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# A case study of a plant-animal relationship: *Cola lizae* and lowland gorillas in the Lopé Reserve, Gabon

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ABSTRACT. The fruits of *Cola lizae*, an endemic tree with a limited geographical distribution, have been a major food source for lowland gorillas in the Lopé Reserve during part of each year over a six-year period. Faecal analysis indicated that 11,000–18,000 *Cola* seeds km$^{-2}$ were deposited by gorillas during the 4-month season in 1989. Gorillas are the only important dispersers of this species: other primates consume the succulent mesocarp, but do not swallow the large seed; elephants do not eat *Cola* fruits. Observations of *Cola* seeds in gorilla faeces showed a very high germination rate and, despite initial high mortality, 18% of seedlings still survived six months after deposition. Survival of seedlings was significantly better in faeces left at nest-sites than in other areas of the forest: 40% of seedlings were viable at nest-sites six months after deposition. This suggests that the open areas of forest, preferred by gorillas as nest-sites, are advantageous to the propagation of this species.

KEY WORDS: *Cola*, frugivory, Gabon, lowland gorilla, *Gorilla g. gorilla*, plant-animal interactions, seed dispersal, seedling survival.

## INTRODUCTION

The role of primates in the dispersal of seeds has been described at length (e.g. Estrada & Coates-Estrada 1984, 1986, Garber 1986, Gautier-Hion 1984, Hladik & Hladik 1967, Howe 1980, Lieberman *et al.* 1979), and has been noted for all species of great apes except gorillas (bonobos: Idani 1986; chimpanzees: Takasaki 1983; orang-utans: Galdikas 1982). An ongoing long-term study of western lowland gorillas (*Gorilla gorilla gorilla* Savage & Wyman 1847) in Gabon has demonstrated that this subspecies is frugivorous (Tutin & Fernandez 1985, Williamson *et al.* 1990). Definitions of frugivory vary and quantitative data on the diet of lowland gorillas are not yet available but, at the Lopé, gorillas eat fruit of at least 78 species and the remains of at least one species of fruit were found in 97% of gorilla faeces (Tutin & Fernandez 1987). Seedlings of several tree species have been seen sprouting in gorilla dung (e.g. *Celtis tessmannii* Rendle, *Parkia bicolor* A. Chev., *Santiria trimera* (Oliv.) Aubr.). Their large body and gut size, together with the considerable quantities of seeds they swallow, make gorillas potentially important dispersal agents for most of the species whose fruits they eat.

This paper concentrates on the relationship between gorillas at the Lopé and one species of tree, *Cola lizae* (N. Hallé 1987), a Sterculiaceae, which is of special interest for three main reasons: 1) in terms of density and dominance (basal area), *Cola lizae* is the most important tree in the Lopé study area (Williamson 1988) and, as such, is significant in the ecology of this area of lowland tropical forest; 2) *Cola lizae* is endemic to Gabon and has a limited geographic distribution (Hallé 1987); and 3) *Cola lizae* provides a major source of food for primates, but only gorillas and occasionally chimpanzees (*Pan troglodytes troglodytes* Blumenbach 1779) swallow and thus disperse the large seeds. Monkeys spit out seeds and no frugivorous bats large enough to disperse the seeds occur at the Lopé. *Cola lizae* fruits dominate the gorillas' diet during a period of two to four months most years.

Mature *Cola* trees are usually of medium height (20–25 m) with very large, simple leaves (up to 100 cm by 125 cm). The fruit is bright crimson when ripe, with four follicles, each a thick rubbery pod containing five to eight seeds in a clear liquid. Each large seed (2.5 cm by 3.5 cm) has two purple cotyledons encased in a fibrous coat and covered with a thin layer of succulent mesocarp, protected by a transparent yellow 'skin' (Figure 1).

The fruits of most tropical forest trees show a range of morphological characters which favour dispersal of their seeds by a particular agent (e.g. Howe & Vande Kerckhove 1979, Janson 1983, Van der Pijl 1972). Fruit characters shown to be adapted to particular groups of animal dispersers include: colour, degree of protection, quality of the flesh, and size. The majority of fruits eaten by gorillas at Lopé fit the 'bird-monkey' dispersal syndrome (succulent or arillate/brightly coloured/unprotected) described by Gautier-Hion *et al.*, (1985), but they also eat some 'ruminant-rodent-elephant' fruits (dry, fibrous flesh/dull coloured/large/ well protected) (Rogers *et al.*, 1988). *Cola lizae* fruits show characters of both these dispersal syndromes, being brightly coloured with succulent flesh, but also large and well protected.

Here we quantify the importance of *Cola lizae* in the diet and examine the role of gorillas in the dispersal and propagation of this species.

## STUDY SITE AND METHODS

Data come from the Lopé Reserve in central Gabon, where research on lowland gorillas and chimpanzees began in 1983. The study area of approximately 40 $km^2$ (0° 10′ S, 11° 35′ E) is mostly mature tropical forest with a zone of savannas and gallery forests in the north-east. Parts of the forest were selectively logged in the early 1960's, when a single species of tree, *Aucoumea klaineana*, was extracted at a rate of 1–2 trees $ha^{-1}$.

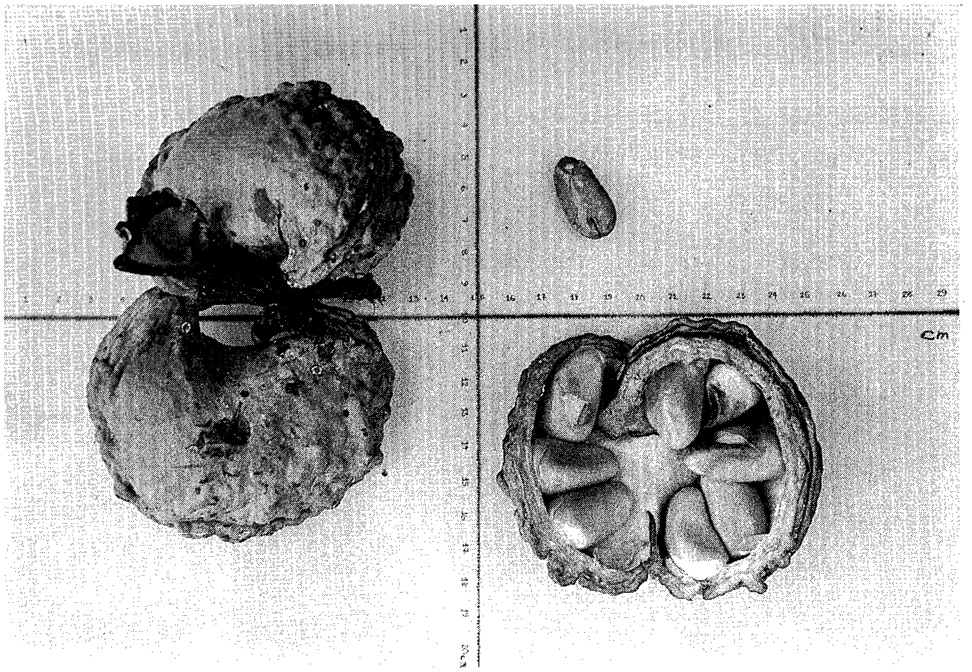

Figure 1. The fruit of *Cola lizae*: a pair of follicles; a cut open follicle showing the seeds with mesocarp, and a cleaned seed showing cotyledons.

