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Seed Dispersal of a Tropical Forest Tree, *Pycnanthus angolensis* (Myristicaceae) by Chimpanzees in the Mahale Mountains National Park, Tanzania

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Abstract Seed dispersal of *Pycnanthus angolensis* by chimpanzees (*Pan troglodytes*) in the Mahale Mountains National Park, Tanzania was studied. Chimpanzees ingested and dispersed large numbers of viable seeds of the forest tree *P. angolensis* and many seedlings became established. The high density of this tree at Kasoje Forest in Mahale is due at least in part to seed dispersal by chimpanzees.

Key words Chimpanzee, Mahale, *Pycnanthus angolensis*, Seed dispersal, Seedling survival

Introduction

The majority of tropical plants rely on animals to disperse their seeds (Jacobs 1988), and the variety of food resources made available by plants in order to attract potential dispersers is said to be one of the factors underlying animal species richness (Whitmore 1990). Interactions between plants and the animals that disperse or destroy seeds are hypothesized to play crucial roles in the life histories of the relevant organisms (Janzen 1970) as well as in community composition and stability (Howe 1977).

Not only the quantity of seeds dispersed but also the quality of dispersal must be considered when evaluating the effectiveness of a disperser (Chapman 1989). Studies of Cercopithecine monkeys (Gautier-Hion *et al.* 1985; Rowell & Mitchell 1991), capuchins (*Cebus*) and spider monkeys (*Ateles*) (Zhang & Wang 1995), howlers (*Alouatta*) (Howe 1980) and patas monkeys (*Erythrocebus*) (Lieberman & Lieberman 1986) have reported variability in the quality of primates as dispersal agents. Differences in the germination and survival of seeds dispersed by primates have been related to differences in time spent feeding, feeding rates and travel distances. Zhang & Wang (1995), for example, found that seeds defecated by capuchins had a 2.6 times greater chance of survival than those defecated by spider monkeys, probably due to decreased seedling competition in the smaller fecal clumps of the capuchins.

Since monkeys usually drop large seeds beneath parent trees and often deposit small seeds in dense fecal clumps they have been viewed as less effective dispersers than other agents such as large frugivorous birds (Howe 1980; Levy *et al.* 1994). Large birds, however, often deposit seeds in large clumps; it has been observed, for example, that hornbills

disperse seeds to nesting tree sites with massive seedling mortality and do not influence seedling composition in the area of the nests (C. Chapman pers. comm.). Great apes with their comparatively large gut sizes (Milton 1984) large home ranges and long daily travel distances (Goodall 1986) may play a more significant role in the dispersal of tropical trees. A number of studies have shown that seeds ingested by great apes remain viable after they are eliminated (chimpanzees (*Pan*): Takasaki 1983; Takasaki & Uehara 1984; Wrangham *et al.* 1994; bonobos (*Pan*): Idani 1986, lowland gorillas (*Gorilla*): Rogers & Parnell 1991; orangutans (*Pongo*): Galdikas 1982). One study indicated that survival of seedlings at gorilla nest sites was higher than at sites elsewhere in the forest (Tutin *et al.* 1991). There have been few studies, however, of the fate of seeds in fecal clumps left by large mammals.

Numerous studies have shown chimpanzees to be largely frugivorous (Nishida 1968, 1976; Ghiglieri 1984; Goodall 1986). The diet of chimpanzees in the Kasoje area of Mahale in particular includes the fruits of 100 species of plants including large forest trees (Nishida & Uehara 1983). During the study M group chimpanzees spent more than 50% of feeding time in any given month feeding on fruits (Turner 2006). Chimpanzees therefore may be particularly important for the dispersal of large-seeded trees. Takasaki (1983) first noted that researchers observed the germination of fruit seeds in chimpanzee feces. He collected seeds of a number of species of chimpanzee food trees from feces and ripe fallen fruit and planted them in a camp garden. When the seeds were examined again a few months later he found that some species collected from feces showed "higher germinability" than those from fallen fruit. Subsequent experiments involving seeds from additional tree species (Takasaki & Uehara 1984) produced similar results.

