

SEED DISPERSAL

Theory and its Application in a Changing World

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Theory and its Application in a Changing World

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Preface

Many researchers working in the field of seed dispersal have recognized that, periodically, the field has begun to lose cohesion and has faced the risk of fraying into a tangle of disconnected directions. This book is the fourth in a series of edited volumes that have appeared at long intervals and have marked the empirical and theoretical position of the field. Our aim, like that of the editors of previous volumes, has been to present recent advances, provide reviews of the state of knowledge and to chart future directions; to provide a reference point in a burgeoning literature. Like its predecessors (Estrada and Fleming, 1986; Fleming and Estrada, 1993; Levey *et al.*, 2002) it has grown from an international symposium/workshop on frugivores and seed dispersal. Most of the chapters in this book are derived from invited presentations given at the *Fourth International Symposium/Workshop on Frugivores and Seed Dispersal* held in Brisbane, Australia, in 2005. A few were invited additions, selected to complement the existing chapters to make a more thorough reference.

The study of seed dispersal and of the plants and animals involved has been developing, and maturing, at an impressive rate. While many concepts and methods used in the past have maintained their currency, many fresh approaches are providing new perspectives and directions. The combination has led to a suite of exciting new questions, new answers to old questions, new approaches, and a reinvigoration of the field. And they point the way for greater progress in the future.

We are proud to be able to present a book that demonstrates the vigour and vibrancy of the field. Without losing touch with its theoretical and empirical past, seed dispersal research has in recent years undergone a renaissance and has surged forward. From a pure science perspective, these are exciting times. But this is also a time when it is becoming ever more important that our knowledge is applied in an effort to meet the growing environmental challenges that threaten natural systems. The

chapters in this volume show that research into the ecology of seed dispersal is focusing on these issues and identifying and applying aspects of research to meet these challenges. Although there is much more to be done, this promises to be one of the growth areas in the field.

The previous three volumes (Estrada and Fleming, 1986; Fleming and Estrada, 1993; Levey *et al.*, 2002) have each represented landmarks in the field and have had enormous impact. We sincerely hope that this fourth volume will live up to the benchmark set by its predecessors and that it serves not only as a reference but also as a source of scientific inspiration and insight.

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I Frugivores and Frugivory

ANDREW J. DENNIS

Introduction

The process of seed dispersal frequently begins with a fruit interacting with a frugivore, and this interaction is a fitting place to begin a book on seed dispersal. The interactions between animals, fruits and their seeds dominate plant reproduction in most habitats. Although we often think of tropical forests, even many desert plants produce fleshy fruit designed to attract animal dispersers, and these plants are frequently abundant species (see Bronstein *et al.*, Chapter 7). Of all the potential vectors for dispersing seeds, animals are the most susceptible to disturbance by humans (see Part IV), making it essential that the process of seed dispersal mediated by animals is understood to the fullest possible extent in our rapidly changing world.

The dawn of research into seed dispersal probably began with naturalists being fascinated by colourful fruits, sometimes flamboyant animals, and the interactions between the two. These interactions have caught the attention of people interested in a range of animal behaviours such as food choice, diet composition, nutrients, and foraging behaviour. However, more than most aspects of animal behaviour, the consumption of fruits and seeds by animals has consequences that can reach far beyond the immediate players. Many animals with non-fruit diets can have impacts on the demography of their food items or can influence community composition (e.g. Augustine and McNaughton, 1998) but few have such complicated and potentially far-reaching consequences as animals that eat fruit (see, e.g. Terborgh *et al.*, 2002).

The act of an animal eating a fruit can influence the survival, dormancy and germination of a seed and the subsequent probability of survival and growth rate for a seedling (see Traveset *et al.*, Chapter 4). The immediate influence an animal has over a seed is determined by how the

seed is handled and the kind of animal doing the handling (e.g. Schupp, 1993). There are four key areas where a frugivore's handling can have significant impacts on the immediate outcomes for a seed. They include the removal of flesh, scarification of the seed coat, other materials deposited with the seed in the dung, and the number and combination of seeds deposited (see Traveset *et al.*, Chapter 4). Combined, these influences can result in a complex array of outcomes, all without considering the location of deposition, which has a whole new suite of influences (see Part III; Schupp, Chapter 21).

While an individual animal can influence an individual seed's fate, assemblages of animals can influence the recruitment of plants and their populations (see Part II). This influence extends to community composition and dynamics and to the evolution of plant traits at individual (see Levey *et al.*, Chapter 2; Schaefer and Schaefer, Chapter 3), regional and continental scales (see Forget *et al.*, Chapter 1; Donatti *et al.*, Chapter 5). Plants and animals have co-evolved in a number of ways. It is common for many species of animals to interact with a single plant (see Dennis and Westcott, Chapter 9), which means that selective pressures and the co-evolution of fruits and their consumers have been diffuse (e.g. Herrera, 1985). However, it is not just the combination of animals consuming a given fruit at any one time or place that influences its evolution, but a combination of past and present selective pressures, and those exerted in different locations (Forget *et al.*, Chapter 1; Donatti *et al.*, Chapter 5).

Despite the diffuse nature of selective pressures, frugivory and seed dispersal have strongly influenced the traits of fruits. For example, colour and bloom on fruits act as visual communication to mutualists and antagonists. Colours and blooms that contrast best with the background appear to have been selected so that fruits can attract those seed-dispersing animals that provide advantages to the plants (see Schaefer and Schaefer, Chapter 3). Clearly, such simple communication is not the full story, and a range of other more subtle messages remain to be fully explored (see Schaefer and Schaefer, Chapter 3). Among these are chemical messages and controls on animal behaviour, which frequently serve complex functions, trading off the benefits of attracting animal dispersers and of deterring pathogens and seed-eating animals (see Levey *et al.*, Chapter 2).

The results of selection can vary from place to place and in subtle and complex ways. For example, the traits of fruits selected by lizards differ considerably between locations. This may be due to different groups of lizards being dominant at different locations, despite lizards seeming to be a uniform group of dispersers throughout the world (see Valido and Olesen, Chapter 6). This pattern is also reflected in patterns of seed size and shape when analysed at a community level and compared between floras on different continents. In this case, differences in animal disperser assemblages are not always reflected, as expected, in the shapes and sizes of seeds (see Forget *et al.*, Chapter 1).

This diffuse co-evolution, brought about by the diversity of the animals potentially interacting with any one plant leads to complex interaction

networks which can have high levels of resilience at community and individual levels (see, e.g. Donatti *et al.*, Chapter 5; Silva *et al.*, Chapter 26). This resilience can be brought about by redundancy in the system, where the loss of one or two dispersers or even whole functional groups of dispersers does not mean the total loss of service to a plant (see Loiselle *et al.*, Chapter 8). Ecological redundancy in the system further complicates our ability to fully understand and predict the outcomes of disruption to the process. In some instances, the ability to persist without dispersal or a range of biotic and abiotic dispersal strategies can mean survival until lost dispersers can be replaced by new ones in different locations or times (see Forget *et al.*, Chapter 1; Donatti *et al.*, Chapter 5). However, as this diversity of dispersal agents and ecological redundancy erodes through human impacts, the system's resilience may also decline (see Part IV).

Because of these complexities, the study of frugivores and the fruits they eat has quickly gone beyond the study of animals and their food resources into the true study of a mutualism – seed dispersal – and all of its consequences. While seed dispersal has developed a range of directions and theories, its foundations still rest on understanding the interaction between fruits and frugivores. This highlights the critical importance of a sound understanding of the natural history of these interactions. Without observing the patterns of food choice and the behaviours of animals after feeding, it will be impossible to navigate the complexities of this process and apply our understanding to managing the sustainability of the earth's ecosystems.

This first section includes some excellent chapters dealing with frugivores and frugivory. It does not attempt to cover all aspects of this broad field but instead provides some novel insights and comprehensive reviews, filling in some gaps and consolidating some lines of investigation. It provides new springboards for continuing research and understanding that can be applied in solutions to ecological problems.

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Seed Allometry and Disperser Assemblages in Tropical Rainforests: A Comparison of Four Floras on Different Continents

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Introduction

A wide range of independent factors can exert selection on plants, influencing the evolution of both fruit and seed size and shape (e.g. Herrera, 1992; Mazer and Wheelwright, 1993; Jordano, 1995a; Lord, 2004). Seed size comes under a range of selection pressures from plant traits such as growth form, seedling size, leaf area and shade tolerance. For example, species with large seeds are usually better adapted to the low-light conditions of mature tropical rainforests (Salisbury, 1974; Foster, 1986; Kelly, 1993; Westoby *et al.*, 1996; Moles *et al.*, 2005a,b). Fruit traits such as secondary compounds (see Levey *et al.*, Chapter 2, this volume) or colour (see Schaefer and Schaefer, Chapter 3, this volume), as well as frugivore traits such as body size, gape width and gut length (Charles-Dominique *et al.*, 1981) may influence the handling and treatment of fruits and seeds and therefore also exert selective pressure on their size (e.g. Jordano, 1995a,b; Rey *et al.*, 1997; Alcantara and Rey, 2003). A number of studies have examined fruit characteristics (Lord, 2004, and references therein) and the size and/or gape width of animals swallowing or regurgitating them (Gautier-Hion *et al.*, 1985; Kitamura *et al.*, 2002) but few have dealt with seed size and shape in relation to endozoochory. Theoretically, as with fruit characteristics, seed size and shape are likely to be selected and constrained by the size of the seed-dispersing animals that swallow them (see, e.g. Tiffney, 1984; Westoby *et al.*, 1996), as well as by the predators that handle them (e.g. Mack, 1998; Dalling and Harms, 1999; Moles and Drake, 1999).

Just as egg allometry is related to birds' body size (Huxley, 1932; Calder, 1979), seed allometry has probably been affected by selective pressures exerted by dispersers via the transportation and passage of seeds

through the body (Lord, 2004). In particular, the diameter of a frugivore's intestinal tube places an upper limit on the size of seeds that it may successfully disperse. In general, the larger the disperser, the bigger the fruit or seed it can handle, swallow and disperse via gut transit (Gautier-Hion *et al.*, 1985). For example, independent of growth form, Peruvian plants dispersed predominantly by mammals have larger seeds than those dispersed mostly by birds, reflecting the greater average size of dispersing mammals compared with birds (Kelly, 1995).

