



Seed-spitting Primates and the Conservation and Dispersion of Large-seeded Trees

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Received August 21, 2003; revision November 10, 2003; 2nd revision June 17, 2004;
accepted July 13, 2004

*Primate frugivory may reduce density-dependent predation on seeds and seedlings via effective seed dispersal. Accordingly, the tendency of cercopithecines to spit and scatter seeds >4 mm wide could represent a prominent means of dispersal. However, the importance of seed-spitting may vary according to the life history adaptations of plants. Indeed, the actions of cercopithecines may be incongruent with the reproductive biology of plants that rely on large frugivores to swallow and defecate their seeds. This possibility raises conservation concerns because large frugivores are often susceptible to extirpation or extinction from hunting and habitat fragmentation. It is therefore important to determine if cercopithecines have a compensatory effect; that is, whether or not seed-spitting effectively conveys large seeds to recruitment sites. To test this concept, we used geospatial techniques to measure and analyze the dispersion of tree species dispersed by elephants, chimpanzees, and cercopithecines to different spatial extents. We studied adult trees of *Balanites wilsoniana*, *Chrysophyllum gorungosanum*, and *Uvariopsis congensis* in a 2.2-ha plot in Kibale National Park, Uganda. Despite the tendency of cercopithecines to spit the seeds of *Uvariopsis congensis*, adult trees were highly clumped, with a modal nearest-neighbor distance of <5 m and a crown overlap of 1.5 m. Virtually identical results for *Balanites wilsoniana* and *Chrysophyllum gorungosanum*, the seeds of which are not spat, suggest that*

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seed-spitting may be a poor mechanism of dispersal for some large-seeded plants.

KEY WORDS: seed dispersal; cercopithecinae; scatter-clump hypothesis; frugivory.

INTRODUCTION

Primates are inferred to have long played a role in the reproductive biology of flowering plants (Sussman and Raven, 1978, Sussman, 1995). Accordingly, their widespread regional reduction or extirpation may pose a prominent threat to the structure, composition, and diversity of tropical forests (Chapman and Onderdonk, 1998). The greatest impact may result from lost interactions between primates and seeds. For instance, a single gibbon can swallow as much as 1 kg of seeds per day (Whitten, 1982). Primates are regarded as effective seed dispersers because their actions favor seedling establishment and survival; they are prodigious frugivores and viable seeds are often dispersed propitious distances (Chapman, 1995). Furthermore, primates reportedly influence the reproductive success and dispersion of some plant species. For example, in the Lopé Reserve, Gabon, several tree species demonstrate improved establishment and growth when gorillas defecate seeds near nest sites (Tutin *et al.*, 1991; Rogers *et al.*, 1998; Voysey *et al.*, 1999). Similarly, vervets, baboons, tamarins, howlers, and capuchins are inferred to also affect the dispersion of some plants (Jackson and Gartlan, 1965; Lieberman *et al.*, 1979; Garber, 1986; Julliot, 1997; Wehncke *et al.*, 2003).

Primates vary in the mechanisms by which they disperse seeds. Whereas some primates consume fruits expressly for seeds, most swallow and defecate viable seeds intact, albeit in varied patterns (Rowell and Mitchell, 1991; Zhang and Wang, 1995; Andresen, 1999; Wehncke *et al.*, 2003). Cercopithecines are notable because they tend to spit seeds >4 mm wide (Gautier-Hion, 1984; Corlett and Lucas, 1990, Kaplin and Moermond, 1998; Lambert, 1999; Otani and Shibata, 2000). The importance of seed-spitting to the reproductive biology of trees is debatable. Expectoration could be a highly effective means of seed dispersal because scattering seeds reduces density-dependant predation (quality dispersal *sensu* Schupp, 1993); or, on the contrary, it may “dispense with seeds rather than disperse them” (Lucas and Corlett, 1998:40). This semantic distinction is a reaction to assumptions in the literature that plant fitness benefits from any mechanism of seed dispersal. From their observations of long-tailed macaques (*Macaca fascicularis*), Lucas and Corlett (1998) concluded that seed-spitting had a negative impact on plant fitness: the dispenser hypothesis. Reports on bonnet macaques are similar: the “role [of *Macaca*

radiata] in the dispersal of plants is negligible” (Balasubramanian and Bole, 1993:35). Interestingly, fossil, molecular, and theoretical studies may bear on the issue of whether cercopithecines are seed-dispersers or seed-dispersers.

