reduced frugivore diversity existed at both community and regional levels in south-east Asia relative to the Neotropics. Palaeotropical frugivores were larger, exhibited greater dietary overlap and dietary breadth and were more nomadic than Neotropical ones. Historical processes potentially causing these patterns included time available for colonization, evolutionary history of floras and pre-emption of feeding niches by ecological competitors¹. Spatio-temporal patchiness (STP) in fruit availability was the major ecological attribute examined¹. The high STP of fruit in forests receiving seasonal rainfall, e.g. monsoonal Palaeotropical forests, should generate greater dietary overlap resulting in fewer co-existing species, thus explaining the more speciose Neotropical frugivore communities. A more constant supply of fruit (low STP) throughout the year should favour dietary specialization, lower food overlap and less nomadic behaviour since individuals need not travel long distances for fruit. Thus, Neotropical toucans are smaller (0.7 kg) and clumsier fliers compared to their Palaeotropical hornbill counterparts (2.5 kg); hornbills fly long distances (up to 290 km) tracking fruit bonanzas³, while toucans have much smaller feeding areas (110 ha)⁴. Other studies confirmed this body mass dichotomy in various frugivorous taxa, including rodents; e.g. within the Sciuridae, masses range from 0.04 to 3 kg in the Palaeotropics and from 0.2 to 1 kg in the Neotropics^{5,6}.

Fruit size differences between tropical regions

Mean and maximum fruit lengths are greater in Palaeotropical plant families important in frugivore diets as compared to Neotropical ones⁵. However, was large fruit size an exaptation or an adaptive response to the already available large frugivorous taxa? Angiosperm fruit size presumably

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increased over several orders of magnitude from the late Cretaceous to the early Eocene, a size change probably driven by climate change rather than sizes of available fruit dispersers⁷. However, pterosaurs as dispersers have been implicated in angiosperm fruit evolution in the Cretaceous⁸ and fruit size also appears to be responding to selection by extant fruit dispersers⁹; e.g. extant fruits in New Zealand are smaller than those in Australia and South America, a pattern attributed to the smaller sizes and lower diversity of the mostly avian New Zealand frugivores⁹. Also, New Zealand fruits are more ellipsoid, apparently resulting from co-evolution with birds of particular gape sizes, and gape size correlated positively with body mass⁹. Thus, of the many physical and chemical traits examined, only fruit size showed recent divergence relative to type of fruit disperser, while other traits showed strong phylogenetic conservatism¹⁰. The primary cause of regional differences in fruit size is still, however, contentious¹¹.

Are regional differences in STP of fruit resources real?

Good comparative data to test the hypothesis that the Palaeotropics have greater STP in flowering and fruiting compared to the Neotropics¹ still remain scarce. However, a recent study and others reviewed by Sakai¹² support this hypothesis. Another feature of the south-east Asian tropics is masting or mass flowering, which may be related to the El Niño–Southern Oscillation phenomenon¹³ (however, see Wich and van Schaik¹⁴), or an evolutionary strategy to cope with seed predators via predator satiation¹⁵. Thus, masting years are periods of community-level fruit abundances followed by periods of fruit shortages. Animals evolving in such forests would need to be adapted to this special ecology of plenitude followed by scarcity. Large body size is one such adaptation. Fleming re-examined the connection between high STP of fruit and greater dietary overlap and found a positive relationship between species richness of mutualistic vertebrates (pollinators and fruit dispersers) and that of their plant resources only in the New World, while these variables were unrelated in the Old World¹⁶. There appear to be more generalists in the Old World, resulting in lower species diversity and niche diversification.

Do tropical forests differ in physiognomy?

Animals are often shaped by the physical attributes of their environment, e.g. streamlined shapes of aquatic fauna. Thus, forest physiognomy could also influence frugivore morphology, locomotion and, consequently, size. Emmons and Gentry¹⁷ related tropical forest structure, specifically the contribution of lianas, to the size and ecology of arboreal vertebrates. They found that the Neotropics had more

lianas than Asia but fewer than Africa, and Neotropical lianas were more fragile than Palaeotropical ones. They also found more gliding vertebrates in the Asian tropics, and prehensile-tailed vertebrates in the Neotropics. Could the fragility of the vegetation have selected for smaller organisms with prehensile tails? While supporting the fragile vegetation hypothesis, Cristoffer⁶ felt that smaller-sized fruit could have contributed to the radiation of small primates in the Neotropics, many of which feed from the fruit of vines or other fragile secondary growth vegetation. Did the fragile vegetation and small fruit come first, followed by small primates? Only studies in palaeo-community ecology can answer this question. Neotropical forests also have a more closed and cluttered forest interior compared to Palaeotropical forests¹⁸. This difference in the distribution of free space within forests may have also contributed to the evolution of larger flying and gliding animals in the Palaeotropics^{18,19}. However, the greater height of Palaeotropical forests, especially those in Asia, may also be responsible²⁰.