Tropical plants tend to have larger fruits and seeds than those of temperate floras, and most are consumed and dispersed primarily by frugivorous or granivorous animals rather than by abiotic vectors (Howe, 1986). Tropical frugivores, ranging in size from tiny ants and dung beetles to massive tapirs, elephants and cassowaries, disperse plant diaspores, ranging in size from 0.1 g to several hundred grams in weight. Rainforest fruits are largest in Africa, where the largest known frugivores occur (Mack, 1993; but see Dubost, 1968, 1987). However, few comparative studies of seed size and allometry have been conducted on a large biogeographic scale. Assuming that differences in mean body size exist between Old and New World frugivores, Mack (1993) predicted corresponding differences between fruits and seeds of these regions and suggested that selection for large seed size should be less constrained in the Old World than in the New World. Indeed, he found evidence that fruits were larger in the Palaeotropics than in the Neotropics, but he could only assume that there was a corresponding difference in seeds. In general, as seed size increases, the number of frugivores likely to disperse them by endozoochory decreases due to the physical constraints associated with transit (e.g. Pratt and Stiles, 1985; Hamann and Curio, 1999; Githiru *et al.*, 2002). However, seeds can change shape as well as size. Lord (2004) found that New Zealand fruit became more ellipsoid (elongate) with increasing size, allowing passage through the gut of smaller frugivores than would be possible with spherical fruits.

If the passage of seeds is constrained by gut diameter, then the elongation ratio of a seed (the ratio of length to width), in combination with the relative sizes of seed and frugivore, will determine whether it is swallowed and defecated or regurgitated or handled without swallowing. Therefore, selection on seed size and elongation imposed by disperser size may be dissipated by disperser behaviour. For example, small frugivores such as scatter-hoarding rodents may sometimes effectively disperse very large seeds by exozoochory (*sensu* Lobova and Mori, 2005; see also Forget and Vander Wall, 2001); seeds that might otherwise be dispersed by endozoochorous megafauna, either extinct or extant (Janzen and Martin, 1982; see Donatti *et al.*, Chapter 5, this volume).

Current patterns of fruit and seed allometry may represent the product of past selection pressures, and the fruits and seeds of extant plants could reflect selection exerted by now extinct dispersers and seed predators (Janzen and Martin, 1982; Eriksson *et al.*, 2000b; see Donatti *et al.*, Chapter 5, this volume). In addition, trans-oceanic dispersal of often large-seeded species (Dick *et al.*, 2003; Pennington and Dick, 2004; de

Queiroz, 2005) could also have led to colonization of islands and isolated continents where the original co-evolved fauna or alternative endozoochorous seed dispersers are absent. Both scenarios would lead to inconsistency between the frequency distributions of the sizes and shapes of fruits and seeds of extant plants and that of the body mass of the frugivores that consume and disperse them (see Donatti *et al.*, Chapter 5, this volume).

Given the myriad selection pressures on seed size, both past and present, can we detect an effect of dispersers on seed size? Does present-day animal size and gut diameter reflect seed size and shape? Paraphrasing Traveset *et al.* (2004), who focused on fruit traits, if frugivores have exerted major selection pressures on seed characteristics in recent history, then frugivore communities that differ in body size in different regions should produce different arrays of seed traits, despite similarities in geographical origin and phylogenetic relatedness. Alternatively, as stated by Kelly (1995), under the exaptation hypothesis, are current seed sizes and shapes the outcome of selection by a now-extinct fauna, which nevertheless remain adapted for dispersal by current frugivores? One way to examine these questions is to compare the distribution of seed sizes and shapes in communities from different continents with different suites of dispersers and different evolutionary histories.

Previous comparisons of tropical fruits have considered geographically restricted floras (e.g. Gabon – Gautier-Hion *et al.*, 1985; Costa Rica – Mazer and Wheelwright, 1993; Thailand – Peru – Kelly, 1995; Kitamura *et al.*, 2002) or floras in two regions (e.g. the Neotropics and Palaeotropics – Mack, 1993; see Corlett and Primack, 2006). The few existing intercontinental comparisons consider temperate floras (e.g. Herrera, 1992; Lord *et al.*, 1995; Edwards and Westoby, 1997; Lord, 2004; Traveset *et al.*, 2004, and references therein) and tropical-to-subtropical forest comparisons (Lord *et al.*, 1997). A worldwide cross-continental comparison of seed size and shape has never been attempted. If disperser size and gut transit capabilities influence seed size and shape then we might predict that the characteristics of a disperser assemblage may influence the general trends in these characters for a particular flora. Given the very different evolutionary histories of the world's tropical rainforest regions (see Corlett and Primack, 2006) and rapid selection for seed size when dispersers are lacking (see Kelly *et al.*, 2004), one might expect that because of long isolation and the recent disappearance of megafauna (see Donatti *et al.*, Chapter 5, this volume), seeds should be smaller and more elongate in tropical America, Asia and Australia than in Africa.

The goals of this chapter are to investigate whether geographically separated plant communities inhabited by frugivores with distinct frequency distributions for body size differ with respect to mean seed size or mean seed elongation. This assumes that endozoochorous dispersal exerts the strongest pressure on seed size and shape. However, exozoochory may relax the limitations on seed size and shape that endozoochory imposes, weakening selection to favour smaller or more elongate seeds in large-

seeded species and allowing smaller-bodied frugivores to disperse and select for large and round seeds that were initially adapted to endozoochory by larger now-extinct frugivores (Janzen and Martin, 1982). This could result in weaker patterns of difference between communities with large dispersers compared with communities with small dispersers. Despite this, we predict that a correspondence between seed size and shape and body size of dispersers, driven by constraints imposed by the passage of seeds through the gut, will be evident when comparing communities from different continents. This should result in:

1. Seeds being smaller and showing greater elongation on continents with smaller-sized dispersing faunas.
2. Plant communities occupied by large dispersers (e.g. megafauna) showing less evidence of constraints on seed diameter relative to those occupied by relatively small frugivores.
3. Guilds of dispersers (e.g. birds, bats, other mammals) differentially affecting selection on the set of seeds that they disperse, resulting in distinct seed size distributions among guilds on different continents.

To test these predictions, we compiled data on the shapes and sizes of seeds consumed and dispersed by frugivores in four neotropical and palaeotropical rainforests. We analysed the relationship between seed width and length, and we compared the mean size and shape of seeds across continents for whole communities and within groups of plants dispersed by particular guilds of animals.

Methods

Data compilation

We compiled a database on tropical plants with seeds known to be consumed and dispersed by frugivores from four rainforest floras on different continents: the Guianas (e.g. Guyane – also known as French Guiana; Suriname – formerly known as Dutch Guiana); Central Africa (e.g. Ivory Coast, Gabon, Cameroun, Uganda); Southern Thailand; and the wet tropics of Australia in Queensland (see Appendices 1 and 2). In some instances, we used data from reports in other countries when information was not available or complete for a region. For example, data for French Guiana included observations of spider monkeys from Suriname (van Roosmalen, 1985b) and Cuvier's toucans from Ecuador (K. Holbrook, Missouri, 2005, personal communication). Much of the data on seed size was obtained from botanical collections at four research stations: Arataye-Nouragues, French Guiana (Belbenoit *et al.*, 2001; Bongers *et al.*, 2001); Makokou, Gabon (Hladik *et al.*, 1987; A. Hladik, MNHN, Brunoy, 2005, personal communication); Khao Yai National Park, Thailand (Kitamura *et al.*, 2002); and the central Wet Tropics Bioregion, Australia (Dennis *et al.*, 2005; A.J. Dennis and D.A. Westcott, 2005, unpublished results). We also

obtained seed size data from the literature on frugivore gut content, including primary literature (Authors, 1961–2005; Jansen-Jacobs *et al.*, 1985–2003; van Roosmalen, 1985a; Vivien and Faure, 1996a,b; Mori *et al.*, 2002), from a thesis (Sabatier, 1983), from the Internet (van Roosmalen and van Roosmalen-Blijenberg, 2003; Mori and Lobova, 2005), and from personal communications (see Acknowledgements). In most instances, the specimens measured were from species whose consumers were known (see references in Appendices 1 and 2). Consumption of a fruit or seed was not treated as necessarily indicating successful dispersal; ‘consumption’ can also result in seeds being dropped and/or killed, since many seed dispersers are also seed predators (e.g. scatter-hoarding rodents, primates with cheek pouches).

Whenever possible, we took measurements (length and width to the nearest millimetre) of at least 5–10 seeds per species (range 1–30). For each species (including morphotypes), we calculated the mean length and width of a seed. Length and width included the two longest dimensions in a two-dimensional space, which are the major constraints to oral handling and gut transit by consumers (Mazer and Wheelwright, 1993). The third dimension, thickness or depth of seeds, was not used because: (i) it is rarely mentioned in flora or studies; (ii) it often equals width; and (iii) it rarely (if ever) constrains oral handling or gut transit. Data were included only for those records that were identified to species level or included referenced morphospecies. This was particularly important for studies relying on gut content, where identification was often uncertain (e.g. Dubost, 1984; Erard *et al.*, 1989a; Henry *et al.*, 2000). Nomenclature was revised according to the International Plant Name Index (Anonymous, 2004). Our data set is not exhaustive, but instead is a sample of plant species that may be consumed by each animal inhabiting a given forest. Therefore, it is representative of the sizes of seeds harvested and potentially transported by animals.