The divergence of extant cercopithecines is estimated to have occurred between 9.5 and 13.5 Ma (Szalay and Delson, 1979; Disotell and Raaum, 2002). Unfortunately, fossils are scant, and few exist before 3.5 Ma (Leakey, 1988). The first recorded cercopithecines in east Africa come from Ongoliba, D.R. Congo, with an estimated date of about 6 Ma, and also from the upper Nawata Formation, Lothagam, Kenya (Gundling and Hill, 2000). Leakey (1988) inferred from this record that cercopithecines radiated into an arboreal niche recently, <1 Ma. The basal position of the semiterrestrial *Allenopithecus nigrovirdis* in the tribe Cercopithecini may support this suggestion (Gautier-Hion *et al.*, 1999; Tosi *et al.*, 2004). However, *Allenopithecus nigrovirdis* tends to consume fruits while in trees (Gautier, 1985), raising the possibility that arboreal seed-spitting has characterized guenon behavior to some extent for as long as 9.5–11 Ma (Disotell and Raaum, 2002). Yet given the discordant evolutionary rates between plants and vertebrates (Herrera, 1985), and the suggestion that large-seeded trees are adapted to a clumped dispersion (Howe, 1989—see below), it is theoretically conceivable that such trees derive few reproductive benefits from seed-spitting monkeys.

Howe’s (1989) scatter-clump hypothesis suggests that birds and bats, which typically scatter seeds widely, will select for seed and seedling traits concordant with the recruitment of isolated individuals. The traits of scatter-dispersed plants are predicted to include an adaptive premium on dispersability, or escape, and minimal investment in chemical or mechanical defense. Plants exhibiting these traits are thus vulnerable to Janzen-Connell effects of density-dependent mortality (Harms *et al.*, 2000; Wang and Smith, 2002). Howe noted, however, that large frugivores regularly deposit large seeds in fecal flocculates (e.g. Alexandre, 1978; Dinerstein and Wemmer, 1988), often near conspecific trees. Thus he argued that consistently clump-dispersed plants should evolve traits designed to deter density-attracted pathogens, insects, and/or vertebrate herbivores. Having evolved to tolerate conspecifics and density-dependent assaults, they will thus ultimately display a clumped dispersion in space. Natural selection would favor such dispersion because large frugivores, such as chimpanzees, tend to be attracted to clumped resources (Bodmer, 1990; Wrangham *et al.*, 1996; Beck and Terborgh, 2002). Indeed, primate foraging can be more sensitive to the spatial aspects of fruiting trees, e.g., crown size, density, and distribution, than to the quality of individual fruits (Janson *et al.*, 1986).

Cercopithecines are anomalous to this model. They are relatively large frugivores that behave like scatter-dispersers. Though attracted to clumped fruiting trees (Homewood, 1978; Lambert, 2001), they spit seeds 0–100 m distant (Kaplin and Lambert, 2002). This tendency to consume fruits that target large frugivores, yet disperse the seeds in a manner inconsistent with their body size, raises the possibility that seed-spitting confers a negative impact on plant fitness. If true, the effectiveness of seed-spitting could be an important conservation issue. In Kibale National Park, Uganda, chimpanzees remove ca. 1400 fruits $\text{km}^{-2} \text{day}^{-1}$ while 3 cercopithecine species remove ca. 33,800 fruits $\text{km}^{-2} \text{day}^{-1}$ (Lambert, 1999). One interpretation of the data is that forest diversity might be maintained by cercopithecine monkeys. They are often less susceptible than chimpanzees, elephants, and other large frugivores to hunting and forest fragmentation.

Goals of the Present Analysis

The goal of our analysis is not to support or to refute the scatter-clump hypothesis (*cf.*, Lambert, 2002). Instead, we provide a quantitative description of spatial clumping in 3 tree species: *Balanites wilsoniana* (Zygophyllaceae), *Chrysophyllum gorungosanum* (Sapotaceae), and *Uvariopsis congensis* (Annonaceae). We selected them because the mechanism of dispersal varies among cercopithecines, chimpanzees, and elephants. Though speculative, we evaluate the effectiveness of seed spitting by comparing the observed versus predicted dispersion of adult trees. We focus on *Uvariopsis congensis* because its dispersion may be clumped or scattered on the basis that chimpanzees or cercopithecines are conferring quality seed dispersal. A highly clumped dispersion may indicate that seed-spitting is a poor dispersal mechanism. We must emphasize, however, that such an analysis does not permit us to infer process unambiguously from pattern. We cannot argue to have teased apart the effects of biotic and abiotic postdispersal factors. Accordingly, our study is intended as a preliminary examination of the dispenser hypothesis.