Mean annual rainfall is 1532 mm (5-year average) with two wet seasons (March–June and October–December) and two dry seasons (January–February and July–September). Mean monthly minimum temperatures vary from 20.1–23.2° and mean monthly maximum temperatures from 27.0–32.8°C.

Field procedure involved searching through the forest for gorillas, or indirect signs of their presence and activities. When gorillas were located we attempted to observe them for as long as possible. At the beginning of the study the gorillas were unused to humans and generally fled when encountered. By 1988, two groups of gorillas were partially habituated to the presence of observers but, as visibility is generally poor, observation is still difficult. Thus, we have concentrated on indirect methods to describe diet, systematically collecting fresh faeces and describing feeding traces left by gorillas (see Tutin & Fernandez 1985 for details of field methods). Faecal samples were collected whole in the field and sealed in plastic bags. They were later weighed, and washed in sieves with 1 mm mesh for examination of the particulate remains. The contents of each faecal sample were listed, large seeds counted, and other items rated as being abundant, common, or few. Schaller (1963: p.90) described differences in the size and diameter of the dung of mountain gorillas related to age-class. The dung of lowland gorillas at Lopé was frequently softer and less well formed than that of mountain gorillas, but a proportion could be assigned to a particular age-class.

All trees over 10 cm dbh (diameter at breast height, measured 1.3 m from the ground) were identified and measured along four 10 m wide transects spread through the study area. The total length of transects was 4 km, giving a 4 ha sample.

Phenological data on leaf, flower and fruit production, have been collected monthly since 1984. The 60 tree species monitored include all those whose fruits are frequently eaten by gorillas and/or chimpanzees. Ten marked individuals of each species were examined each month and the relative quantities of flowers and fruits scored from zero to a maximum of four.

Samples of gorilla foods have been collected and dried for chemical analysis (Rogers *et al.* 1988, 1990). Unripe and ripe *Cola* pods were collected from several different trees, and processed by removing the seeds and scraping off the succulent mesocarp and 'skin'. These were analysed separately, because only the mesocarp is digested. Samples were dried in an oven over paraffin lamps at not more than 50°C. When they were of constant weight, they were sealed in plastic bags and transported to the UK for chemical analysis. Assays were done of acid-detergent fibre, crude lipid and protein, water soluble sugars, total phenols, and condensed tannins, using standard techniques. We also checked for the presence of alkaloids.

## RESULTS

Gorillas at the Lopé eat 182 plant foods from 134 species and 36 families (Williamson *et al.* 1990). Appendix I lists 75 species, identified at least by family, of which gorillas consume succulent or fibrous pericarp/mesocarp. For 87% (65) of these species, gorillas excrete all, or the majority of, seeds intact and presumably unharmed. The large seeds of another five species are occasionally swallowed but usually rejected after the flesh has been removed.

The phenology data on production of flowers and fruit by *Cola* from December 1984 to April 1989 are summarised in Figure 2. The patterns observed from 1986 to 1989 were similar, with flowers appearing in August, peaking in September–October and fruit being most abundant in January–March. In 1985 very few fruit were present in January–March, but *Cola* trees produced flowers from March onwards and a minor crop of fruit in July (heavily exploited by gorillas, see below). The total fruit scores for the 10 trees monitored each month, with a theoretical maximum score of 40 are presented in Figure 2. The actual scores are low, with a maximum of 10.5 in March 1987, for two reasons: 1) the fruits of *Cola* tend to be hidden by the trees' enormous leaves and this probably leads to an underestimation of each tree's crop; and 2), individual *Cola* trees produced variable quantities of fruit and ripening was spread over several months giving a long, though obvious, fruiting season for the species. All trees in the phenology sample flowered each year but, as well as inter-annual variation in the total quantity of fruit produced, individual trees showed different fruiting patterns (see Figure 3): one tree produced fruits in each of the five years; five trees fruited in four years; one in three years; two in two years, and one tree has not yet been seen to fruit. No attempt was made to count individual fruit, but a phenology