We extracted two subsets of the original database. In the first, which we named the Plant Data Base (PDB), we pooled all the data from frugivore diets within each continent in order to compare rainforest floras. In the second, the Animal Data Base (ADB), we pooled all species according to their occurrence in the diets of members of different frugivore groups (e.g. volant birds, arboreal mammals, ruminants/ungulates). Therefore, in the ADB each individual species of plant may be listed more than once if it is dispersed by more than one group of frugivores. Most of our frugivore groups were based on high-level taxonomy (e.g. Order or higher; see Table 1.5). However, some groups were less taxonomically constrained. For example, our megafauna group includes the tapir (*Tapirus terrestris*; Tapiridae), cassowary (*Casuaris casuaris*; Casuaridae) and elephant (*Loxodonta africana*; Elephantidae), which we consider comparable, as they all swallow very large items and pass them intact. This differentiates the group from ruminants/ungulates, which either spit out or chew large seeds (e.g. Feer *et al.*, 2001). In addition, all arboreal mammals are pooled. This group includes, and is

dominated by, scansorial and arboreal primates, but also includes carnivores and marsupials.

In this chapter we present a summary of seed traits across continents based on species in the diets of neo- and palaeotropical animals. These animals range in size from a weight of several grams (manakins) to several tonnes (elephant). Body mass data are from Gautier-Hion *et al.* (1999) and C. Erard (MNHN, 2005, personal communication) for Central Africa; Emmons and Feer (1990) and a few other sources (see Appendix 2) for the Guianas; Kitamura *et al.* (2002) for Thailand; and A.J. Dennis and D.A. Westcott (unpublished data), Strahan (1995); Baker *et al.* (1997) and Dennis (1997) for Australia. Values for body mass are the average for males and females. Mean weights for all species in our samples, and within guilds, were compared between locations using log-transformed values and ANOVA but excluding animals weighing >100 kg from the whole-community analysis. Animals of this size, including *Gorilla gorilla* (Hominidae), *Loxodonta africana*, *Tapirus terrestris*, *Cervus unicolor* (Cervidae) and *Elephas maximus*, were excluded due to their disproportionate impact on the means.

Analyses

Relationship between size and elongation in seeds

There are two ways to investigate the allometry of seed size across continents. The first approach is based on an ecological or 'static' perspective, examining the bivariate relationship between seed size and shape among extant species in which seeds are dispersed by animals. In this approach, each phenotype represents an independent data point, regardless of its relationship to other species in the data set. This approach asks the question: Do seed width and length increase proportionally or is there evidence that seed diameter is constrained relative to changes in seed length? For these 'cross-species' analyses, we regressed seed width against seed length using log-transformed data (to improve normality) and standardized, major-axis regressions, with the software utility SMATR (Warton *et al.*, 2006, <http://www.bio.mq.edu.au/ecology/SMATR>). When the resulting slope is <1.0 and the 95% confidence interval does not overlap with 1.0, the relationship is one of 'negative allometry', indicating that seed width increases more slowly than seed length. Negative allometry supports the hypothesis that large seeds have evolved greater elongation in response to constraints imposed by their dispersers.

The second approach is based on an evolutionary perspective and incorporates the phylogenetic relatedness of plants in a given community. It examines the correlated evolution of length and width among frugivore-dispersed seeds. This approach also asks: 'Do seed width and length increase proportionally?' but uses phylogenetically independent contrasts (PICs; Felsenstein, 1985; Harvey and Pagel, 1991) to examine this relationship without the complication of particular families or genera

driving observed patterns. This approach necessarily results in fewer data points than the ecological or static approach because only cases in which closely related taxa have diverged will contribute a 'contrast' to the data set. We expect that if seed length and width evolve at the same rate, a 50% increase in length would be accompanied by a 50% increase in width: an isometric relationship. However, if gut diameter places an upper limit on the width of seeds that can be swallowed and dispersed, then we would expect that an increase in length would be accompanied by a proportionally smaller increase in width.

To use this approach, we compiled data by identifying evolutionary divergences between pairs of closely related taxa (measured as phenotypic differences). These divergences were identified after mapping trait values on a cladogram which represented the phylogenetic relationships between co-occurring species of plants. We used *Phyloomatic* (Webb and Donoghue, 2005) to construct pruned cladograms for the angiosperm communities in each of our four study regions. The cladograms were pruned (or incomplete) because they only contained data on species that were known to occur in the diets of animals in each area. They represent relationships among the included taxa based on the dynamic, family-level phylogeny available online (Stevens, 2004), a hypothesized relationship between species. Given that the precise phylogenetic relationships among many species and genera within families are unknown, confamilial genera and congeneric species are often represented as polytomies on the resulting tree. Nevertheless, among many of the included taxa, phenotypic divergences between pairs of confamilial and/or congeneric taxa were identified.

We used the 'Analysis of Traits' module (version 3.0; Ackerly, 2004) in *Phylocom* version 3.22 (Webb *et al.*, 2004) to identify phylogenetically independent contrasts within each phylogenetic tree. The values of each independent contrast for seed length and width were calculated at each node where the pair of descendent taxa differed in either trait. The trait values of internal nodes were estimated using a weighting procedure that assumes that traits evolve by Brownian motion (Felsenstein, 1985). The treatment of polytomies is described by Ackerly (2004).

To maintain consistency in the bivariate relationship, we consistently subtracted the phenotypic value of the taxon or node with the shorter seed(s) from that with the longer seed(s), which yields contrasts for seed length that are always positive. The corresponding contrast for seed width could, in theory, be either positive or negative. Generally, though, where seed length increased between two taxa or nodes, seed width did as well.

Once divergences were identified and contrasts calculated, we regressed seed width against length using log-transformed data (to improve normality) and standardized, major-axis regressions (using *SMATR*) and fitting regression lines forced through the origin (Garland *et al.*, 1992; Warton *et al.*, 2006). As with the previous analysis, a slope significantly <1.0 suggests that evolutionary changes in seed width are constrained relative to those in seed length, and that larger seeds are more elongate than smaller ones.

Seed attributes across rainforests and frugivore guilds

Using ANOVAS, we tested whether the mean seed length and the width : length ratio (W:L estimates roundness) across all species differed between rainforests and frugivore guilds on different continents. Following Mazer and Wheelwright (1993) and Mack (1993), we used one dimension and one index to analyse size and shape of seeds harvested by animals. They were: (i) length (L; mm), which is an indication of seed size and is highly correlated with width (handling constraint); and (ii) the W:L ratio, a measure of roundness and gut transit constraints. Values of W:L range between 0 and 1; when width equals length, W:L is 1 and the seed is spherical. The greater the deviation of W:L from 1, the greater the elongation of a seed. Seed length was log-transformed and W:L ratios were square-root-transformed for ANOVA. Species were nested within genus and family for each continent (see Appendix 1).

Results

We compiled seed size and shape data (PDB) for 1558 species and morphospecies belonging to 650 genera and 119 families which were consumed by frugivores in four neo- and palaeotropical rainforests (Appendix 1). We also compiled records of plant species with seeds consumed by a total of 154 species in the four rainforests (Appendix 2).

Disperser sizes on different continents

The disperser assemblages sampled in this analysis differed between continents in the distributions of weights (Fig. 1.1). Australia had a much higher frequency of small-sized dispersers than the other locations. The Guianas had a more even distribution of body sizes up to about 100 kg but lacked very large species. Central Africa and Thailand were the most similar. Australia had a mean disperser weight statistically less than that of Central Africa (Fig. 1.2; $F_{(3, 143)} = 6.92$, $P < 0.001$, Tukey HSD) but a trend was also evident, with Central Africa > the Guianas ~ Thailand > Australia.

Birds sampled from Africa and Guiana were heavier than those from Thailand and Australia ($F_{(3, 71)} = 7.81$, $P < 0.001$). Bats were lighter in the Neotropics (Guiana) than in parts of the Palaeotropics (Africa and Australia; $F_{(2, 10)} = 7.57$, $P < 0.01$). Similarly, primates were lighter in the Neotropics than in parts of the Palaeotropics (Africa and Thailand), although this was only marginally significant ($F_{(2, 19)} = 3.42$, $P = 0.054$). Rodent and ruminant/ungulate groups did not differ between regions ($F_{(3, 19)} = 2.15$, $P = 0.13$ and $F_{(2, 7)} = 0.39$, $P = 0.69$, respectively). The largest dispersers were elephants in Africa and Thailand, tapir in the Guianas and cassowary in Australia.

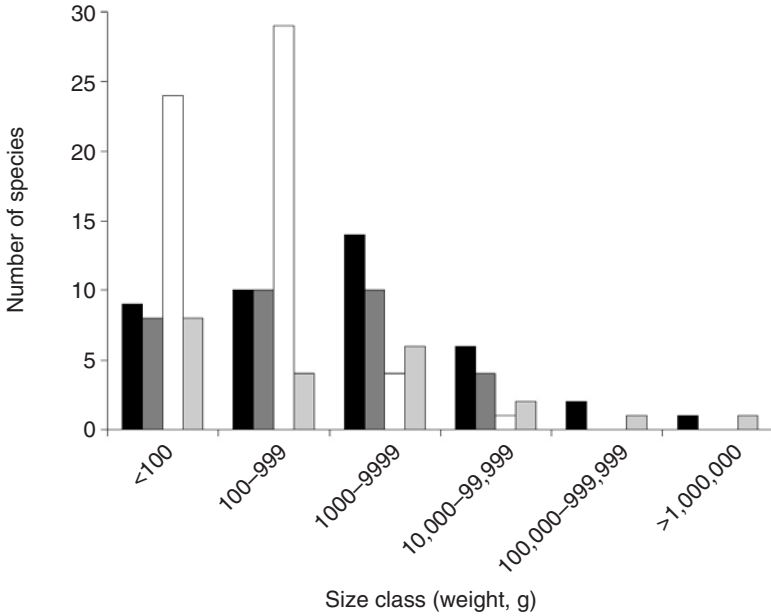


Fig. 1.1. The number of species of disperser known to consume fruits and seeds in different size classes (weight, g) in our databases for Central Africa (black bars), the Guianas (dark grey bars), Australia's wet tropics (white bars) and Thailand (light grey bars).