Morphological constraints on body size evolution and solutions

Having particular morphological attributes, e.g. claws versus nails, can determine the maximum size achievable by an arboreal species. Nail-bearing arboreal vertebrates are significantly larger than those bearing claws, e.g. larger primates compared to smaller squirrels²¹, since larger animals cannot support their weight using claws and may need to acquire more flexible digits to increase grasping ability. Many large arboreal mammals are, thus, morphologically specialized for arboreality; e.g. the shoulder girdle of the giant squirrel *Ratufa*, which is confined to the Asian tropics, shows specializations associated with arboreal gigantism²². Among squirrels, only *Ratufa* has wrist architecture that suggests greater use of its thumbs for grasping²³, a prediction confirmed by behavioural observations (pers. obs.). The large Asian flying squirrels *Petaurista* and *Pteromyscus* also have proportionately longer digits than other flying squirrels and use these effectively for grasping²⁴. *Ratufa* also has a relatively longer tail than any other arboreal squirrel²⁵, which is probably an adaptation for balancing a large body during a highly arboreal existence.

Could savannas have contributed to body size evolution of rainforest taxa?

In the past, extensive savannas occurred in Africa and Asia; Africa, especially, was a huge evolutionary theatre for savanna vertebrates²⁶. The savanna biome of the Old World is old, dating to the Miocene with large animal population densities²⁶. According to Cristoffer and Peres²⁷, such large savanna populations could have spilled over into other

biomes, e.g. rainforests, where their members would occur as immigrants. If the rainforest biota thus came to include species that had originated in the savanna, its composition would consist of larger-bodied species, as such taxa would, by virtue of their greater mobility, invade forests. In this way, rainforests could have received species that were already large and already pre-adapted to the conditions of higher STP of food resources²⁷. Consistent with this is the larger mean body mass of extant rainforest mammals in Africa and Thailand compared to Amazonia²⁷; furthermore, the largest fossil African squirrel, *Kubwaxerus pattersoni*, is from the Miocene savanna of Kenya and equals the giant squirrel *Ratufa* in size²⁸. Although, today, the savanna biome in tropical Asia is small, it was extensive in the Pleistocene²⁹ and could have contributed larger-sized animals to the rainforest biota.

Islands, sea level fluctuations and squirrel evolution in the Cenozoic of Asia

Extant squirrels are morphologically primitive and are considered to be living fossils³⁰. The evolution of giant squirrels such as *Ratufa* may have occurred in the south-east Asian arena³¹. The Cenozoic history of the Sunda Shelf is central to the dispersal and vicariance history of Asian biota³². In the Late Pleistocene, much of the land of the Sunda Shelf was above water, with land connections between the Malay Peninsula, Sumatra, Java and Borneo, and also with ancient river courses^{29,32,33}. Pleistocene savannas on the Sunda Shelf were extensive²⁹; the wetter vegetation would, therefore, have been confined to riparian forests that could have facilitated the dispersal of large arboreal vertebrates such as giant squirrels throughout the Sunda Shelf, explaining their present distribution on islands throughout this region. In a classic demonstration of palaeoecology bearing on present-day ecology, the body size and distribution of the tree squirrel *Callosciurus prevosti* in southeast Asia has been linked to past and present island area and ensuing food limitation and inter-specific competition³⁴. Heaney³⁵ also pointed out that the rate of phylogenesis (generation of new species) on large islands is likely to be higher than that for small islands. Thus, the spatial area within which evolutionary forces can act is also extremely important in evaluating community-wide patterns of body size.