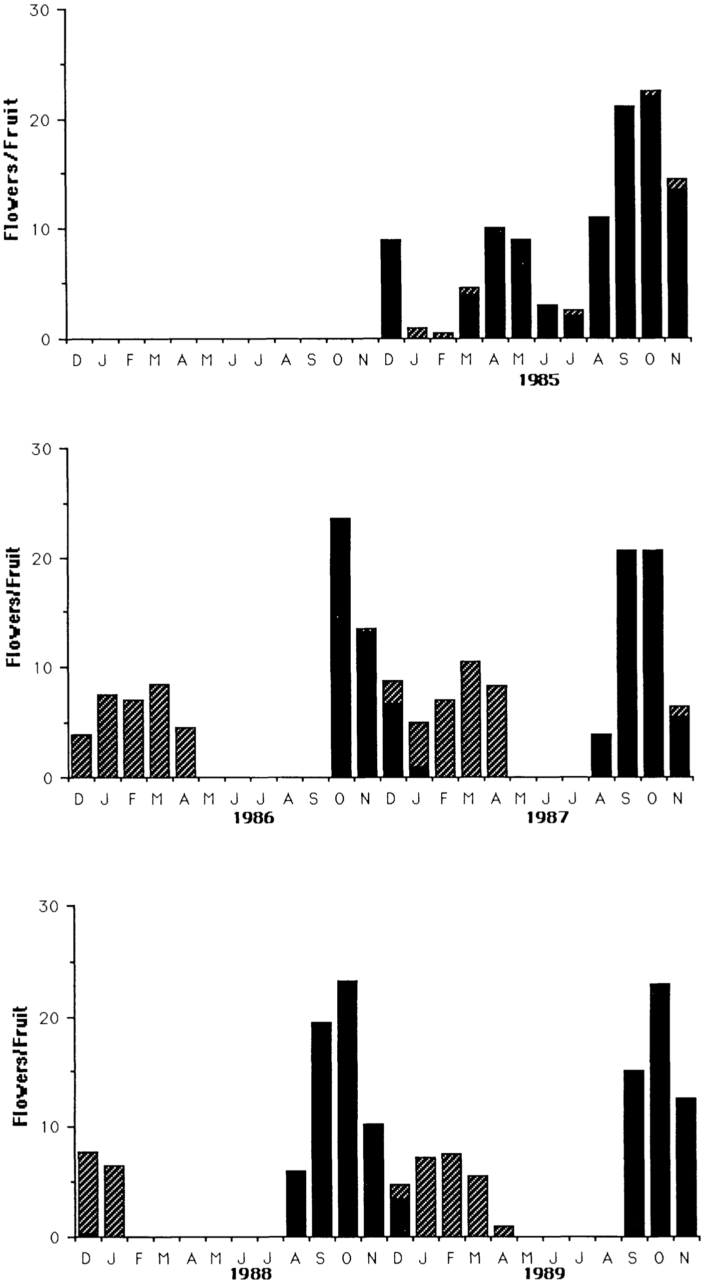

Figure 2. Production data summed for 10 *Cola lizae* trees over a five-year period. Flowers solid bar; fruit hatched bar.

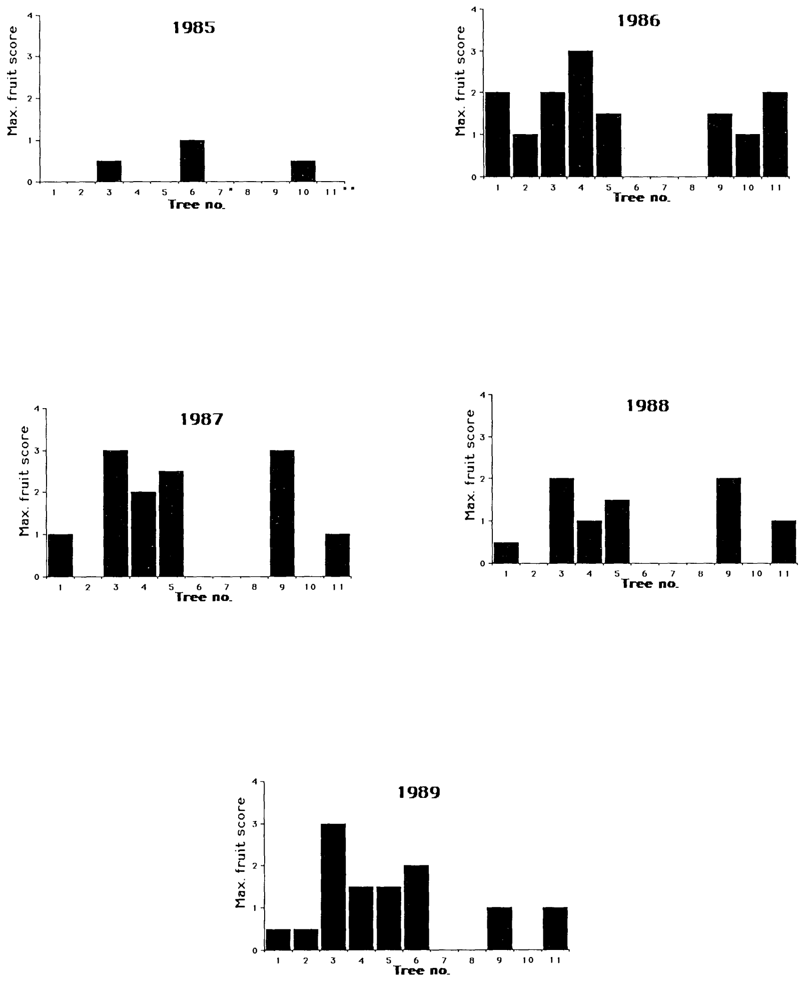

Figure 3. Annual fruit production by the 10 *Cola lizae* trees in the phenology sample, 1985–1989. *Tree 7 died in November 1985. **Tree 11 was added in November 1985 to replace tree 7.

score of one represents approximately 50 fruits (or 200 follicles).

Figures 2 and 3 do not suggest that fruit is abundant. However, *Cola* occurs at high frequency: 394 trees with dbh $\geq$ 10 cm were recorded in 4 ha of transects (Williamson 1988). Trees of < 15 cm dbh are not sufficiently mature to produce fruit, but nonetheless this sample included 244 *Colas* of $\geq$ 15 cm dbh, giving a mean density of 6100 mature trees $km^{-2}$ in the central study area. This is a particularly high density as *Cola* has a patchy distribution and a 2 ha sample in an area 7 km west of our study area recorded a mean density of only 100 mature *Cola* $km^{-2}$ (Harrison, pers. comm.).

*Cola* seeds were found in 522 of the 3123 gorilla faecal samples examined between December 1983 and April 1989. Figure 4 shows the percentage of samples containing *Cola* by month for this period. *Cola* was eaten each year and,