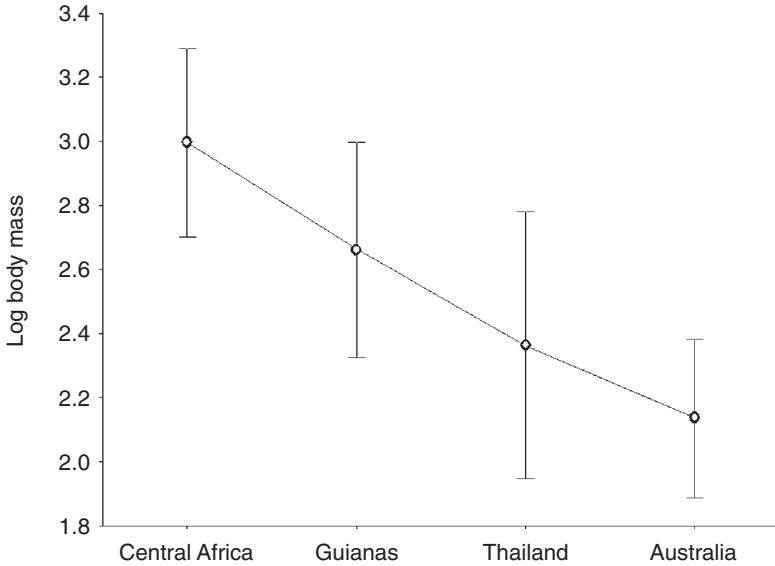


Fig. 1.2. Mean body mass (log-transformed) of disperser communities for our sample floras in Central Africa, the Guianas, Thailand and Australia, excluding species over 100 kg.

Relationship between size and elongation in seeds

The relationship between seed width and seed length differed among floras, and the differences depended on the analysis conducted. The cross-species analyses were more likely to detect evidence of negative allometry than were the PIC analyses (Table 1.1; Figs 1.3 and 1.4).

Among the cross-species analyses, the slope of the regression of $\log(\text{seed width})$ on $\log(\text{seed length})$ was significantly <1.0 in Central Africa and in Thailand (Fig. 1.3; Table 1.1): longer-seeded species were more elongate than shorter-seeded species. In contrast, seed width increased significantly more rapidly than seed length in the Guianan flora (the slope was significantly >1.0), meaning that large seeds were more spherical than small seeds. In Australia's wet tropical flora, width and length increased isometrically, so seeds retained a similar shape independent of size.

PIC analyses revealed similar patterns, although fewer results were significant. Large seeds were more elongate than small seeds only for species from Thailand (Table 1.1; Fig. 1.4; $s = 0.942$; 95% CI 0.890–0.997). In the three other regions, seed length increased either isometrically with width (Central Africa and Australia) or evolutionary increases in seed length were accompanied by disproportionately large increases in seed width (the Guianas).

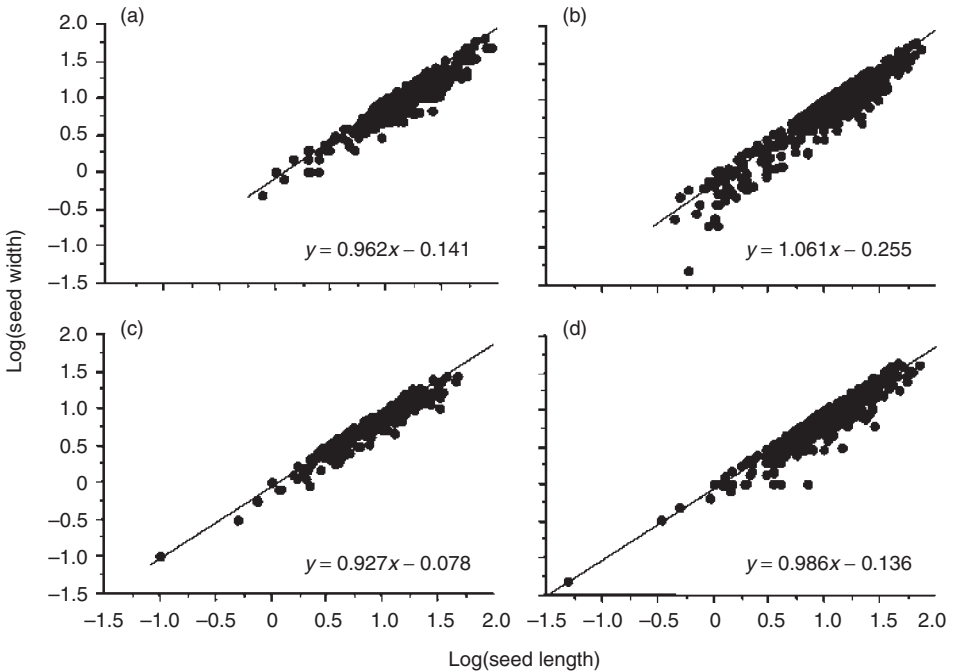


Fig. 1.3. Standardized major axis regressions of the cross-species analysis for $\log(\text{seed length})$ versus $\log(\text{seed width})$ in tropical rainforest seeds from (a) Central Africa, (b) the Guianas, (c) Thailand and (d) Australia.

Table 1.1. Relationship between seed width and seed length for species of plants dispersed by animals in four rainforests on different continents. Summary of the standardized major-axis regressions of the cross-species means (intercept unconstrained; see Methods) and the phylogenetically independent contrasts (PICs; intercept forced through origin) for log(seed width) versus log(seed length). Slopes with 95% confidence intervals that remain below 1.0 indicate that larger seeds are more elongate than smaller seeds. $P < 0.05$ indicates regressions in which the slope is significantly different from 1.0 and these have a slope summary in bold type.

Continent	n^*	Slope	Slope summary	95% CI	R^2	Intercept (CI)	P value of $H_0 : s = 1$
<i>Cross-species</i>							
Central Africa	304	0.962	$s < 1$	0.932–0.993	0.922	–0.141 (–0.177 – –0.104)	0.0167
Guianas	556	1.061	$s > 1$	1.035–1.088	0.913	–0.255 (–0.284 – –0.226)	< 0.0001
Thailand	250	0.927	$s < 1$	0.901–0.952	0.95	–0.078 (–0.102 – –0.054)	< 0.0001
Queensland	442	0.986	$s = 1$	0.959–1.012	0.918	–0.136 (–0.163 – –0.108)	0.2893
<i>PICs</i>							
Central Africa	122	1.001	$s = 1$	0.941–1.065	0.881	0	< 0.0001
Guianas	202	1.092	$s > 1$	1.032–1.155	0.836	0	0.0025
Thailand	122	0.942	$s < 1$	0.890–0.997	0.90	0	0.0416
Queensland	174	1.001	$s = 1$	0.946–1.059	0.86	0	0.9810

* Number of species for cross-species regression, number of contrasts for PIC-based regression.

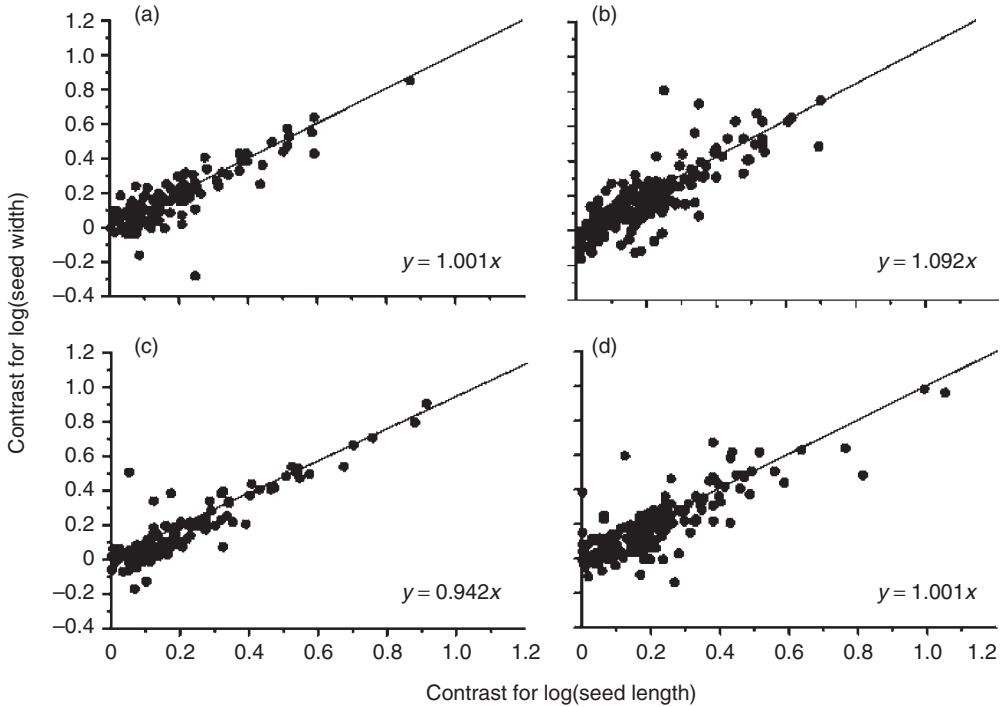


Fig. 1.4. Standardized major axis regressions for the phylogenetically independent contrasts (PICs) of log(seed length) versus log(seed width) in tropical rainforest seeds from (a) Central Africa, (b) the Guianas, (c) Thailand and (d) Australia.

Seed attributes across rainforests on different continents

Length of seeds consumed by frugivores differed significantly among rainforests ($F_{(3, 1180)} = 22.114$, $P < 0.001$). Species in Central Africa had significantly longer seeds (mean 19 mm) than species in the Guianas (14.9 mm), Australia (12.8 mm) and Thailand (10.1 mm) (Fig. 1.5a; post hoc Bonferroni test: Central Africa > Guianas = Australia > Thailand; see grand mean for all families in Table 1.2). Seed roundness was also significantly different among continents ($F_{(3, 1180)} = 15.302$, $P < 0.001$); species in Thailand and Australia had significantly rounder seeds than species in Central Africa and the Guianas (Fig. 1.5b; see grand mean in Table 1.2).