Ecological significance of large body size in giant squirrels

The giant squirrel genus *Ratufa*, with four species, is restricted to the Asian tropics; of three species that occur in India, only one, *R. indica*, is endemic³⁶. *Ratufa* includes the largest tree squirrels in the world, with individuals reaching a 2-kg body mass³⁶. The Indian giant squirrel *R. indica* subsists entirely on a diet of leaves and bark when

its preferred fruit are unavailable^{37–39}; this is enabled by an enlarged caecum which facilitates post-gastric digestion and the consumption of such a nutritionally poor diet³⁶. The large size of *Ratufa* buffers it against food shortages and is ideal to cope with increased STP of fruit in the monsoonal forests that it occupies. Unlike temperate squirrels, that hoard seeds in larders to tide over unfavourable periods of seed shortages, tropical arboreal squirrels such as *Ratufa* are not known to hoard seeds, with only one exception reported recently in a population inhabiting a seasonal cloud forest with extreme monsoon conditions in the Western Ghats⁴⁰. Diurnal *Ratufa* also often shares its forests with nocturnal flying squirrels, including the giant *Petaurista petaurista*, which is the largest flying squirrel²⁵ with an enlarged caecum and a highly folivorous diet²⁴. Thus, the Asian giant arboreal squirrels *Ratufa* and *Petaurista* diversify their diets to include leaves and bark, a diversification that is only possibly because of their large body size.

Phytochemistry, productivity, species richness and body size

Since biomass and ecological dominance are related, it is important to ask why some forests support a higher biomass of certain taxa. Poor leaf chemistry was correlated with lower total biomass of leaf-eating primates⁴¹. Primary productivity of forests in the Neotropics was positively correlated with rainfall and with high species diversity of frugivorous primates⁴². Similarly, the high species richness of browsing mammals in the Miocene was correlated with high primary productivity of woodland vegetation while larger savanna grazers appeared later under conditions of global climatic change⁴³. Therefore, besides conventional factors such as forest area, others such as phytochemistry and productivity must be considered when evaluating the ecological potential for generating and maintaining herbivorous communities. Perhaps we also need new theories such as the one linking the absence of large herbivores from Australia to concentrations of micronutrients such as iodine, cobalt and selenium⁴⁴.

An ecological clock?

An analysis of primate communities in Africa, Madagascar, Asia and South America using ecological variables such as size, diet and locomotion found more inter-continental than intra-continental differences, indicating diverse evolutionary trajectories on different continents⁴⁵; for example, Africa had more terrestrial taxa, whereas more suspensory taxa occurred in Asia. Moreover, divergence time and ecological distance between taxa within a community were linearly related on all four continents. This led to the novel idea of an ecological clock⁴⁵. Just as a molecular

clock can time the divergence between genes that have descended from a common ancestor using the assumption of regular mutation rates⁴⁶, so can ecological divergence be measured in terms of divergence in phenotypic traits of community members. An important caveat in the use of the ecological clock, as with its molecular counterpart, is that it is calibrated based on the distance and divergence time for extant taxa; whether the tempo and mode of evolution have remained constant through time and space remains unknown. The idea of the ecological clock is nevertheless useful as it helps to foster a research agenda that uses a cross-taxa community-level approach.

Coda: The ghosts of taxa past

It appears, then, that a metabolic and more integrated approach to community structure is required^{47–49}. This approach should examine the relationship between land area, body mass and food requirements for various extant and extinct ecological groups, such as carnivorous versus herbivorous dinosaurs, carnivorous versus herbivorous endotherms and ectotherms. Such analyses will allow more meaningful investigations of potential and actual co-existing taxa using evidence from the fossil record as well^{50–52}. This approach would necessitate examination of trophic competitors as well as the co-evolution of all interacting taxa, not just those in the focal phyletic group⁵³. Unfortunately, the big picture often fades from view, owing to the taxonomic specialization of investigators. For example, squirrels may have been constrained from evolving to certain sizes or into certain trophic niches because these niches were already pre-empted by non-squirrel competitors. We need to ask whether the rodent pacas and agoutis of the Neotropics are analogues of the mouse deer of the Palaeotropics, and whether giant squirrels are analogues of primates⁵⁴. This investigation of functional and morphological analogues must be performed with all interacting and possibly co-evolving taxa, which should include plants as well. Palaeobotany and palaeozoology, conducted with physical or molecular fossils, should provide novel perspectives on present-day plant–animal interactions. The ghosts of taxa past could be extremely instructive.

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