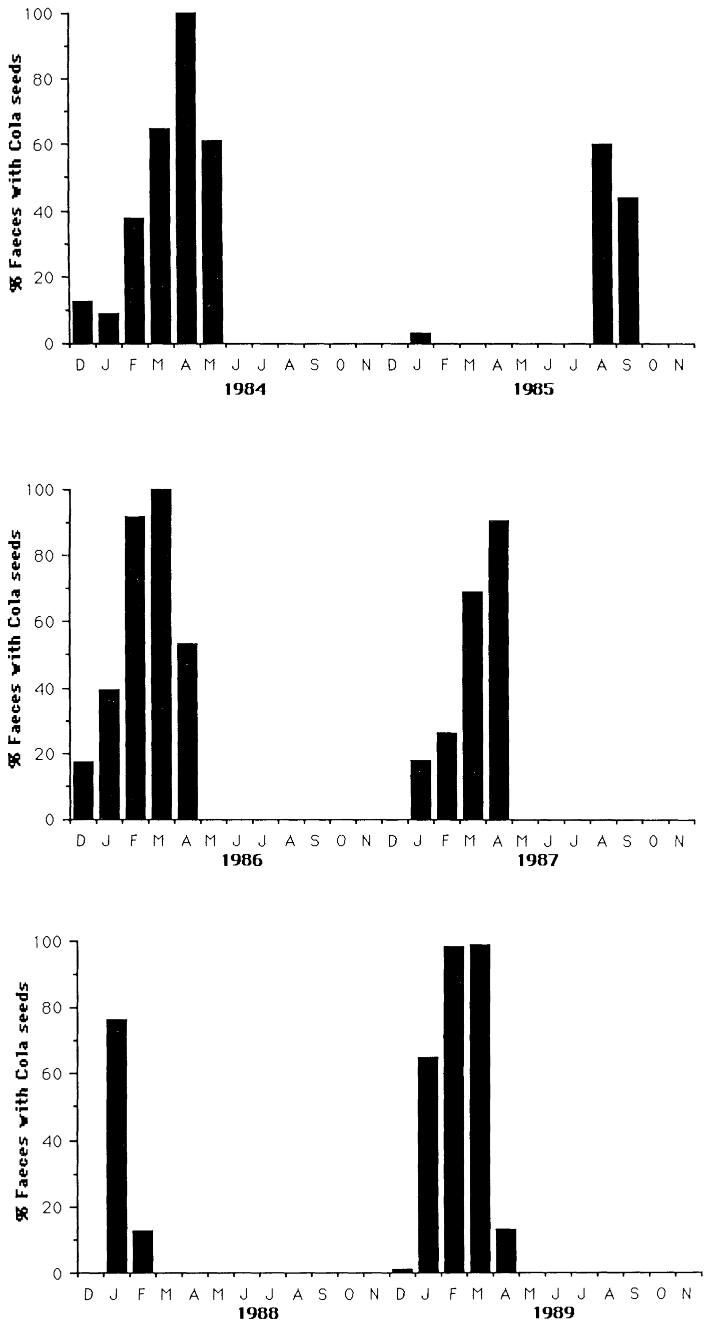

Figure 4. Percentage of gorilla faeces containing *Cola lizae* over a six-year period.

except in 1985, consumption by gorillas was most frequent during the first four months of the year.

Gorillas process *Cola* fruits by biting into the pod, letting the clear fluid drain and then opening the pod with mouth and hands and extracting the individual seeds by mouth. The pod is then dropped and another plucked. Processing involves not only the removal of individual seeds, but also piercing of the transparent yellow 'skin' around the mesocarp: if this is not done, the mesocarp is not digested. Generally, gorillas ate fully ripe, red, fruits but some full-sized, green, fruits were eaten at the beginning of the season and in 1988, when there was an unusual scarcity of ripe fruit, most of the *Cola* crop was consumed in January before it was ripe (see Figure 4). Gorillas have been observed feeding for up to 11 minutes in a *Cola* tree and examination of feeding remains showed that a group of eight gorillas had consumed over 100 pods at one tree. Trail data from the 1989 season showed that gorillas visited up to six *Cola* trees in a day.

In 1989 *Cola* fruits were eaten from January to April. Overall, 81% (N = 234) of gorilla faeces collected during this four-month period contained *Cola* seeds. This proportion reached 98% (N = 177) between 23 January and 28 March, when fruits were ripe and abundant.

Table 1 shows the mean number of seeds in each faecal sample containing *Cola* during the 1989 fruiting season, and that this is directly related to the rank order of body (and faecal) weight. The mean number of seeds in each sample was 30.9 for the 234 faeces collected from January–April and 38.1 for the 190 faeces that contained *Cola.*

*Cola* seeds represented a considerable proportion of the weight of faecal samples collected during the season. The total weight of the 190 samples containing *Cola* was 72.4 kg, and the 7232 *Cola* seeds contained within them weighed 34.4 kg. Thus, the average proportion of the faecal weight formed by *Cola* seeds was 47% (Range (R) = 1–98%). The average wet weight of mesocarp by seed was 1.4 g (N = 14), so the 'meal' represented by the average *Cola*-containing faecal sample was 53.3 g of mesocarp (R = 1.4–336 g).

The chemical analysis of *Cola* mesocarp, the only part of of the fruit which is

Table 1. Number of Cola seeds in gorilla faeces, January–April 1989.

| Age-class | No. faeces containing *Cola* | Mean No. *Cola* seeds/faeces | Range |
|---|---|---|---|
| Silverback | 18 | 55.3 | 1–218 |
| Adult | 47 | 53 | 1–164 |
| Juvenile | 38 | 23.5 | 1–87 |
| Infant | 2 | 3.5 | 1–7 |
| Unassigned | 85 | 33.5 | 1–240 |
| TOTAL | 190 | 38.1 | 1–240 |

digested, revealed a high content of soluble carbohydrate (Table 2). As can be seen, the sugar content rises as the fruit ripens, but it is already high in full-sized unripe fruit. The levels of condensed tannins measured are not exceptionally high for gorilla foods at Lopé (Rogers 1989, Rogers *et al.* 1990), but might contribute to the low digestibility of the 'skin' surrounding the mesocarp, and the relative unpalatability of unripe mesocarp. No measurable alkaloids were detected in either *Cola* seeds or seed coats.

Defaecation rates of gorillas at Lopé are unknown at present, but it is clear from nesting sites and trails that an individual defaecates several times each day, and an estimate of 3–5 times each 24 hours is conservative. The mean number of *Cola* seeds in faecal samples collected during the season was 30.9, which gives 93–155 seeds excreted per gorilla each day, making a total of 11,160–18,600 seeds excreted by each gorilla during the four month *Cola* season. The density of gorillas in the study area is approximately one individual $\text{km}^{-2}$; therefore between 11,000 and 18,000 *Cola* seeds are distributed $\text{km}^{-2}$ of forest.

### *Germination of* Cola *seeds and survival of seedlings*

Faeces collected in the field were kept, sealed in their plastic bags, for up to a week at camp before sieving. Seven faecal samples collected from a gorilla nest-site of 20–21 March 1989 were sieved two days later. We noted that 252 out of 364 *Cola* seeds they contained had begun to germinate and five days later, an additional 54 (kept on damp paper) had also germinated, giving 84% germination success seven days after deposition in faeces.