Following Mack (1993), we also compared seed traits across pantropical plant families (Table 1.2). Overall, eight of 12 families showed significant ($P < 0.05$) or marginally significant ($P < 0.1$) differences in seed size across rainforests and continents (Table 1.3). For instance, seeds in the families Annonaceae and Sapotaceae had significantly longer seeds in Central Africa than in the Guianas, and Arecaceae seeds were longer in Central Africa than in Australia. In contrast, Moraceae and Rubiaceae had

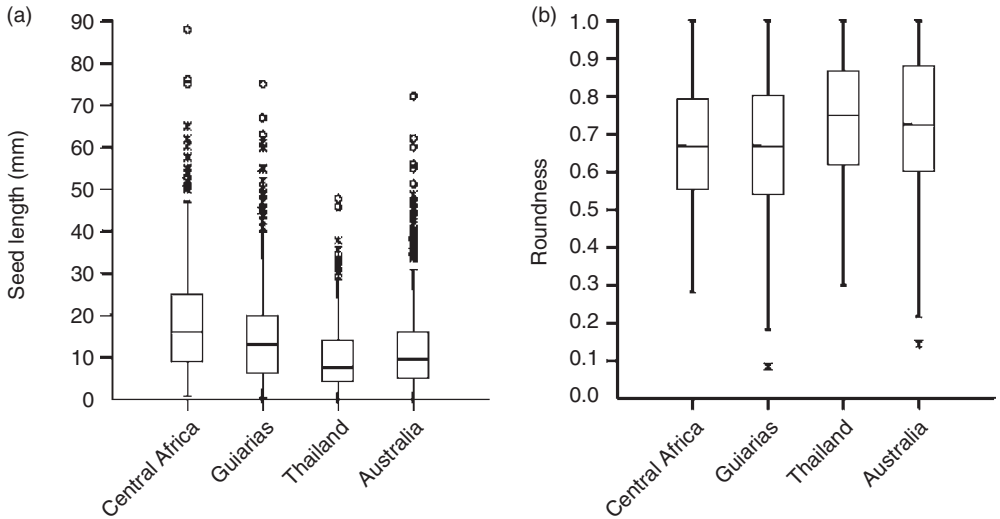


Fig. 1.5. Comparative length (a) and roundness (b) of seeds consumed and dispersed by frugivores in four rainforests from different continents. Box plot showing the median of the sample: each box shows the range within which the central 50% of the values fall, with the box edges at the first and third quartiles. Values between the inner and outer fences are plotted with asterisks, and outside values are plotted with empty circles.

longer seeds in the Guianas than in Central Africa, and Euphorbiaceae were smaller in Australia than in the three other continents. Anacardiaceae, Lauraceae, Meliaceae and Myristicaceae did not differ across continents (all $P > 0.05$ for both L and W:L). Clusiaceae had rounder seeds in Australia than in the Guianas ($P = 0.026$) but no other family differed in seed shape among continents (all W:L < 0.6).

Seed attributes across frugivore guilds

Bats

Fruits consumed by neotropical bats fall into two classes for which seed size and shape are not equally constrained: (i) those with seeds that are swallowed and defecated (endozoochory); or (ii) those carried away in the mouth (exozoochory). As an example, in the Guianas, endozoochorous seeds average 2×1.3 mm (L range 0.5–7 mm, $n = 71$), while exozoochorous seeds average 25.3×17 mm (L range 6.0–63 mm, $n = 83$). We found no difference in seed length or shape among any of the three continents tested for either of these two classes (no data available for Thailand; all $P > 0.452$; Table 1.4). We then pooled the data across classes and retested; again, neither size nor shape differed across continents (Table 1.5). The species dispersed by bats ranged from those with minute seeds such as *Clidemia octona* (Melastomataceae; 0.5×0.3 mm) and

Table 1.2. Seed dimensions and shape for species of plant from four rainforests on four continents for each of 12 pantropical families and the grand mean for all families (CA – Central Africa; GA – the Guianas; TH – Thailand; AU – Australia’s wet tropics). Values with the same superscript letters indicate those values that were not significantly different in Bonferroni post hoc tests when P was significant ($P < 0.05$).

Plant family	Mean length (mm)					Average roundness (W:L)					No. spp.			
	CA	GA	TH	AU	P	CA	GU	TH	AU	P	CA	GU	TH	AU
Anacardiaceae	24.3	19.7	23.1	13.9	0.500	0.665	0.708	0.719	0.818	0.104	11	4	5	4
Annonaceae	17.1 ^a	12.1 ^b	15.1 ^{ab}	14.4 ^b	0.019	0.588	0.655	0.674	0.685	0.169	30	21	14	8
Arecaceae	31.4 ^a	20.9 ^a	20.0 ^{ab}	13.0 ^a	< 0.001	0.760	0.781	0.704	0.794	0.967	6	16	3	13
Clusiaceae	27.1	13.8	25.1	22.2	0.378	0.627 ^{ab}	0.509 ^a	0.511 ^{ac}	0.784 ^{bc}	0.029	7	17	2	4
Euphorbiaceae	12.6 ^a	13.0 ^a	5.6 ^b	10.4 ^a	< 0.001	0.774	0.710	0.818	0.808	0.065	23	14	18	15
Lauraceae	35.8	17.0	14.7	22.2	0.273	0.610	0.739	0.668	0.745	0.257	3	12	15	53
Meliaceae	14.1	20.7	18.9	16.4	0.082	0.675	0.662	0.737	0.636	0.645	7	10	10	16
Moraceae	4.2	6.7 ^b	3.2 ^a	1.9 ^a	< 0.001	0.920	0.804	0.864	0.695	0.195	11	28	21	25
Myristicaceae	24.2	21.6	21.3	17.3	0.596	0.665	0.711	0.718	0.802	0.405	5	17	2	2
Rubiaceae	4.0 ^a	7.5 ^b	5.3 ^a	4.8 ^a	< 0.001	0.754	0.744	0.665	0.658	0.707	17	14	26	11
Sapindaceae	19.8 ^a	12.6 ^{ab}	14.8 ^{ab}	12.9 ^b	0.011	0.569 ^a	0.764 ^b	0.768 ^b	0.715 ^b	0.044	8	13	7	25
Sapotaceae	26.6 ^a	19.4 ^b	16.5 ^{ab}	20.7 ^{ab}	0.052	0.575	0.571	0.635	0.610	0.771	21	41	2	15
Grand mean	20.2 ^a	12.7 ^b	12.0 ^c	11.8 ^b	< 0.001	0.682 ^a	0.652 ^a	0.732 ^b	0.747 ^b	< 0.001	54	70	61	75

Table 1.3. A comparison of seed length and shape across rainforest floras on different continents with genera nested within family. Significant differences among continents are indicated with Tukey post hoc probabilities between brackets (CA – Central Africa; GU – Guianas; TH – Thailand; AU – Australia’s wet tropics).

Family*	df	Length (mm)		Observed trends	Roundness		Observed trends
		F	P		F	P	
Anacardiaceae	3,8	0.859	0.500		2.864	0.104	
Annonaceae	3,31	3.835	0.019	CA > GU (0.032)	1.794	0.169	
Arecaceae ^a	3,12	12.821	< 0.001	CA = GU > AU (0.001)	0.085	0.967	
Clusiaceae ^a	2,13	1.051	0.378		4.134	0.029	GU < AU (0.026)
Euphorbiaceae ^a	3,42	13.231	< 0.001	CA = GU = AU > TH (0.01)	2.741	0.065	
Lauraceae ^{a,b}	2,65	1.326	0.273		1.387	0.257	
Meliaceae	3,25	2.502	0.082		0.562	0.645	
Moraceae ^a	3,59	12.997	< 0.001	GU > CA = TH = AU (0.04)	1.618	0.195	
Myristicaceae	3,16	0.647	0.596		1.031	0.405	
Rubiaceae ^a	3,28	16.882	< 0.001	GU > CA = AS = AU (< 0.001)	0.468	0.707	
Sapindaceae	3,21	3.032	0.052	CA > AU (0.042)	3.204	0.044	CA < GU (0.056)
Sapotaceae ^{a,b}	3,52	4.061	0.011	CA > GU (0.011)	0.376	0.771	

* Significant effect ($P < 0.05$) of Genus nested within Family and Continent for ^a Length and ^b Roundness.

Table 1.4. Seed size and shape for species of plant consumed by different frugivore guilds, for each of four rainforests on different continents, with seed treatment and body mass of the frugivores.

Group	Rainforest/ animal	Treatment*	Body mass (g)	Mean length (mm)				Mean width (mm)				Average roundness (W:L ratio)	No. spp.
				sd	Min.	Max.	sd	Min.	Max.				
Bats	Central Africa	C – Sw	250–300	18.2	19.4	1.0	88.0	13.1	14.0	0.8	65.0	0.720	37
	Guianas	C – Sw	15–70	13.2	14.4	0.5	63.0	8.8	10.0	0.2	40.0	0.668	155
	Australia	C – Sw	700	13.3	13.4	0.5	60.0	9.2	9.2	0.5	35.0	0.698	49
Volant birds	Central Africa	R – Sw	250–1,300	18.0	8.3	3.4	40.7	11.3	4.8	3.1	23.6	0.663	53
	Guianas	P – Sw	13–3,000	12.9	7.9	0.5	45.0	8.7	5.0	0.3	28.0	0.701	191
	Thailand	R – Sw	<50–3,000	9.1	7.5	0.1	35.6	6.1	4.4	0.1	20.3	0.744	151
	Australia	P – R – Sw	10–2,270	9.2	7.2	0.1	40.4	6.5	5.3	0.1	35.0	0.737	311
Arboreal mammals	Central Africa	P – Sw – Sp	1,100–175,000	18.7	14.2	0.8	88.0	12.0	9.9	0.5	60.8	0.673	222
	Guianas	P – Sw	300–10,500	14.9	9.4	0.5	67.0	9.5	6.4	0.2	60.0	0.652	326
	Thailand	P – Sw – Sp	4,000–9,000	12.8	9.1	0.1	47.8	8.2	5.2	0.1	27.7	0.715	86
Rodents	Central Africa	Ca – P	20–1,000	23.8	15.6	1.0	76.2	16.0	11.5	1.0	60.8	0.686	111
	Guianas	Ca – P	35–3,500	24.7	15.5	1.3	75.0	16.9	11.8	0.5	60.0	0.684	124
	Thailand	Ca – P	300–1,400	13.9	10.2	0.1	47.8	9.0	6.1	0.1	27.7	0.718	103
	Australia	Ca – P	80–650	22.3	13.6	1.5	56.0	16.8	11.4	1.0	41.9	0.734	56
Terrestrial marsupials	Australia	C – Ca – P – Sw	520–4,500	26.1	14.6	2.1	62.1	20.1	11.6	1.0	42.3	0.772	56
Ruminants/ ungulates	Central Africa	P – Sp – Sw	4,900–68,000	21.8	14.1	1.0	76.2	14.5	10.1	1.0	51.4	0.679	123
	Guianas	P – Sp – Sw	16,000–44,000	16.7	9.7	1.3	45.5	11.0	6.3	0.5	35.0	0.675	91
	Thailand	P – Sp – Sw	24,000–222,500	17.5	10.6	0.1	47.8	10.6	6.1	0.1	27.7	0.658	46
Megafauna	African elephant	P – Sw	5,000,000	26.6	17.4	0.8	88.0	17.2	11.7	0.5	51.4	0.667	81
	Brazilian tapir	Sw	250,000	18.3	13.7	1.5	55.0	12.1	9.5	0.9	45.0	0.668	30
	Asian elephant	Sw	4,000,000	17.9	11.2	1.0	30.2	11.3	7.4	1.0	22.9	0.673	9
	Cassowary	Sw	60,000	16.3	13.1	0.1	72.2	11.6	9.5	0.1	41.7	0.732	228