These experiments were the first to provide evidence that chimpanzees may disperse the seeds of a number of tree species, however they did not allow investigation of the possible effects of deposition site, seedling density and predators on germination and seedling survival. Differences in the ground layer, canopy cover, soil and drainage create variations in microclimate that may influence germination and seedling survival (Whitmore 1990). Seed handling may also affect the outcome of germination experiments. The goal of this study, therefore, was to examine germination and survival of *Pycnanthus angolensis* (Myristicaceae) seedlings in chimpanzee dung deposits in the forest. Although general studies of chimpanzee seed dispersal are increasing in number, no study thus far has followed the interaction between chimpanzee and food plant from seed ingestion to germination. A number of indications suggest that chimpanzees may be important seed dispersers, but before any conclusions may be drawn it must be established that not only do seeds left in dung piles germinate but also that seedlings become established and survive. The role of deposition site may also be critical to the effectiveness of seed dispersal; the present study therefore sought to investigate the effectiveness of dispersal into both gaps and closed canopy forest.

Natural history of *Pycnanthus angolensis*

Pycnanthus angolensis (Welw.) Warb. or the "cardboard tree" is a native of Central and West Africa. It is a characteristic species of moist, intermediate-stage successional

forest in parts of East Africa (Lind & Morrison 1974). Trees can reach 25 m in height and exceed one meter in diameter (Vivien & Faure 1985). The tree produces clusters of fruits with a yellowish, two-valved pericarp (fruiting season is from June-February at Kasoje), 3-4 x 1.5 cm in size, which dehisces to reveal a thin, finely divided bright red aril surrounding a single, large black seed.

P. angolensis is a common tree in lowland forest at Kasoje (Turner 2006) and the fruit is an important resource for chimpanzees (Nishida 1977, 1991) as well as food for a number of other animal species in the habitat. Because the habitat is a mosaic of different vegetation types the distribution of *P. angolensis* is patchy (Turner 2006), and during fruiting season chimpanzees will sometimes feed at more than one patch in a single day.

Methods

Chimpanzees (*Pan troglodytes*) in the Mahale Mountains National Park, Tanzania, were observed to eat fruit and swallow seeds of *Pycnanthus angolensis* during 41 visits to trees on 28 separate days during the study for a total of 938 minutes feeding time. To determine the number of seeds ingested and defecated by chimpanzees, *P. angolensis* seeds were counted in dung deposits left by chimpanzees during follows of the study group. To study seed germination and seedling establishment a total of 564 seeds were monitored at 30 forest sites under closed canopy and in gaps (sites without canopy cover and exposed during the day to the sun) over a period of 4 months. Sites were chosen in late October through mid-November, labeled with stakes and surveyor's tape and their location recorded. Sites were checked on a weekly basis until all seeds had germinated and seedlings were established or until seeds rotted or were lost (Some seeds may have been carried away by predators while others were washed down slopes in heavy rainfall). Data on feeding by other frugivores at *P. angolensis* trees were collected during chimpanzee follows and extended watches at fruiting trees. Seeds of fruits eaten by chimpanzees but not previously tested for germinability (Takasaki 1983; Takasaki & Uehara 1984) were planted in a camp garden and checked for germination and survival.

Results

Chimpanzee feeding and defecation

Chimpanzees were observed during 41 visits to *P. angolensis* trees on 28 separate days during the study for a total of 938 minutes feeding time. The number of chimpanzees feeding at *P. angolensis* trees at one time ranged from 1-20 (mean no. in feeding party = 4.4) and feeding episodes lasted from 6 to 30 minutes. Chimpanzees usually consumed fruits while sitting in the parent tree but occasionally climbed down to the ground with a fruit-laden branch. They only ate ripe fruits and always swallowed seeds whole. Feeding rates were difficult to measure when chimpanzees were high in the canopy, but four adult males consumed 13-15 fruits in a one minute period and an adult female ate 10 fruits in

one minute. Chimpanzees defecated a mean number of 11.7 seeds per feces (SD 12.68, range 1-63, N=104). Wild chimpanzees have been noted to defecate 6.7 times per day (Wrangham *et al.* 1994); this would mean a single chimpanzee could disperse approximately 78 seeds of this species per day or 19,110 seeds during the entire fruiting season. The size of the chimpanzee group was approximately 56 individuals in 1994-95, therefore the entire group could potentially disperse over 1 million seeds during the peak season of feeding on *P. angolensis* fruit. Because chimpanzees commonly experience diarrhea during the *P. angolensis* fruit-eating season (S. Uehara pers. comm.) the frequency of defecation and therefore the actual number of seeds dispersed may be much higher than estimates from the present study.