We also followed the fate of *Cola* seeds in undisturbed gorilla faeces, and made casual observations on seeds dropped below *Cola* trees by monkeys, and those in whole fruits which fell to the ground and rotted. We monitored germination and survival of seedlings in 34 undisturbed gorilla faecal samples at four-week intervals for six months after deposition. Sixteen of the monitored faecal samples were at a nest-site dating from 17–18 March 1989. The other 18 faeces were found in the forest between 14 March and 6 April and had been deposited by gorillas

Table 2. Chemical analysis of *Cola lizae* seeds and seed coats. (ND, not done because of shortage of material; NA, values not available separately because ripe seeds were dried with adhering mesocarp which was easier to scrape off without loss.)

| | Unripe mesocarp | Ripe mesocarp | Ripe seed | Ripe 'skin' |
|---|---|---|---|---|
| *% Dry Matter* | | | | |
| Crude protein | 12.3 | 3.9 | 7.7 | ND |
| Water soluble carbohydrate | 31.4 | 58.4 | 10.0 | ND |
| Crude lipid | 0.3 | 0.3 | 1.0 | ND |
| Acid-detergent fibre | 22.5 | 16.5 | 5.3 | 20.6 |
| Total phenols | 8.8 | 1.9 | 1.8 | 3.8 |
| Condensed tannins | 28.5 | 10.4 | 6.2 | 20.2 |
| % Water | 83.0 | NA | NA | 65.9 |

during travel and/or feeding. *Cola* seeds were counted at the first observation and on subsequent visits, the number and condition of surviving seedlings were noted and causes of mortality assessed when possible. Despite high germination rates, early seedling mortality was very high and, from 1043 seeds in the total sample, there were only 416 seedlings (40%) 7–9 weeks after deposition. After six months, this figure had dropped to 195 (19%).

There was a striking difference between seedling survival in faeces left at nest-sites compared with other areas of forest (Figure 5). Two months after deposition, 341 surviving seedlings (from 476 seeds) were present at the nest-site with a mean of 21.3 (4–100) in each faecal sample. In the faeces from other areas of forest, only 75 surviving seedlings (from 567 seeds) remained, giving a mean of 4.2 (0–12). This difference is highly significant: $\chi^2 = 221$, DF = 1, $P < 0.001$. While seedling mortality continued to take its toll (Figure 5), six months after deposition 189 (40%) seedlings still survived at the nest-site. By this time, only 6 (1.1%) of those in faeces elsewhere in the forest were still viable. Figure 6 shows a group of healthy seven-week-old *Cola* seedlings 20–30 cm high) in faeces left beside a nest. Major identifiable causes of seedling mortality were: feeding on leaves by insects or ungulates, trampling by elephants, and disease.

Systematic data were not collected from *Cola* seeds spat out by primates or from those in fruits that fell from trees, but very few surviving seedlings were found below *Cola* trees seven weeks after the 1989 fruiting season.

Of 79 chimpanzee faecal samples collected during January–April 1989, five contained *Cola* seeds and an additional 25 had no seeds but contained the characteristic transparent skin that covers *Cola* mesocarp. Thus, although 38% of chimpanzee faecal samples included remnants of *Cola* fruit, only 6% contained seeds, with a mean of 4.2 (N = 5) seeds in each sample (R = 1–11).

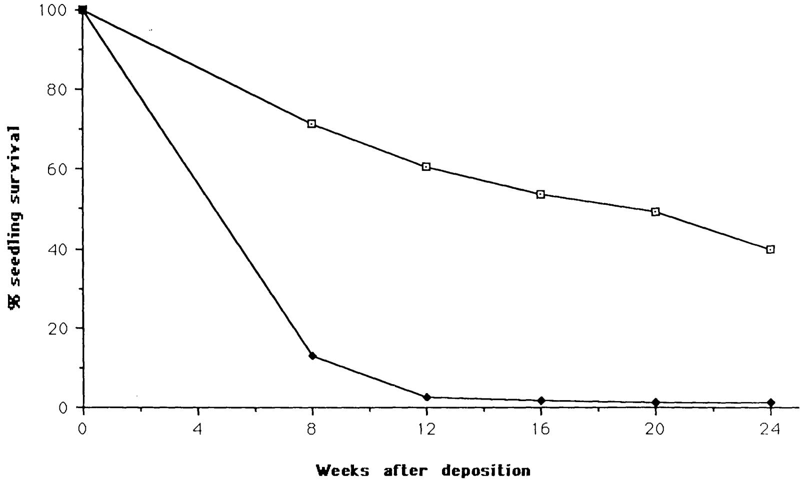

Figure 5. Survival of *Cola lizae* seedlings in undisturbed gorilla faeces. □—□, seedlings at nest-sites; ◆—◆, seedlings in other areas of the forest.

Figure 6. A group of *Cola lizae* seedlings in gorilla faeces left at a nest-site, seven weeks after deposition.

## DISCUSSION

The fruit of *Cola lizae* has formed a major part of the diet of gorillas at the Lopé during the six consecutive years of this study. Despite inter-annual variation in fruit production (Figures 2 & 3), the abundance of *Cola* trees in the study area allowed gorillas to feed intensively on the fruit each year. The high level of *Cola* fruit consumption, even when phenology data indicated fruit to be relatively uncommon (see Aug–Sept 1985 data in Figures 2 & 4), suggest that it is a highly preferred food. *Cola* mesocarp has one of the highest sugar levels (WSC in Table 2) of all the gorilla foods analysed from Lopé (Rogers *et al.* 1990) and this may explain its particular attraction.

The availability of all fruits eaten by gorillas at Lopé varies seasonally, but not all tree species have such a regular annual rhythm of production as *Cola lizae*. While *Cola* dominated the gorillas' diet for 2–4 months in each year, it was not the most commonly-eaten fruit on an annual basis, ranking seventh in 1984–85 (Williamson 1988) and tenth in 1988 (unpublished data). *Cola lizae* is one of the 15 species whose fruit is ranked as consistently important in the diet of the Lopé gorillas (see Appendix I): these are fruit which are eaten whenever they are available and the spatial distribution of which influences ranging patterns of the gorillas (Tutin *et al.* in prep.). So, in terms of gorilla nutrition, *Cola lizae* is an important but not exceptional fruit, but for *Cola lizae* gorillas are important and exceptional dispersers of seeds, depositing 11,000–18,500 $\mathrm{km}^{-2}$ in the 1989 season.

A major aspect of seed dispersal is the transport of seeds away from the parent plant. This is particularly important for a colonising species, such as *Cola lizae*, which thrives in light-gaps, as the probability of germination in dense shade below the large-leaved parent tree appears low (pers. obs.). There are likely to be other advantages of transport away from the parent as species-specific seed and seedling predation have been found to be greater near conspecific trees (Janzen 1970). Gorillas at Lopé travel an average of 1.2 km each day (R = 0.3–2.6 km) (Tutin *et al.* in prep.). Gut passage time is not known for wild gorillas, although Milton (1984) found a long and variable transit time of 17–84 hours in captive gorillas. Thus, ingested seeds could be carried considerable distances before deposition.