*Seed treatment: C – carried; Ca – cached; P – predated; R – regurgitated; Sw –swallowed; Sp – spat.

Table 1.5. Results of ANOVA showing differences in seed length and shape among rainforests on different continents for species of plants consumed by different groups of animals (species nested within genus and family). Significant differences are indicated in parentheses with probabilities from Tukey post hoc tests; CA – Central Africa; GU – Guianas; TH – Thailand; AU – Australia's wet tropics.

Guild	df	Length (mm)		Contrast	Roundness		Contrast
		F	P		F	P	
Bats	2,213	1.828	0.163		1.475	0.231	
Birds	3,541	22.923	0.000	CA > GU > TH = AU (< 0.004)	4.901	0.02	CA = GU < TH = AU (0.045)
Arboreal mammals	2,441	4.634	0.010	CA > TH (0.007)	2.664	0.071	
Rodents	3,293	16.707	< 0.001	CA = GU = AU > TH (< 0.001)	2.241	0.084	
Ruminants/ungulates	2,180	1.488	0.233		0.234	0.791	
Megafauna	2,345	10.032	< 0.001	CA > AU (< 0.001)	5.136	0.005	CA < AU (0.013)

Pothomorphe peltata (Piperaceae; 0.5×0.5 mm) up to large stones such as *Dipteryx odorata* (Fabaceae; 60×35 mm) and *Caryocar villosum* (Caryocaraceae; 55×39 mm) in the Guianas, and *Balanites wilsoniana* (Zygophyllaceae; 88×47 mm) in Central Africa. Shape ranged from seeds as round as *Andira coriacea* (Fabaceae; W:L ratio = 1.0) to elongated ones such as those of *Dipteryx* spp. (Fabaceae; W:L ratio = 0.57).

Volant birds

In contrast to bats, and despite comparable body mass range (Table 1.4), both the length and shape of seeds consumed by birds differed significantly across continents (Table 1.5). Species consumed by birds had larger seeds in Central Africa than in the Guianas, and these were in turn larger than those of Thailand and Australia (Table 1.5). Seeds in Central Africa and the Guianas were more slender than those consumed by birds in Australia and Thailand. In Central Africa, the largest seed was dispersed by hornbills (*Annonidium mannii*, Annonaceae; 41×24 mm); in Ecuador by toucans, *Rhamphastos cuvieri* (*Iryanthera grandis*, Myristicaceae; 45×28 mm). In Thailand and Australia, *Canarium euphyllum* (Burseraceae; 36×17 mm) and *Endiandra sideroxylon* (Lauraceae; 40×22 mm), respectively, had the largest dimensions for seeds dispersed by volant birds. A seed length of approx. 40 mm appears to reflect an upper threshold size limit for dispersal by volant birds.

Arboreal mammals

Species of plants with fruits consumed by this group had larger seeds in Central Africa (18.7 mm in length) than in the Guianas (14.9 mm) and Thailand (12.8 mm), although only the difference between Thailand and Central Africa was significant ($P = 0.007$; Table 1.5). Seeds from fruit consumed by arboreal mammals in Thailand were marginally rounder than those in Central Africa and the Guianas ($P = 0.07$; Table 1.5). It appears that even the largest scansorial frugivores, such as *Pan paniscus* (Hominidae) and *Gorilla gorilla*, do not swallow large seeds (> 30 – 40 mm). Instead, they extract the pulp and reject the seeds of fruits with large seeds or nuts such as *Baillonella toxisperma* (Sapotaceae; 58×34 mm), *Panda oleosa* (Pandaceae; 54×38 mm), *Diospyros manii* (Ebenaceae; 52×23 mm) and *Parinari holstii* (Chrysobalanaceae; 52×42 mm). The largest-seeded species dispersed via endozoochory and defecated by arboreal mammals were *Platonia insignis* (Clusiaceae; 42×24 mm), *Gnetum* spp. (Gnetaceae; 40×20 mm) and *Dussia discolor* (Fabaceae; 36×21 mm) in the Guianas. In contrast, large seeds of *Elaeagnus latifolia* (Elaeagnaceae; 33×10 mm) and *Beilschmiedia maingayi* (Lauraceae; 32×14 mm) in Thailand and a wide range of species with seed length 20–42 mm in Central Africa are spat out after processing. The contrast in seed shape and size across neo- and palaeotropical primates will be further analysed in another study (P.-M. Forget et al., 2006, unpublished results).

Rodents

Large rodents are well documented as seed dispersers in the Guianas and Australia (Forget and Vander Wall, 2001; Theimer, 2001), but little is known about the role of large rodents as seed dispersers in Central Africa (but see Ewer, 1965; Emmons, 1980) and Thailand (but see Yasuda *et al.*, 2000; Kitamura *et al.*, 2004). Because rodents hoard the same species they consume, we consider them seed dispersers despite the frequent high cost of seed loss to the plants. Seeds taken by rodents appeared to be smaller in Thailand ($L = 14$ mm) than in the three other continents ($L > 22$ mm; $P < 0.001$), which may be an artefact of the smaller mean seed size in Thailand. In Central Africa, the range of seed sizes harvested by rodents overlapped with that of seeds handled by primates, fruit bats and elephants (Tables 1.4 and 1.5). Seeds taken by rodents in Central Africa and the Guianas were very similar in shape but marginally more elongate than those in Australia and Thailand ($P = 0.08$; Table 1.5). In the Guianas, dasyproctid rodents are dispersers of large seeds such as *Parinari montana* (75×48 mm), *Couepia bracteosa* (Chrysobalanaceae; 63×40 mm), *Dipteryx odorata* (60×35 mm), *Attalea maripa* (Arecaceae; 55×28 mm) and *Caryocar villosum* (Caryocaraceae; 55×39 mm). In Central Africa, a large terrestrial squirrel *Epixerus ebii* (Sciuridae; Emmons, 1980) and the nocturnal rodent *Cricetomys emini* (Muridae; Debroux, 1988) may disperse seeds of comparable size, such as *Baillonella toxisperma*, *Panda oleosa*, *Parinari holstii* (52×42 mm) and *Irvingia grandifolia* (Irvingiaceae; 45×22 mm; Emmons, 1982; Debroux, 1998). In Australia, *Endiandra xanthocarpa* (56×29 mm), *Beilschmiedia bancroftii* (49×42 mm) and *Syzygium gustavioides* (Myrtaceae; 47×42 mm) are among the largest-seeded species scatter-hoarded by rodents such as *Uromys caudimaculatus* (Muridae). In Thailand, the largest seeds taken by rodents overlap with those dispersed by primates.

Ground-dwelling marsupials

Overall, seeds swallowed or carried by ground-dwelling marsupials in Australia were large (mean = 26×20 mm) and round (Table 1.4). Data for this group were dominated by a single species, the musky rat-kangaroo, *Hypsiprymnodon moschatus* (Hypsiprymnodontidae), which carries and disperses relatively large seeds (mean = 22.6×18.5 mm; $n = 48$). These animals scatter-hoard fruits and seeds and play a comparable ecological role to that of large rodents in dispersing large-seeded species that sometimes lack alternative dispersal modes, although usually with less seed consumption than large rodents (Dennis, 2003).

Ruminants/Ungulates

Seeds consumed by ruminants in the Palaeotropics and by ungulates in the Neotropics usually do not survive passage of the digestive tract. However, seeds with hard integuments may be spat out and dispersed. For this guild

of consumers, there was no significant difference in seed allometry across three rainforests (Tables 1.4 and 1.5).