METHODS

Study Site and Subjects

From April–July 1999 we measured the dispersion of *Balanites wilsoniana*, *Chrysophyllum gorungosanum*, and *Uvariopsis congensis* in the Kanyanchu sector of Kibale National Park, Uganda (0°13'N–0°41'N; 30°19'E–30°32'E). The forest in Kibale ranges from moist evergreen forest

(closely related to moist montane forest) to lowland tropical rain forest (with affinities to both montane rain forest and mixed tropical deciduous forest) (Struhsaker, 1997). Kanyanchu is a tourist area (Mason and Rubens, 1992) with a floristic composition similar to Ngogo, ca. 10 km to the north at 1350 m a.s.l. At Ngogo, yearly rainfall averages 1500 mm (1977–1984) and it falls in 2 distinct rainy seasons: March-May and August-November (Chapman *et al.*, 1999).

Balanites wilsoniana is a tall (35 m), deciduous tree that produces single-seeded fruits 6–10 cm long. When mature, the fruits are green-brown, unpleasant smelling, and toxic (Hamilton, 1991; Chapman *et al.*, 1992). The seeds, which measure ca. 9×6 cm, are often in the dung of elephants (Wing and Buss, 1970; Lieberman *et al.*, 1987), to which they appear dependent for dispersal (Chapman *et al.*, 1992; Hawthorne and Parren, 2000; Cochrane, 2001). Bush pigs (*Potamochoerus porcus*) are frequent seed predators (Ghiglieri *et al.*, 1982). In Kibale, seeds of *Balanites wilsoniana* were in 11% of elephant dung boluses; 51–61% of which germinated successfully (Chapman *et al.*, 1992; Cochrane, 2001). Germination success is considerably worse (<1%) in seeds collected from fruiting trees. In general, *Balanites wilsoniana* is rare in Kibale, existing at a density of 1.7 individuals ha^{-1} (Chapman *et al.*, 1999). However, seeds and saplings are common in and around grasslands (Lwanga, 2003).

Chrysophyllum gorungosanum is a tall tree (40 m) on valley slopes; it features a small, dense crown (Hamilton, 1991). At Ngogo, density reaches 65 trees ha^{-1} (Chapman *et al.*, 1999). The seeds, measuring ca. $2.1 \times 1.2 \times 0.7$ cm, are identical to those of *Chrysophyllum albidum*, which is also present in Kibale. Although bush pigs are reported to macerate or swallow seeds of *Chrysophyllum albidum* (Ghiglieri *et al.*, 1982), elephants in Ghana appear to provide high quality dispersal (Hawthorne and Parren, 2000). In Kibale similar effects are inferred. Cochrane (2001) reports that 5% of elephant dung boluses included seeds of *Chrysophyllum* spp., of which 42% germinated. At Ngogo, 7.2% of chimpanzee dung samples contained seeds, of which 33% germinated (Wrangham *et al.*, 1994). Control seeds collected from fruiting trees did not germinate. Red-tailed monkeys (*Cercopithecus ascanius*) spit seeds of *Chrysophyllum*, whereas chimpanzees and gorillas swallow them (Lambert, 1999; Stanford and Nkurunungi, 2003).

Uvariopsis congensis is a common understory tree (20 m) on valley slopes. At Ngogo, density exceeds 100 trees ha^{-1} (Chapman *et al.*, 1999). The fleshy fruit is ca. 3 cm long and contains 2–7 seeds, which average 1.3 cm along the longest axis (Chapman and Chapman, 1996). The fruits are a top-ranking food of Kibale chimpanzees (Wrangham *et al.*, 1996), with seeds in 15% of Ngogo dung specimens (Wrangham *et al.*, 1994). In a detailed study of foraging on *Uvariopsis congensis*, Lambert (1999) observed

chimpanzees swallowing and spitting seeds. Spitting of *Uvariopsis congensis* seeds characterized 81% of chimpanzee fruit eating events, with seeds raining ≤ 1 m from parent trees. In addition, for all trees studied, chimpanzees defecated seeds beneath conspecifics on 21 of 81 occasions (26%). In germination trials, 15.5% of seeds collected from chimpanzee dung germinated, whereas control seeds did not (Wrangham *et al.*, 1994). Notably, seedlings thrive beneath conspecifics (Chapman and Chapman, 1995), where the preponderance of seeds is deposited (Lambert, 1999). In this regard, it is noteworthy that *Uvariopsis congensis* is the preferred nesting tree of chimpanzees in Kibale (R. W. Wrangham, personal communication) and Kalinzu Forest (Furuichi and Hashimoto, 2004). Primate sleeping sites can exert a strong effect of plant dispersion (Julliot, 1997; Rogers *et al.*, 1998).