Germination of seeds in chimpanzee feces

Although seeds were found in feces soon after *P. angolensis* fruits became available in June, germination was not observed during the dry season or early rainy season but was rapid once the rains became established around mid-November . Within three weeks 56.7% of seeds had germinated. Many of the seeds which did not germinate had seed coat damage in the form of bore holes or narrow "tracks" presumably made by insects. Some seeds (13%) could not be located, possibly removed by predators or washed away in heavy rains.

Differences in time to germination and seedling establishment at the two different types of sites (closed forest and gap) were noted (Fig. 1). More seeds (69.9%) germinated in closed canopy forest than in forest gaps (36.1%). Seeds in gaps were subject to desiccation and slow to germinate or did not germinate. Seedlings could not become established at sites where leaf litter completely covered the ground or on rocks.

Four months after deposition, 143 or 44.7% of the original 320 seedlings (25.4% of the original number of seeds) were still alive at deposition sites. Seedling survival is thought

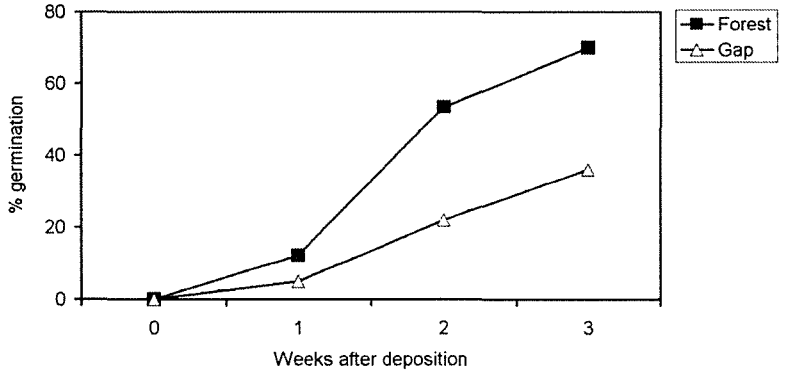

Fig. 1. Germination of *Pycnanthus angolensis* seeds in chimpanzee feces deposited in forest sites and in gaps.

Table 1. Consumers of *Pycnanthus angolensis* fruit at Kasoje.

Family Common name (Latin name)	Type of consumption
Musophagidae	
Ross's turaco (*Musofaga rossae*)	disperser
Sciuridae	
Giant forest squirrel (*Protoxerus stangeri*)	disperser
Viverridae	
African Civet (*Viverra civetta*)	neutral consumer?
Cercopithecidae	
red-tailed monkey (*Cercopithecus ascanius*)	neutral consumer
blue monkey (*Cercopithecus mitis*)	neutral consumer
red colobus (*Colobus badius*)	predator
Pongidae	
chimpanzee (*Pan troglodytes*)	disperser

to be even higher because many seeds may have germinated and become established on other sites after being washed down slopes by heavy rains or scattered by animals. Seedling survival was significantly higher in closed canopy forest than in gaps (chi-square = 67.9, df = 1, $P < .0001$). Seedlings often showed herbivore damage but still survived.

Seed handling by other frugivores

Six species of diurnal vertebrates were directly observed to feed on fruits of *P. angolensis* during the study (Table 1). Hornbills removed fruits from the shells and swallowed them whole. The fruit was also eaten by red-tailed monkeys (*Cercopithecus ascanius*) and blue monkeys (*Cercopithecus mitis*) who removed the aril with their teeth and spat out the seeds which fell to the ground beneath the parent tree. Red colobus monkeys (*Colobus badius*) bit through unopened shells; the whole fruit including the seed was thoroughly chewed and the remainder discarded. A giant forest squirrel (*Protoxerus stangeri*) was also observed gnawing and discarding partially-eaten fruits under the parent tree.

Whole, undamaged seeds were found in civet (*Viverra civetta*) feces on two occasions. These seeds later germinated in a camp garden. Dense clumps of seeds, sometimes in combination with the undigested fibers of oil palm fruits were also found at a distance from *P. angolensis* trees. These seed clumps, which later developed into luxuriant mats of seedlings, may have been dispersed by civets or guinea fowl which return repeatedly to the same spot to defecate. It is likely, however, that the majority of seedlings left in civet middens will die due to intense competition or some other factor: one researcher who has monitored a midden for 8 years has never seen a seedling survive to more than 20 cm. (C. Chapman pers. comm.).