Additional benefits of endozoochory are that seeds are surrounded by a dung matrix, which reduces desiccation and may provide an advantageous substrate for germination. Whether seeds benefit from any chemical or mechanical action of the digestive tract, or not, is debatable (Estrada & Coates-Estrada 1986, Lieberman & Lieberman 1986), but we can conclude that the gorilla's digestive system appears not to inhibit germination of *Cola* seeds as 84% of seeds from faeces had germinated seven days after deposition. Gorillas avoid chewing the unprotected cotyledons of *Cola*, but the fibrous coat of ripe seeds in faeces was either totally removed or loosened, presumably during passage through the gut. Assertion of positive effects of passage through a gorilla's gut on germination success cannot be made as non-ingested seeds were not monitored systematically in this study. However, Ibikunle & Mackenzie (1974) found significantly higher germination rates in seeds of *Cola nitida* Schott & Endl. which had either been soaked in water or had had the two cotyledons mechanically separated before sowing, compared with untreated seeds.

The likely advantages of gorillas as dispersal agents of *Cola lizae* may, to some extent, be counteracted by the large number of seeds swallowed. Gorillas ingest the seeds in vast quantities with up to 240 seeds counted in a single faecal sample. Thus, while many seeds are transported from the parent tree and germination rate is high, seedlings may be subject to intense competition within faecal clumps (cf. Howe 1980). Observations of seedling survival indicate that even six months after deposition, dominant seedlings had not clearly emerged.

Dispersal does not imply the fate of the seed (Janzen 1983), but a high-quality propagator should deposit seeds at sites favourable, or at least not adverse, to their germination. Wheelwright & Orians (1982) state that seed dispersal lacks the precision of pollen dispersal and that, whereas 'plants can control pollinators' movements by providing nutritional and reproductive incentives at the appropriate site (flower) . . ., there is no similar incentive for seed dispersers to drop seeds in appropriate places' (page 405). However, gorillas excrete up to 50% of their daily faeces at sleeping-sites (Schaller 1963:203), the rest being deposited during daily feeding and travel. Gorillas construct a new sleeping 'nest' each night and tend to choose open areas (where the herbaceous plants used for nest construction are common). At the Lopé, 63% of nests had no overhead cover (Williamson 1988). These conditions are likely to favour the rapid germination and growth of *Cola lizae*, which seems to be well adapted to colonising light gaps. The present study indicates that seedling survival is higher at nest-sites than in other parts of the forest. Observations suggest that seedlings at nest-sites are less vulnerable to trampling by elephants, or browsing by ungulates, and their good state of health and 40% survivorship 24 weeks after deposition, suggest that typical gorilla nest-sites provide favourable micro-habitats for *C. lizae*.

It is clear that gorillas are reliable, high-quality, dispersers of *Cola lizae* and out data show that chimpanzees are the only other member of the diverse community of frugivores at Lopé which also disperse *Cola* seeds. Birds, bats and rodents have not been observed feeding on *Cola* fruit. The absence of mammalian seed predation suggests that the cotyledons are chemically protected. Five species of monkey eat the mesocarp, but never ingest seeds. Normally, monkeys drop seeds (unharmed) below the parent tree, but some may be transported short distances, in cheek pouches, before processing. Chimpanzees eat large amounts of *Cola* mesocarp but swallow relatively few seeds. The seeds' large size, 2.5–3.5 cm long, is obviously an important factor in their dispersal. For a small primate it is costly to fill the gut with a large non-usuable volume, so monkeys invest time and energy separating the pulp from the seeds. The different patterns of seed ingestion shown by gorillas and chimpanzees are striking given the similarity of the relationship between body and gut size (Chivers & Hladik 1984) and gut passage time (Milton 1984) in the two species.

Elephants (*Loxodonta africana cyclotis* Blumenbach 1797) at the Lopé are opportunistic frugivores and show considerable dietary overlap with the apes but they do not eat *Cola* fruit. We can only speculate about the reasons for elephants' avoidance of this fruit. Certainly, seed size is not the explanation, as elephants are known dispersers of considerably larger seeds than *C. lizae*, e.g. *Panda oleosa* Pierre, *Saccoglottis gabonensis* (Baill.) Urb, *Klainedoxa gabonensis* Baill., and *Pentadesma butyracea* Sabine (pers. obs.; Alexandre 1978; Lieberman *et al.* 1987). Elephants are skilful manipulators and able to extract large pulp-covered seeds from fruits such as *Mammea africana* Sabine (pers. obs.). The cotyledons of *C. lizae* are not physically protected either by a rigid fruit shell, or by a lignified seed coat, but they may be chemically defended: the clear fluid found in the fruits of certain *Cola* species contains a substance that inhibits growth of other seedlings (Miège *et al.*, 1970) and which may have an adverse effect on the metabolism of mammals. The unusual form of *Cola* fruits may render them difficult for elephants to manipulate without ingesting the fluid. This hypothesis gains support from our observation that primates empty this fluid from the pods of *Cola* before they eat the mesocarp. It is also possible that the crimson cotyledons of *C. lizae* contain caffein, as do the seeds of the commercially exploited *Cola nitida* (Ogutuga 1975). If so, elephants may not eat the fruit, because they are unable to avoid biting into the cotyledons during feeding.

Gorillas at Lopé disperse seeds of at least 65 species of plants and their impact on the ecology of the forest must be considerable. The fruit eaten by gorillas at Lopé are diverse both in morphological characters and chemistry (Rogers *et al.* 1990). It seems that gorillas bridge the broad vertebrate disperser categories, having a combination of morphological characters that set them slightly apart (large gut, climbing ability, strong jaws). Patterns of ranging and other behaviours (e.g. choice of nesting sites) also make them seed dispersers 'par excellence', at least for light-tolerant plant species.

In the absence of historical data, co-evolution between gorillas and *Cola lizae* can only be suggested but such specialization to a single species of disperser is unusual (Herrera 1986, Wheelwright & Orians 1982). As *C. lizae* is the commonest tree in the study area, it appears to be a system that works well. However, the important local differences in the density of *C. lizae* and its restricted geographical range, require explanation. Gorillas still occur in the majority of Gabon's forests (Tutin & Fernandez 1984), but *C. lizae* is restricted to a small area in the centre of the country (Hallé 1987).