Focal tree observations indicate that cercopithecines also rely on the fruits heavily (Chapman and Chapman, 1996). However, Lambert (1999) showed that seeds spat by red-tailed monkeys rained significantly further from parent crowns than those spat by chimpanzees (Figure 1A). Furthermore, red-tailed monkeys defecated seeds beneath conspecifics in only 4 of 135 instances (3%). Accordingly, Lambert (1999) viewed chimpanzees and red-tailed monkeys as clump- and scatter-dispersers, respectively, of seeds of *Uvariopsis congensis*.

To quantify the dispersion of each tree species, we established a 2.2-ha plot in an area accessed by bisecting trails. The size of the plot is arbitrary

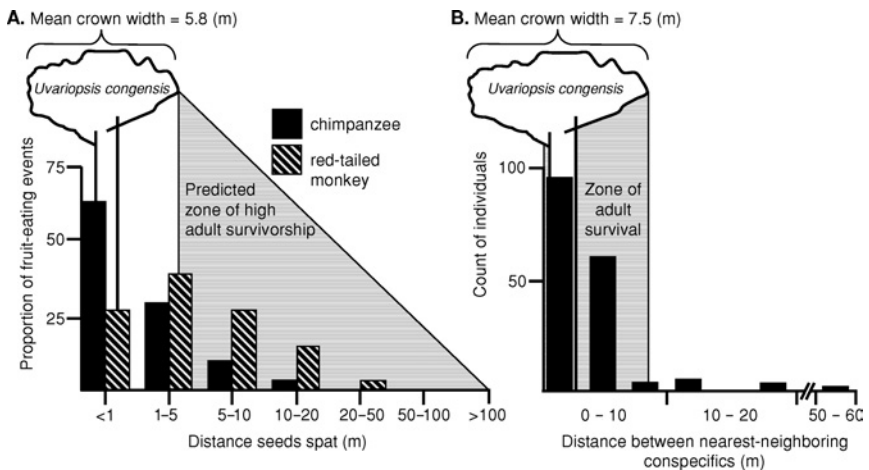


Fig. 1. The distances seeds of *Uvariopsis congensis* are spat by chimpanzees and red-tailed monkeys (after Lambert, 1999) and the zone where recruitment is predicted to be highest based on the premise that scattering seeds confers quality dispersal (A). The frequency of nearest-neighbor distances observed in an adult population (B).

to some extent; that is, time permitted treatment of only 2 ha, a scale we considered sufficient to capture dispersion arising from dung-based seeds or from seeds spat by primates occupying/exiting fruiting trees.

GPS Measurements

The Navstar Global Positioning System (GPS) refers to the group of 24 geosynchronous satellites owned and maintained by the U.S. Department of Defense (USDOD). GPS data are expressed as latitudes and longitudes relative to a mathematical model called the World Geodetic System 1984 datum (or WGS-84). The coordinates of WGS-84 are based on an origin point and the GRS-80 ellipsoid, the standard most closely approximating the shape of the earth. Before the presidential decision directive of 1 May 2000, the greatest source of GPS error was called Selective Availability (S/A), which referred to ephemeris errors (epsilon) and satellite clock errors (dithering) deliberately induced by the USDOD. Accordingly, autonomous accuracies of 10–30 m were restricted to the U.S. military and its allies. The combination of S/A and other sources of error, e.g., ionospheric and tropospheric delay, resulted in 95% of all civil GPS positions being somewhere within 100 m of truth (Dominy and Duncan, 2001). Although the presidential decision to remove S/A improved civil GPS accuracy to 10–30 m, differential correction is necessary to correct this degree of error.

To achieve greater accuracy, we used a 12-channel GPS Pathfinder Pro XRS (Trimble Navigation, Sunnyvale, California) subscribed to a satellite differential correction service (Fugro-OmniSTAR, Houston, Texas). Selection of the unit was based on the demands of a rain forest environment and the need for 1-2 m accuracy; in addition to being lightweight (1.35 kg) and battery powered, several features of this backpack GPS were suited to our needs: (i) the capacity to simultaneously track 12 satellites, (ii) real-time differential correction capability, (iii) a rugged, waterproof housing; and, (iv) built-in, multipath rejection technology.

We configured the unit to the suggested critical settings of the manufacturer. We set the Position Dilution of Precision (PDOP) mask to <6 , the Signal to Noise ratio (SNR) to >6 , and Elevation mask to 15° . PDOP is a measure of satellite clumping in space and the strength of the trilateration base for determining earthly positions. Evenly distributed satellites produce a better trilateration base, or lower PDOP. The SNR is a measure of satellite signal strength; a higher number is a stronger signal. The elevation mask prevents the GPS from using unfavorable satellites by eliminating ones low on the horizon. After configuring the critical settings, we established a link between the Pro XRS and the satellite differential service (XSAT satellite,

1538.053 MHz, data rate: 2400 bps). In an ideal physical environment and the above configurations, Fugro-OmniSTAR specifies 1-m accuracy for our study location. Preliminary tests in Kibale were consistent with this expectation (Dominy and Duncan, 2001).