Modern megafauna

Finally, we independently considered the three largest ground-dwelling frugivores: the tapir, *T. terrestris*, in the Guianas (insufficient data for Thailand), the elephant, *L. africana*, in Central Africa (insufficient data for Thailand, but see Williams, 1978), and the cassowary, *C. casuarius*, in Australia. Along with the rhinoceros (Dinerstein and Wemmer, 1988; Dinerstein, 1991), these are the only species likely to play a role as megafauna seed dispersers (*sensu* Janzen and Martin, 1982). Seeds dispersed by *L. africana* were larger and more slender than seeds dispersed by *T. terrestris* or *C. casuarius* (Tables 1.4 and 1.5; Fig. 1.6). In Central Africa, the largest elephant-dispersed seeds were *Balanites wilsoniana*, *Tieghemella africana* (Sapotaceae; 65 × 35 mm), *Detarium macrocarpum*, *Baillonella toxisperma*, *Maranthes glabra* (Chrysobalanaceae; 55 × 33 mm), *Panda oleosa* and *Raphia leptobothrys* (Arecaceae; 54 × 34 mm), some of which were also listed as dispersed by bats, primates and rodents. Similarly, many seeds dispersed by *T. terrestris* in the Guianas, including large palm nuts such as *Attalea maripa* (55 × 28 mm), *Mauritia flexuosa* (Arecaceae; 45 × 45 mm), *Astrocaryum paramaca* (Arecaceae; 33 × 19 mm) and *Jessenia bataua* (Arecaceae; 32 × 20 mm), were also

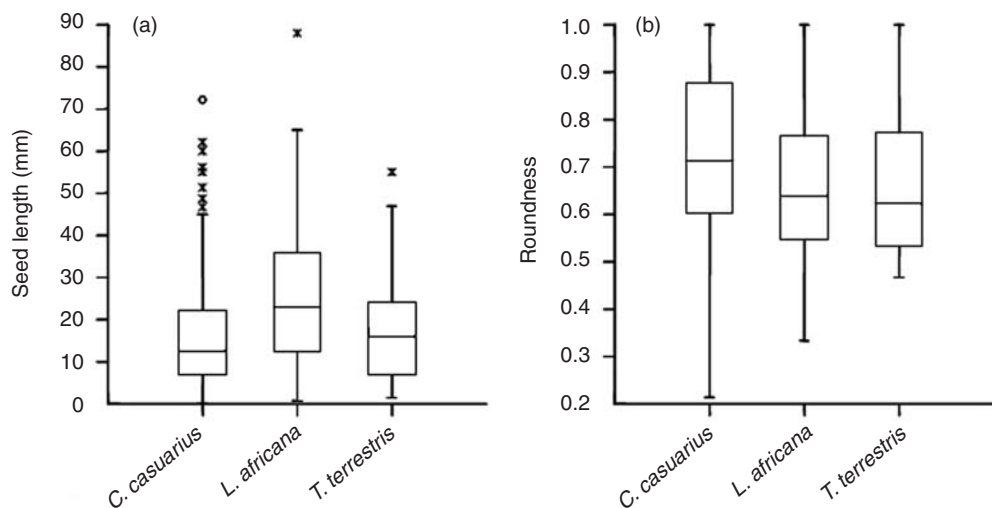


Fig. 1.6. Comparative length (a) and roundness (b) of seeds consumed and dispersed by three megafauna species (the cassowary, *C. casuarius*, in Australia; the elephant, *L. africana*, in Africa; the tapir, *T. terrestris*, in the Guianas) in three rain forests on different continents. Box plot showing the median of the sample: each box shows the range within which the central 50% of the values fall, with the box edges at the first and third quartiles. Values between the inner and outer fences are plotted with asterisks, and outside values are plotted with empty circles.

dispersed by scatter-hoarding Dasyproctid rodents. In Australia, species dispersed by *C. casuarius*, such as *Endiandra microneura* (62 × 33 mm) and *Elaeocarpus stellaris* (Elaeocarpaceae; 51 × 38 mm), on the one hand, and *Beilschmeidia bancroftii* (49 × 42 mm) on the other, are also scatter-hoarded by *H. moschatus* and *U. caudimaculatus*, respectively, while *Terminalia catappa* (Combretaceae; 60 × 35 mm) appears to be dispersed by both *C. casuarius* and the flying fox, *Pteropus* spp.

Discussion

The flora with the largest mean seed size, that of Central Africa, exhibited negative allometry, suggesting that the larger-seeded species were constrained with respect to their diameters (cross-species analysis; see Table 1.1; Fig. 1.1). This is surprising given the availability of megafauna in Africa, as well as the large size of its bats, primates and ruminants. However, while large seeds are more elongate today, there was no evidence that selective pressures created elongate seeds; the PIC analysis demonstrated that seed shape remained similar between small and large seeds within taxonomic groups (Table 1.1; Fig. 1.4). This suggests that taxa with elongate seeds encountered no constraints as larger seed sizes were selected for.

The sampled flora of southern Thailand, on the other hand, exhibited negative allometry in both static and evolutionary contexts (Table 1.1; Figs 1.3 and 1.4), suggesting strong constraints on seed shape both present and past. In addition, Thailand had a relatively small mean seed size despite the availability of large volant birds, primates and, potentially, elephants and rhinoceros as seed dispersers (Table 1.4). However, volant birds, primates and rodents in Thailand were all observed to consume relatively small-seeded species, so collectively they may place an upper limit on the size of seeds likely to be successfully dispersed. Together, these results suggest selective pressures limiting the enlargement of seeds and restricting increases in seed size to a single dimension. The strength of the pressure necessary to create this effect depends on the concurrent pressures selecting for large seed size. Conditions that reduced selection for large seeds could allow a weak selective pressure for small or elongate seeds to have an impact.

In contrast to Thailand, the Guianas demonstrated positive allometry in both analyses (Table 1.1; Figs 1.3 and 1.4); seed width increased more than length as seeds became larger, and large seeds were relatively rounder than small ones. This occurred even though seeds in general were more elongate in the Guianas than in Thailand. This result suggests that large seeds in the Guianas do not rely on passage through a gut for dispersal, or if they do, the animals in question impose less constraints on seed width than animals that eat smaller fruit do.

In Australia's wet tropics, the relationship between seed length and width remained isometric for both analyses, suggesting little or no selective

constraints on seed shape despite Australia having the smallest dispersers. While mean seed size was smaller than in Africa and South America, Australian seeds were rounder. This may be due to large seeds being carried rather than swallowed and passed through the gut. Alternatively, when swallowed and dispersed, the disperser did not or does not constrain the size of the seeds. It may be worth mentioning that rodents and marsupials in Australia and rodents in the Guianas handle quite large-seeded species (comparable to those handled by rodents in Central Africa), potentially releasing them from selection based on gut-width limitations.

The lack of concordance between seed characteristics and frugivore sizes on different continents is not easily explained. We initially predicted that as the size of animals in disperser assemblages decreased, fruit size should also decrease (see below), and that large fruit should be more elongate and show evidence of selection for elongation. This was not clearly demonstrated in our results, suggesting that selective pressures exerted by disperser communities cannot be analysed at the broad level attempted here, or that seeds may not respond to selection in the manners predicted. The optimum fruit shape and size may differ among floras and it may be affected by the relative abundances of different frugivore guilds, an issue that we were unable to examine with the current data. One productive way of evaluating this hypothesis more carefully would be to examine cross-species and evolutionary relationships between seed width and length within each frugivore group and continent. In this way, one may be able to detect differences among floras in the pattern or strength of selection imposed by individual guilds, which may be obscured when all of the guilds are pooled.

Contrast in seed size and shape and frugivore guilds across four rainforests

In this comparison of floras on different continents, we found that seeds were larger (longer) in Central African rainforests than in other rainforests (Table 1.2). Thus, we confirm the previous assumption by Mack (1993) that seed size is greatest in Africa, the continent with the largest frugivores. Although this was the overall trend, these differences were not demonstrated by all pantropical families (Tables 1.2 and 1.3). In addition, the trend across the four floras was not a reflection of the largest frugivores but was instead a reflection of the community mean excluding the largest species (Fig. 1.2; Table 1.2). Seed shape was relatively comparable across continents, although seeds were more elongate in Central Africa and the Guianas than in Thailand or Australia (Fig. 1.5).

Among birds and megafauna, we found correspondence between the size of seeds and the size of dispersers across the four rainforests (see Results and Table 1.5) However, we also found that small frugivores such as bats and scatter-hoarding rodents or marsupials dispersed seeds as large as those dispersed by megafauna (Table 1.4), regardless of whether megafauna were present in a community. Thus, we conclude there is no

clear relationship between the size of the seeds and the size of the frugivores dispersing them.

We assume that after the break-up of the continents, the floras of different places experienced different selective pressures based, in part, on differing disperser assemblages on each continent. Selective pressures have continued to change with the recent extinction (i.e. 10,000–40,000 years ago) of a variety of megafauna in many locations (see, e.g. Donatti *et al.*, Chapter 5, this volume). This may have led to the disappearance of some plants, but others are now dispersed by smaller animals that filled the gap or continued to disperse the same seeds after megafauna declined. The use of new tools has shown that radiation of plants throughout the tropics might be more recent than previously thought; many species may have recently colonized new continents after their seeds floated long distances across oceans (de Queiroz, 2005). Therefore, fruit and seed attributes that might have evolved in one rainforest, may be pre-adapted or exapted to other seed dispersers in another rainforest lacking the original fauna.

Together, the historical changes in dispersing animals within an area and the spread of plants to new areas creates mechanisms for the disjunction between seed attributes and their dispersing fauna. We have collated a large number of examples of seeds that appear primarily adapted to endozoochory (elongate) but are also dispersed through exozoochory by small animals, as well as fruit that are large (but not elongate) that are dispersed both by large and small animals (Table 1.6). For example, on Polillo Island in the Philippines, the gigantic lizards, *Varanus olivaceus* (up to 180 cm, 10 kg; Varanidae) swallow and disperse the large seeds of *Canarium ovatum* (54 × 21; Burseraceae) (Bennett, 2005; D. Bennett, Brisbane, 2005, personal communication), which resemble palm nuts. In the Neotropics, the large *Attalea* palm nuts, *Canarium*-like seed, are primarily dispersed by tapirs (Fragoso, 1997; Fragoso *et al.*, 2003), secondarily dispersed by agoutis *Dasyprocta leporina* and depredated by various vertebrates (Forget *et al.*, 1994, Silvius and Fragoso, 2003). In Central Africa, *Raphia leptobothrys*, a species related to *Attalea* (Pennington and Dick, 2004), is dispersed by elephant and the giant rat *Cricetomys emini* (Debroux, 1988) and possibly by terrestrial squirrels that scatter-hoard (Ewer, 1965). In New Guinea, large-seeded *Meliaceae* (*Aglaiia* spp.) are dispersed by cassowary and occasionally by large fruit bats (Mack, 1995). In Thailand, seeds in another related *Aglaiia* species are dispersed by hornbills and cached by scatter-hoarding rodents (Kitamura *et al.*, 2004; see also Becker and Wong, 1985). These parallel observations from different rainforests suggest the possibility that many of these seeds might have once been dispersed by giant reptiles (today represented by giant *Varanus*) now extinct, and that large size in seeds (i.e. > 25–35 mm L) and elongated shape is exapted to their current dispersal agents.