The discovery that the commonest tree in our study area at Lopé was an undescribed species was surprising and provides yet another example of the incompleteness of the understanding of tropical forest ecosystems. The specialised disperser relationship between *C. lizae* and gorillas is an example of the delicate links that can exist within an ecosystem. Alexandre (1978) found indications that local extermination of elephants (by hunting) in some areas of forest in Ivory Coast led to the absence of young trees of species with elephant-dispersed seeds. If gorillas in central Gabon had been as heavily persecuted as those in some areas, perhaps *Cola lizae* would not have survived long enough to have been identified and described.

## SUMMARY

1. Gorillas in the Lopé Reserve, central Gabon, are the most frugivorous population of this species studied to date (Williamson *et al.* 1990) and they disperse seeds of at least 65 plant species. The fruits eaten by gorillas are morphologically and chemically diverse (Rogers *et al.* 1990). Lowland gorillas are likely to exert a strong influence on the ecology of tropical forests in which they occur.
2. As part of an on-going study of the behavioural ecology of lowland gorillas at the Lopé, faeces are collected and analysed to describe the gorillas' diet, and phenology data collected monthly on leaf, flower and fruit production of 60 species of trees whose fruits are regularly consumed by gorillas.
3. Analysis of these data over a six-year period revealed that gorillas eat large quantities of *Cola lizae* fruits whenever they are available. *C. lizae* is an endemic species with a limited geographical distribution (Hallé 1987), but is the commonest tree in the Lopé study area. The fruits are eaten by other primates, but the large seeds are very rarely swallowed except by gorillas.

Gorillas deposited between 11,000 and 18,000 *Cola* seeds km$^{-2}$ in the four-month season in 1989.

4. Given this specific disperser relationship, we examined the fate of a sample of 1043 *Cola* seeds in undisturbed gorilla faeces. The germination rate was high, but seedling mortality in the first eight weeks after deposition was also high. There was a very significant difference between seedling survival rate in faeces deposited at nest-sites, and those in other areas of the forest. Seedlings thrived at nest-sites which are typically in areas of forest where overhead cover is sparse, such as light gaps, and six months after deposition 40% of nest-site seedlings were surviving, compared with only 1% in other areas.
5. Chemical analysis of *C. lizae* fruits revealed that the mesocarp (the only part digested by gorillas) has a high sugar content. Data from a related species, *C. nitida*, suggest that the fruit may be chemically protected from some potential consumers by the composition of the clear fluid surrounding the seeds and by concentrations of caffein in the cotyledon (Miège *et al.* 1970, Ogutuga, 1975).
6. *Cola lizae* is exceptional because gorillas appear to be the sole dispersers of its large seeds. Such a specific plant-animal relationship is unusual (Herrera 1986, Wheelwright & Orians, 1982) but appears successful as mature *Cola* trees occur at a mean density of 6100 km$^{-2}$ in the study area.

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Appendix 1. Characteristics of fruit consumed by lowland gorillas at the Lopé, fate of seeds and importance in the diet

| | | Fruit characteristics | | | | |
|---|---|---|---|---|---|---|
| Scientific Name or Number | Family | Size | Colour | Seed size | Fate of seeds | Import in diet |
| *Aframomum longipetiolatum* Koech. | ZINGIBERACEAE | L | RED | S | 1 | 3 |
| *Aframomum sp. nov.* | ZINGIBERACEAE | L | RED | S | 1 | 1 |
| *Aframomum ?leptolepis* Shum. | ZINGIBERACEAE | L | RED | S | 1 | 3 |
| *Antidesma vogelianum* Müll. Arg. | EUPHORBIACEAE | S | PURPLE | S | 1 | 2 |
| *Antidesma sp* #251 | EUPHORBIACEAE | S | PURPLE | S | 1 | 3 |
| *Antrocaryon klaineanum* Pierre | ANNONACEAE | M | YELLOW | L | 1 | 3 |
| *Celtis tessmannii* Rendle | ULMACEAE | M | GREEN | M | 1 | 1 |
| *Chrysophyllum subnudum* Baker | SAPOTACEAE | L | GREEN | L | 1 | 3 |
| *Cissus dinklagei* Gilg & Brandt | VITACEAE | M | ORANGE | M | 1 | 2 |
| *Cola lizae* N. Hallé | STERCULIACEAE | L | RED | L | 1 | 1 |
| *Dacryodes normandii* Aubr. & Pellegr. | BURSERACEAE | M | PURPLE | L | 1 | 1 |
| *Detarium macrocarpum* Harms. | CAESALP. | L | GREEN | VL | 3 | 4 |
| *Dialium ?soyauxii* Harms. | CAESALP. | M | BROWN | M | 2 | 1 |
| *Dialium sp* #118 | CAESALP. | M | BROWN | M | 1 | 3 |
| *Diospyros abyssinica* (Hiern) F. White | EBENACEAE | S | RED | S | 1 | 3 |
| *Diospyros dendo* Welw. ex Hiern | EBENACEAE | M | RED | M | 2 | 1 |
| *Diospyros cf. iturensis* (Gürke) R. Let. & F. White | EBENACEAE | M | YELLOW | M | 1 | 4 |
| *Diospyros polystemon* Gürke | EBENACEAE | M | RED | M | 2 | 1 |
| *Diospyros suaveolens* Gürke | EBENACEAE | L | BROWN | L | 1 | 5 |
| *Drypetes sp* #264 | EUPHORBIACEAE | M | GREEN | M | 1 | 4 |
| *Duboscia macrocarpa* Bocq. | TILIACEAE | L | BROWN | S | 1 | 5 |
| *Enantia chlorantha* Oliv. | ANNONACEAE | M | RED | M | 1 | 2 |
| *Ficus macrosperma* Mildbr. & Hutch. | MORACEAE | L | GREEN | S | 1 | 5 |
| *Ficus mucuso* Ficalho | MORACEAE | M | GREEN | S | 1 | 5 |
| *Ficus polita* Vahl | MORACEAE | M | GREEN | S | 1 | 5 |
| *Ficus recurvata* De Wild | MORACEAE | M | GREEN | S | 1 | 5 |
| *Ficus thonningii* Bl. | MORACEAE | S | GREEN | S | 1 | 5 |
| *Gambeya africana* Pierre | SAPOTACEAE | L | ORANGE | L | 1 | 1 |
| *Grewia sp* #343 | ANACARDIACEAE | M | RED | M | 1 | 3 |
| *Heisteria parvifolia* Engl. & Diels | OLACACEAE | M | WHITE | M | 1 | 2 |
| *Hexalobus crispiflorus* A. Rich. | ANNONACEAE | L | ORANGE | M | 1 | 2 |
| *Irvingia gabonensis* Baill. | IRVINGIACEAE | L | GREEN | VL | 4/1 | 1 |