We restricted our measures to trees with a diameter at breast height (dbh) ≥ 8 cm. Although this measure was intended to capture all trees of reproductive size, it probably underestimates the reproductive status of *Balanites wilsoniana*. To measure tree dispersion, we placed the GPS antenna against individual boles. If differential (DGPS) readings were unobtainable at ground level, we ascended trees to reduce SNR attenuation and improve PDOP (Dominy and Duncan, 2001). Although this procedure worked reliably for large trees, smaller understory trees required manual measurement. We used a compass and measuring tape to determine the direction and distance of small trees relative to those with DGPS data. Our error for such measurements was 1–2 m (when checked against trees with known DGPS positions). We downloaded spatial and physical attributes, e.g., height, dbh, and crown width, of all trees from the Trimble data logger onto a portable laptop computer and exported them into geographic information systems (GIS) software (ArcView v3.1, Environmental Systems Research Institute, Redlands, California).

Spatial Analyses

We produced a 3-dimensional map of our plot and subdivided it into 40 quadrants (Figure 2). To determine the degree of clumping, we calculated the standardized Morisita index of dispersion (I_p), which ranges from -1.0 to 1.0 , with 95% confidence limits at 0.5 and -0.5 (Krebs, 1999). Random patterns produce an I_p of zero, clumped patterns >0 , and uniform patterns <0 . The standardized Morisita index is one of the best measures of dispersion for quadrant data because it is insensitive to quadrant size and is independent of population density and sample size (Myers, 1978; Upton and Fingleton, 1985). To understand the extent to which species are potentially competing for resources, we used ArcView to calculate distances between the boles and crown perimeters of every tree and its nearest-neighboring conspecific. Spatial competition could be indicated by the extent to which crowns overlap.

RESULTS

In total, we studied 275 individual trees. All 3 species were clumped ($P < 0.05$; Table I). The modal distance between nearest-neighboring

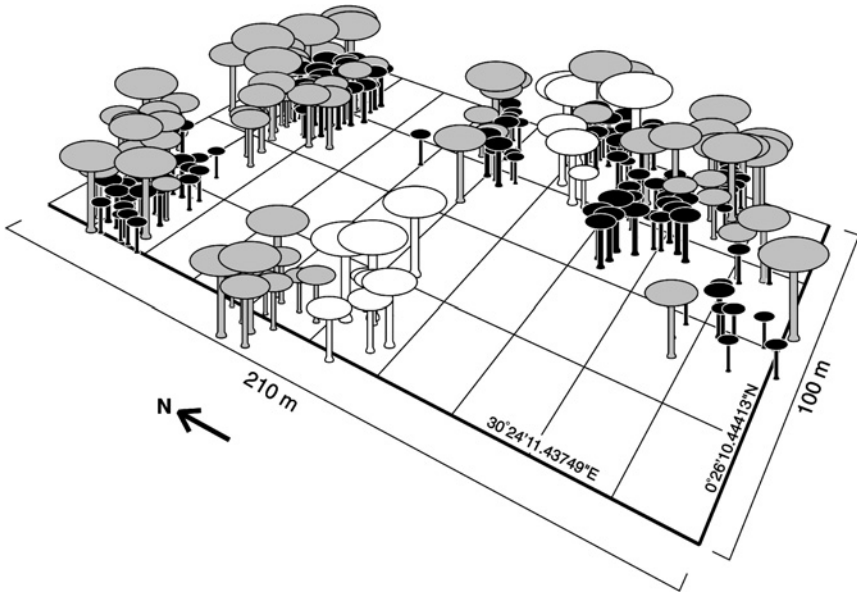


Fig. 2. Three-dimensional rendering of our 2.2-ha study plot in Kanyanchu, Kibale National Park, Uganda. Tree heights and crown widths are scaled to the size of the plot. Species portrayed are *Balanites wilsoniana* (white), *Chrysophyllum gorungosanum* (gray), and *Uvariopsis consgensis* (black). After Lucas *et al.* (2001).

conspecifics is ≤ 5 m for *Uvariopsis consgensis* (Figure 1B) and *Balanites wilsoniana* (Figure 3A). For *Chrysophyllum gorungosanum*, nearest-neighbors were equally likely to exist 0–5 or 5–10 m distant (Figure 3B). Mean physical attributes are portrayed in Figure 4, which also depicts the extent to which crowns of nearest-neighbors overlap. The modal distance between crown perimeters was overlapping for each species. The effect was identical in *Chrysophyllum gorungosanum* and *Uvariopsis consgensis* (1.5 m)