Germination of other chimpanzee food species

Germination of seeds of some species not previously tested by Takasaki (1983) and Takasaki & Uehara (1984) was noted during this study. Seeds of Cissus ?petiola Hook. f. and *Psychotria peduncularis* (Salisb.) Steyerm. (Rubiaceae) were found already germinated in chimpanzee wadge. Germination of *Syzygium guineense* (Myrtaceae) seeds was also noted in discarded chimpanzee wadge, revealing that chimpanzees do not always destroy seeds even when they chew them.

Cordia africana Lam. (Boraginaceae) seeds from fallen fruit and chimpanzee feces and *Harungana madagascariensis* Poir. (Guttiferae) seeds from chimpanzee wadge, feces and fallen fruit all failed to germinate in a camp garden and recovered seeds were rotten. Seeds dispersed earlier in the fruiting period while rain continues to fall or in continuously moist environments i.e. near stream beds or grassland areas where the water table is close to the surface may be more successful at germinating. Seeds of *Afrosersalisia cerasifera* (Welw.) Aubrev. (Sapotaceae) did not germinate in the garden but germinated seeds were seen in chimpanzee feces deposited on rocks near a permanent stream.

Discussion

P. angolensis seeds were monitored in chimpanzee dung deposits to examine the effect of deposition site on seed germination and seedling survival. Survival of seedlings on canopy-covered forest sites was found to be greater than in gaps. Various tree species have different microsite preferences for seed germination and seedling growth (Whitmore 1990). *P. angolensis* falls into the secondary (non-pioneer) group of tree species, the seeds of which germinate quickly and often cannot withstand desiccation (Whitmore 1989, 1990).

In addition to chimpanzees, a number of other animal species were observed to consume fruits of *P. angolensis.* Hornbills and turacos transported fruits from trees and swallowed whole seeds with attached arils. Monkeys and squirrels dropped seeds beneath parent trees. Civets were indirectly found to disperse this species by the discovery of viable seeds in their feces and at civet middens.

One hypothesized explanation for fruit transport is that it may lessen the risk of predation (Howe 1979). *P. angolensis* is an emergent tree with open foliage where birds and small mammals would be easily visible to predators. When feeding on *P. angolensis,* frugivorous birds will quickly gather fruits, then fly to a neighboring dense foliage tree to consume their meal undisturbed. Monkeys and squirrels will remain only briefly in trees, feeding on a few fruits and dropping the seeds before leaving the canopy. Chimpanzees have little fear of predation and even after they are no longer hungry will linger in the branches of a large tree to rest and groom, and sometimes begin to feed again after a period of rest. This allows them to consume large amounts of fruit, the seeds of which are then dispersed as they travel through the forest.

Seedling mortality has been shown to be density-dependent and therefore greatest near the parent, presumably due to the effects of pathogens and predators (Whitmore

1990). In the forest at Kasoje, seed rain causes dense carpets of seedlings to develop beneath the canopies of *P. angolensis* trees. Seeds which are transported away from parent trees may have an advantage for survival. The morphological characteristics of *P. angolensis* fruits (bright color, conspicuous display, arillate fruit and large seed size) indicate that it is adapted for dispersal by specialist frugivorous birds (Gautier-Hion *et al.* 1985). Still, the tree probably gains an advantage from multiple dispersers by an increase in both the number of seeds dispersed and number of dispersal sites (Thompson 1982 cited in Gautier-Hion *et al.* 1985).

The forests at Kasoje were highly disturbed in the past due to a long history of human activity. Following the relocation of local inhabitants in 1974 (Nishida 1985) Kasoje chimpanzees continued to range in areas of abandoned fields and to feed there on remnants of agricultural crops such as the pith of banana plants (Nishid 1973). Utilization of human disturbed-zones by chimpanzees was probably important for tree colonization and forest recovery at Kasoje through the transport of seeds to those areas of the habitat. The common and widespread occurrence of *Pycnanthus angolensis* in lowland forest is due at least in part to seed dispersal by chimpanzees.

Although a number of animal species disperse *P. angolensis* seeds, chimpanzees may be particularly important for the dispersal of this tree due to the fact that they swallow large numbers of seeds, travel long distances and deposit seeds in many places. The chances of seedling survival from seeds left in chimpanzee dung deposits are probably greater than that of seeds left in dense deposits at hornbill nesting sites or civet middens because of less competition for resources and perhaps less risk from disease or predation. Further long-term research about seed survivorship and also information about the effectiveness of other animal species as dispersers is needed to fully understand the role chimpanzees play in the dispersal of *P. angolensis* and other tropical forest trees.

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