| | | Fruit characteristics | | | | |
|---|---|---|---|---|---|---|
| Scientific Name or Number | Family | Size | Colour | Seed size | Fate of seeds | Import in diet |
| *Irvingia grandifolia* Hallier | IRVINGRACEAE | L | GREEN | VL | 4/1 | 4 |
| *Klainedoxa gabonensis* Baill. | IRVINGIACEAE | L | GREEN | VL | 4/1 | 2 |
| *Klainedoxa sp* #208 | IRVINGIACEAE | L | GREEN | VL | 4/1 | 3 |
| *Lecaniodiscus cupanoides* Planch. ex Benth | SAPINDACEAE | M | BROWN | M | 1 | 1 |
| *Mammea africana* Sabine | GUTTIFERAE | L | BROWN | VL | 4 | 3 |
| *Mangifera indica* Linn. | ANNONACEAE | L | GREEN | VL | 4/1 | 3 |
| *Megaphrynium gabonense* Koech. | MARANTACEAE | M | RED | M | 1 | 4 |
| *Megaphrynium macrostachyum* (Benth.) M.-Redh. | MARANTACEAE | M | ORANGE | M | 1 | 4 |
| *Monanthotaxis congensis* Baill. | ANNONACEAE | M | RED | M | 1 | 4 |
| *Monodora angolensis* Dunal | ANNONACEAE | L | GREEN | M | 1 | 3 |
| *Myrianthus arboreus* P. Beauv. | MORACEAE | VL | YELLOW | M | 1 | 4 |
| *Nauclea didderichi* (De Wild.) Merrill | RUBIACEAE | L | BROWN | S | 1 | 2 |
| *Nauclea vandeguchtii* (De Wild.) Petit | RUBIACEAE | L | GREEN | S | 1 | 3 |
| *Parkia bicolor* A. Chev. | MIMOSACEAE | VL | PURPLE | M | 1 | 2 |
| *Parkia filicoidea* Welw. ex Oliv. | MIMOSACEAE | VL | GREEN | M | 1 | 2 |
| *Pentadesma butyracea* Sabine | GUTTIFERAE | VL | BROWN | VL | 4/3 | 1 |
| *Plagiostyles africana* (Müll. Arg) Prain | EUPHORBIACEAE | M | RED | M | 1 | 3 |
| *Porterandia cladantha* (K. Shum.) Keay | RUBIACEAE | M | ORANGE | S | 1 | 2 |
| *Pseudospondias longifolia* Engl. | ANACARDIACEAE | M | RED | M | 1 | 3 |
| *Pseudospondias microcarpa* Engl. | ANACARDIACEAE | M | PURPLE | M | 1 | 5 |
| *Psidium sp* #53 | MYRTACEAE | M | YELLOW | S | 1 | 1 |
| *Psychotria peduncularis* (Salisb.) Steyerm. | RUBIACEAE | S | BLUE | S | 1 | 3 |
| *Psychotria vogeliana* Benth. | RUBIACEAE | S | WHITE | S | 1 | 2 |
| *Rutidea dupuisii* De Wild. | RUBIACEAE | M | ORANGE | S | 1 | 4 |
| *Saccoglottis gabonensis* (Baill.) Urb. | HUMIRIACEAE | L | GREEN | L | 4 | 3 |
| *Santiria trimera* (Oliv.) Aubr. | BURSERACEAE | M | PURPLE | M | 1 | 1 |
| *Scytopetalum ?klaineanum* Pierre ex Engl. | SCYTOPETALAC. | M | PURPLE | M | 1 | 3 |
| *Treculia africana* Decne. | MORACEAE | VL | GREEN | M | 3/1 | 3 |
| *Trichoscypha acuminata* Engl. | ANACARDIACEAE | L | RED | L | 1 | 2 |
| *Uapaca ?acuminata* (Hutch.) Pax ex K. Hoffm. | EUPHORBIACEAE | M | GREEN | M | 2 | 3 |
| *Uapaca guineensis* Müll. Arg. | EUPHORBIACEAE | M | GREEN | M | 2 | 1 |
| *Uapaca cf sansibarica* Pax. | EUPHORBIACEAE | M | GREEN | M | 2 | 3 |
| *Uapaca sp* #299 | EUPHORBIACEAE | M | GREEN | M | 2 | 3 |
| *Uvaria sp* #256 | ANNONACEAE | M | ORANGE | M | 1 | 3 |
| *Vitex doniana* Sweet | VERBENACEAE | M | BLACK | M | 1 | 5 |
| *Zanha golungensis* Hiern | SAPINDACEAE | M | ORANGE | M | 1 | 1 |
| SEGC #36 | APOCYNACEAE | L | ORANGE | L | 1 | 3 |
| SEGC #46 | APOCYNACEAE | VL | ORANGE | L | 1 | 3 |
| SEGC #58 | APOCYNACEAE | L | ORANGE | L | 1 | 3 |
| SEGC #56 | CELASTRACEAE | L | RED | S | 1 | 4 |
| SEGC #288 | RUBIACEAE | M | WHITE | S | 1 | 3 |
| SEGC #291 | RUBIACEAE | M | ORANGE | S | 1 | 3 |
| SEGC #318 | SAPOTACEAE | M | GREEN | M | 1 | 3 |

*KEY:*

Fruit Size, classed by largest diameter of whole fruit:

S = Small, < 5 mm

M = Medium, 10–30 mm

L = Large, 30–100 mm

VL = Very Large, > 100 mm

Seed Size, classed by largest diameter:
S = Small, < 5 mm
M = Medium, 5–15 mm
L = Large, 15–40 mm
VL = Very Large, > 40 mm

Fate of Seeds:
1: Passed intact in faeces
2: Majority of seeds passed intact, minority destroyed by chewing
3: All seeds destroyed in feeding
4: Seeds not swallowed
N.B. If two categories listed, first is the usual pattern for ripe fruit.

Importance in the diet:
1: Eaten whenever available;
2: Frequency/quantity of consumption less than would be expected from availability;
3: Uncommon species, thus availability always limited;
4: Consumed infrequently and/or in small amounts;
5: Large differences in patterns of consumption either between years or between groups.

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