Table I. Standardized Morisita index of dispersion (I_p), range, and mean distance (\pm one standard deviation) between nearest-neighboring conspecifics for three tree species in Kanyanchu, Kibale National Park, Uganda

Species studied	<i>N</i>	I_p	Range of distances between conspecifics (m)	Mean distance between nearest conspecifics (m)
<i>Balanites wilsoniana</i>	16	0.608	1.4–25.8	7.1 \pm 6.5
<i>Chrysophyllum gorungosanum</i>	97	0.518	1.5–28.8	6.5 \pm 4.3
<i>Uvariopsis consgensis</i>	162	0.525	0.02–55.6	4.0 \pm 5.0

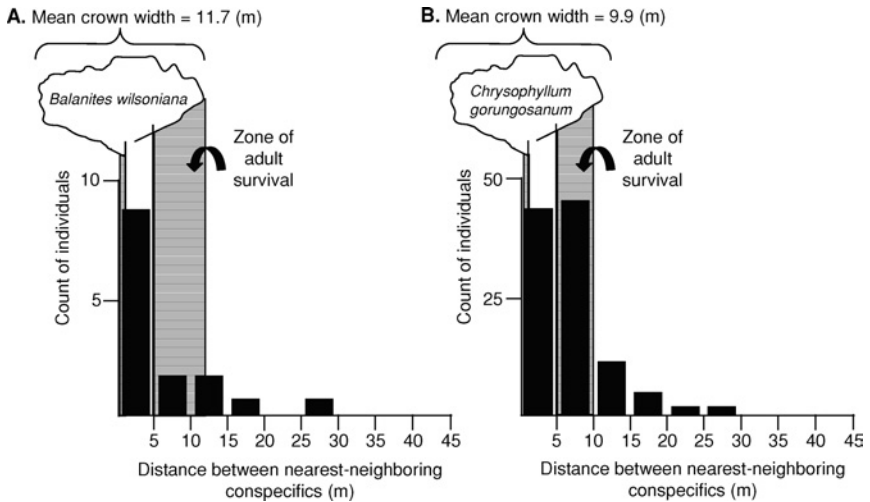


Fig. 3. The frequency of nearest-neighbor distances observed in adult populations of *Balanites wilsoniana* (A) and *Chrysophyllum gorungosanum* (B).

and greatest in *Balanites wilsoniana*, for which modal crown overlap is 2.5 m (Figure 4C).

A caveat regarding *Balanites wilsoniana*: Individuals can produce adventitious shoots, or suckers (C. A. Chapman, personal communication). Accordingly, adult aggregations may not always reflect zoochorous seed dispersal. On this basis, a reviewer advocated the removal of *Balanites wilsoniana* from our analysis. We acknowledge this suggestion and the implications to our results, but we opt to include it in our analysis because the species is mainly recorded (in small or large sizes) in or close to areas inhabited by elephants (Hawthorne and Parren, 2000). Although a few isolated large trees are reported outside of the ranges of present-day elephants, seedlings have not been reported, which suggests that the species seldom regenerates in the absence of elephants.

DISCUSSION

Here we show that 3 large-seeded tree species are clumped in space. Of special interest are the seeds of *Uvariopsis congensis*, which are spat by red-tailed monkeys and chimpanzees. A key distinction is that chimpanzees spit seeds nearer to fruiting parents than red-tailed monkeys do and they defecate some seeds beneath conspecifics; ca. 38% of seeds spat by red-tailed monkeys land away from the crowns of parent trees (Lambert, 1999).