There is no broad correspondence between the size of seeds and the body mass of current dispersers, which may be because the same (or similar) seeds might be ingested whole and defecated (e.g. *Varanus*, tapir, elephant), regurgitated (hornbill), spat out (primates), scatter-hoarded

Table 1.6. Examples of large-seeded plants from pantropical families dispersed by endozoochores and/or exozoochores in four rainforests on different continents (CA – Central Africa; GU – Guianas; S-EA – South-east Asia; AU – Australia's wet tropics).

	Species	Family	L × W (mm) or weight (g)	Endozoochores (swallower, spitter)	Exozoochores (carrier)	References	
CA	<i>Beilschmiedia mannii</i>	Lauraceae	50 × 33	<i>Pan troglodytes</i> , <i>Cercopithecus cephus</i>	?	Gautier-Hion <i>et al.</i> , 1985	
	<i>B. obscura</i>	Lauraceae	33 × 15	<i>Ceratogymna atrata</i> , <i>C. cylindricus</i>	?	Gautier-Hion <i>et al.</i> , 1985	
	<i>Canarium sweinfurthii</i>	Burseraceae	35 × 16	<i>Loxodonta africana</i>	?	Alexandre, 1978	
	<i>Carapa</i> spp.	Meliaceae	30 × 25	<i>L. africana</i>	<i>Cricetomys</i> spp.	Debroux, 1988	
	<i>Dacryodes buttnueri</i>	Burseraceae	34 × 15	Hornbills, Primates	?	Gautier-Hion <i>et al.</i> , 1985; Ebigbo, 2005	
	<i>Parinari curatellifolia</i>	Chrysobalanaceae	35 × 25	<i>L. africana</i> ?	<i>Eidolon helvum</i>	Ebigbo, 2005	
	<i>P. holstii</i>	Chrysobalanaceae	52 × 42	<i>L. africana</i> , Primates	<i>E. helvum</i>	Gautier-Hion <i>et al.</i> , 1985	
	<i>Raphia leptobothrys</i>	Arecaceae	54 × 34	<i>L. africana</i>	?	Alexandre, 1978	
	<i>Symphonia globulifera</i>	Clusiaceae	25 × 12	Hornbills, Primates	?	Gautier-Hion <i>et al.</i> , 1985	
	<i>Spondias mombin</i>	Anacardiaceae	32 × 20	? unknown	<i>Eidolon helvum</i>	Okon, 1974	
	GU	<i>Attalea maripa</i>	Arecaceae	55 × 28	<i>T. terrestris</i>	Dasyproctidae	Forget <i>et al.</i> , 1994; Fragoso, 1997; Fragoso <i>et al.</i> , 2003; Silvius and Fragoso, 2003
		<i>Carapa</i> spp.	Meliaceae	30–35 × 20–25	? extinct	Dasyproctidae	Forget, 1996; P.-M. Forget and P.A. Jansen, personal observation
<i>Mauritia flexuosa</i>		Arecaceae	45 × 45	<i>T. terrestris</i>	Dasyproctidae	van Roosmalen, 1985a	
<i>Parinari campestris</i>		Chrysobalanaceae	40 × 26	? extinct	<i>Artibeus</i> spp.	Charles-Dominique, 1986; van Roosmalen, 1985a	
<i>P. exelsa</i>		Chrysobalanaceae	32 × 21	? extinct	<i>Artibeus</i> spp.	Charles-Dominique, 1986; cf. van Roosmalen, 1985a	
<i>P. montana</i>		Chrysobalanaceae	75 × 48	? extinct	Dasyproctidae	P.-M. Forget, personal observation	
<i>Symphonia globulifera</i>		Clusiaceae	20 × 14	<i>T. terrestris</i>	<i>Rhynophylla pumilio</i> , <i>Artibeus</i> spp.	Charles-Dominique, 1986; Henry <i>et al.</i> , 2000	
<i>Spondias mombin</i>		Anacardiaceae	32 × 20	<i>T. terrestris</i> , <i>Mazama</i> spp., <i>Ateles paniscus</i> , <i>Alouatta seniculus</i>	Bats	Guillotin <i>et al.</i> , 1994; Henry <i>et al.</i> , 2000; Janzen, 1985; van Roosmalen, 1985b	

S-EA	<i>Aglaia harmsiana</i>	Meliaceae	17.9 diam.	<i>Varanus olivaceus</i>		Auffenberg, 1988
	<i>A. spectabilis</i>	Meliaceae	30–46 × 17–28	Hornbills	<i>Maxomys surifer</i>	Kitamura <i>et al.</i> , 2004
	<i>Aglaia</i> sp.	Meliaceae	25–45 × 15–27	<i>Anthracoseros malayanus</i>	<i>Callosciurus prevostii</i>	Becker and Wong, 1985
	<i>Beilschmiedia maingayi</i>	Lauraceae	32 × 14	<i>Ducula badia</i> , Hornbills, <i>Hylobates</i> spp., <i>Macaca nemestrina</i>	Rodents	Kitamura <i>et al.</i> , 2002
	<i>Canarium hirsutum</i>	Burseraceae	26 × 20	<i>V. olivaceus</i>	?	Auffenberg, 1988; D. Bennett, personal communication
	<i>C. indicum</i>	Burseraceae	30–60 × 20–30	<i>Cynopterus sphinx</i>	?	Docters van Leeuwen, 1935
	<i>C. ovatum</i>	Burseraceae	54 × 21	<i>V. olivaceus</i>	?	Auffenberg, 1988; D. Bennett, personal communication
	<i>C. euphyllum</i>	Burseraceae	36 × 17	Hornbills, <i>Ducula badia</i> , <i>Cervus unicolor</i> , <i>Muntiacus muntjak</i>	<i>Menetes berdmorei</i>	Kitamura <i>et al.</i> , 2006
	<i>Spondias spinnata</i>	Anacardiaceae	25.8 diam.	<i>Varanus olivaceus</i>	?	Auffenberg, 1988
	AU	<i>Beilschmiedia bancroftii</i>	Lauraceae	49 × 42	<i>Casuarium casuarium</i>	<i>Hypsiprimnodon moschatus</i> , <i>Uromys caudimaculatus</i>
<i>Entiandra microneura</i>		Lauraceae	62 × 33	<i>C. casuarium</i>	<i>H. moschatus</i> , <i>U. caudimaculatus</i>	Stocker and Irvine, 1983; Dennis, 2003
<i>E. xanthocarpa</i>		Lauraceae	56 × 29	<i>C. casuarium</i>	<i>H. moschatus</i> , <i>U. caudimaculatus</i>	Stocker and Irvine, 1983; Dennis, 2003
<i>Aglaia cf. flavida</i>		Meliaceae	118 g	<i>Casuarium bennettii</i>	<i>Dobsonia moluccensis</i>	Mack, 1995

(rodents, *Hypsiprymnodon*) or dispersed by abiotic means. This combination of dispersal modes and vectors means that selective pressures on seed size and shape could vary considerably among different places and times.

Another example of such exaptation is given by *Symphonia globulifera* (Clusiaceae), which evolved in the Palaeotropics and then later dispersed by drifting on oceanic currents to colonize the Neotropics (Pennington and Dick, 2004). The palaeotropical form is known in Central Africa from fossils as old as 45 MYBP (Dick *et al.*, 2003), and is now dispersed by hornbills (regurgitated), primates (spat out; Table 1.6) and cephalophes (swallowed; *Cephalophus monticola* and *Hyemoschus aquaticus*). In the Neotropics, where it arrived some 15 MYBP, *S. globulifera* it is now dispersed by endozoochory through tapirs and by exozoochory through bats and later consumed by granivores such as *Tinamou major*, small rodents, primates (*Pitheca pithecia*) and deer. While *S. globulifera* do not differ in the size and shape of their seeds across continents, there are two forms that differ in seed size in the Guianas: one small (10–20 mm in length) and the other large (>30 mm). The small-seeded form grows on hills and would benefit from a wide array of vertebrate dispersal services, perhaps constraining seed size. The large-seeded form grows in flooded and swamp forests and benefits from both vertebrate and water dispersal, perhaps relieving the constraints on seed size. Both forms are known to be dispersed by bats and tapir. The debate remains open.

Conclusions

Is there a relationship between seed size and shape and the size of the animals that disperse them? Differences in the mean size of seeds in plants from four rainforests on different continents reflected the mean size of the animals handling them. However, the relationship was a tenuous one and, when examined in more detail, the expected or straightforward patterns broke down. Large seeds from our African sample were elongate relative to smaller ones, though we expected few constraints on the shape of large seeds there. Large seeds in Thailand were also relatively elongate and showed strong selective pressure to become elongate as seed size increased. Given that they had the second smallest mean disperser size, this is not surprising. However, Australia, with the smallest mean disperser size, had seeds that did not show a change in shape as a function of seed size, nor any selective pressure to do so. In contrast, seeds from the Guianas, with the second largest mean disperser weight, had large seeds that were rounder than small ones and demonstrated strong selection for this to occur. These patterns indicate that different trends in seed allometry do occur at the broad community scales investigated here, but also that the evolution of seed size cannot easily be unravelled by examining patterns at this broad community scale. Why patterns in seed size and shape should be so different on different continents is an interesting question requiring further investigation. Clearly, different animal behaviours, such as carrying

and dispersing seeds rather than swallowing them, can exert opposing selection on seed size and shape. For example, the largest seeds in the Guianas may no longer be swallowed but only dispersed externally, releasing them from selection for elongation, whereas in Africa the largest seeds may still be swallowed as well as carried, resulting in continued selection for elongate seeds. To unravel the reasons for these patterns further, we need more data on the diets, behaviours and relative contributions of dispersers.

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