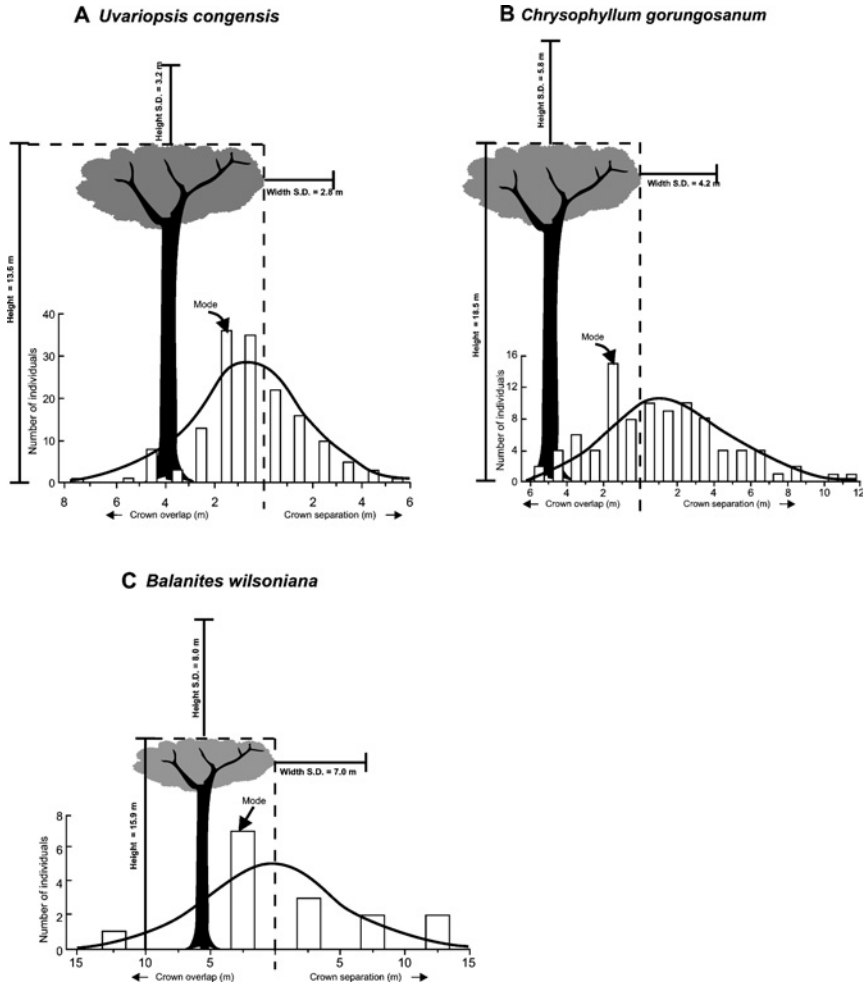


Fig. 4. Mean physical attributes of each taxon and the frequency of distances between crowns of nearest-neighboring conspecifics. Modal distances between crown perimeters were overlapping for each species.

If strong Janzen-Connell effects of density-dependant predation were acting on *Uvariopsis congensis*, one would predict a modal nearest-neighbor distance beyond the perimeters of tree crowns. The prediction was not observed. Virtually identical results for *Balanites wilsoniana* and *Chrysophyllum gorungosanum*—the seeds of which are not spat—suggest that none of the observed dispersions are the result of seed spitting.

However, although these results are conceptually consistent with the seed dispenser hypothesis, our analysis does not address some important factors. First, the premise that mature tree dispersion is directly related to zoochorous seed rain is confounded by the fact that “a plant’s surroundings may be as important in determining its seed shadow as its set of dispersal-related heritable attributes” (Herrera, 1985:136). Plant dispersion is often governed by abiotic factors, such as aspects of slope, soil depth, or over-story coverage (Lewis, 1987; Schupp, 1988, 1990, 1995). In fact, spatial discordances between seed depositional patterns and seedling survival are well documented (Herrera *et al.*, 1994; Jordano and Herrera, 1995; Schupp *et al.*, 2002). In such cases, scattering improves the probability that seeds will reach favorable sites for growth and survival. The failure of seeds to reach potential recruitment sites is regarded as one of the major factors contributing to high species diversity in tropical forest trees (Nathan and Muller-Landau, 2000; Muller-Landau *et al.*, 2002; Howe and Miriti, 2004). Accordingly, the conclusions that can be drawn from our analysis are limited. Although the species we studied appear to exhibit characteristics that are consistent with clump-adaptations (*sensu* Howe, 1989), we cannot exclude the possibility that our dispersions are simply a reflection of favorable microhabitats.

Furthermore, dung beetles and rodents are attracted to the presence and density of dung (Andresen, 2001, 2002). Although their actions decrease seed aggregations (Shepherd and Chapman, 1998), the scale is unlikely to produce a random dispersion (Plotkin *et al.*, 2002). Rodents hoard seeds <20 m distant (Yasuda *et al.*, 2000) and large caviomorphs bury 64% of seeds \leq 20 m away (Jansen and Forget, 2001). It is plausible, however, that such behaviors are sufficient to reduce selection for clump-dispersed traits. Accordingly, the generalities of the scatter-clump hypothesis appear untenable. Birds and bats disperse large or small seeds into a clumped dispersion, and some large frugivores scatter seeds widely (Wenny and Levey, 1998; Schupp *et al.*, 2002). In Bukit Timah, Singapore, the scattered dispersion of rattans may be due largely to long-tailed macaques (Lucas and Corlett, 1992). However, in general, long-tailed macaques are regarded as ‘spoilers’ providing few dispersal benefits to most forest species (Ridley, 1930). This notion, emphasized by Lucas and Corlett (1998), stresses a distinction between oral and digestive seed scattering. As Daniel H. Janzen noted over 20 years ago:

“What now needs to become of interest is not what [fruits] an animal likes to eat . . . , but rather what traits influence seed spitting, [and] what is the ideal germination pattern of the clutch of seeds that emanate from the rears and fronts of the disperser” (Janzen, 1983:105).

Seeds emanating from the fronts of ungulates can produce latrines of fruit trees (Bodmer, 1990; Freer, 1995; Fragoso, 1997; Fragoso *et al.*, 2003). The spitting of a seed after rumination may resemble the benefits of gut passage (Traveset and Verdú, 2002). Accordingly, our evaluation of the dispenser hypothesis does not devalue the importance of seed-spitting *per se*. Instead, we suggest that one factor in the failure of *Uvariopsis congestis* to reach recruitment sites away from clumps may be the fact that cercopithecine seed-spitting is preceded by oral processing. Although some preliminary digestion occurs in the cercopithecine buccal pouch (Murray, 1975), oral processing is often insufficient to clean a seed of its flesh, leaving a spat seed susceptible to fungal pathogens (personal observation). However, our interpretation is only speculative, we cannot soundly argue to have teased apart the effects of biotic and abiotic postdispersal factors on the dispersion of *Uvariopsis congestis*. Furthermore, the adherence of fruit flesh to an endosperm varies. Oral processing may be an effective mechanism for some species. In Kibale, *Strychnos mitis* (Loganiaceae) exists in dense groves but the seeds are uncommon in chimpanzee dung (Wrangham *et al.*, 1994). Aggregation could result from cercopithecines (Lambert, 2001).

Cercopithecines also consume unripe fruits, destroying the seeds (Wrangham *et al.*, 1998). Because this behavior reduces the availability of ripe fruits, the cercopithecine radiation is inferred to have contributed to the widespread collapse of the hominoid lineage (Andrews and Aiello, 1984). The collective nature of these observations implies that extensive coevolution between plants and seed-spitting monkeys is implausible. Herrera (1985) noted that adaptations of plants for successful dispersal should be of a generalized, coarse nature, matching broad taxonomic groups of dispersers (whose species are and have been similar enough in some respects so as to make their pressures persistent and additive), rather than particular groups of species (p. 137; and see Tiffney, 1984). In this regard, plant species targeting vertebrates appear to depend on 2 forms of dispersal: (1) seed swallowing followed by defecation; or (2) seed swallowing followed by rumination and expectoration. The advantages to a plant of evolving adaptations to cope with the partial cleaning and spitting of seeds by one monkey subfamily are ambiguous, despite the advantages of a scattered dispersal.

It is clear, however, that the differential actions of frugivores are necessary for preserving forest diversity (Howe, 1989; Chapman and Onderdonk, 1998; Cordeiro and Howe, 2003). One immediate threat to forest diversity is the widespread reduction or extirpation of large-bodied frugivores (Walsh *et al.*, 2003). They are susceptible to hunting and habitat fragmentation and their absence can have short- and long-term effects on the recruitment of

large-seeded taxa (Howe, 1985; Chapman and Onderdonk, 1998; Corlett, 2002). The advantages of large, vertebrate-dispersed seeds (Foster, 1986; Lord *et al.*, 1997; Eriksson *et al.*, 2000) cannot overcome the fact that large frugivores are required for dispersal (Kitamura *et al.*, 2002). Accordingly, cercopithecines could be inferred to have a compensatory effect; that is, in the absence of large frugivores, cercopithecines might preserve large-seeded trees through an effective means of seed dispersal: seed-spitting. Our preliminary analysis suggests that this inference should be made with caution. Further, our case study of 3 species should not be generalized to entire forest systems. Additional data are required if we are to determine how alternative mechanisms of seed dispersal affect the dispersion of adult trees.

ACKNOWLEDGMENTS

We thank Lindsay Magnuson and Mary Glenn for inviting us to participate in the Conservation of African Monkeys Symposium at the 26th annual meeting of the American Society of Primatologists. We also thank L. J. Alport, B. Balyeganira, C. A. Chapman, M. Huff, P. Kagoro, J. E. Lambert, P. W. Lucas, M. Musana, C. Preuss, E. Ting, R. H. Tuttle, R. W. Wrangham, and 2 anonymous reviewers. The Makerere University Biological Field Station, Ugandan National Council for Science and Technology, and the Uganda Wildlife Authority granted research permission. Financing was received from the Croucher Foundation, Explorer's Club, National Geographic Society, Research Grants Council of Hong Kong, and Sigma Xi. We acknowledge with gratitude the software, equipment, and technical assistance received from Environmental Systems Research Institute Inc., OmniSTAR Inc., and Trimble Navigation Ltd.

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