Mutualism between a leguminous tree and large African monkeys as pollinators

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Abstract. Observations of a monkey community in a forest of the Zaire Basin show that four species intensively lick the nectar of *Daniellia pynaertii* (Caesalpinoideae) for 5 months of the year; nectar makes up a mean of 20% and a maximum of 50% of monthly plant feeding records (Fig. 3). Such intensive nectar-feeding by monkeys of up to 8 kg body weight probably developed in these basically frugivorous primates as an alternative strategy to cope with a shortage of fleshy fruits. This would have been possible due to the high density of the plant species, the synchrony and abundance of its flowering (Fig. 2), and the large size of the nectar drop and its nutritional value. Patterns of monkey movements among *Daniellia* trees show that one flowering tree may receive up to 10 species visits and 30 individual visits per day, for a total of up to 141 min. (Table 1). A monkey troop can visit 12 trees in succession over less than 3 h (Fig. 4). This suggests that monkeys are able to promote pollen transfer both among flowers of the same tree and between conspecific trees. The individual tree fruiting index is positively correlated with its flowering index and with the amount of visits by monkeys, indicating at least that monkeys do not inhibit the reproductive ability of flowers (Fig. 5). These results suggest that monkeys can be considered as a guild of effective pollinators. Long-term coevolution between the plant and its present-day pollinators seems unlikely, and we suggest that monkeys replaced other pollinators, such as Lepidoptera. This hypothesis is supported by the fact that tubular flowers adapted for pollination by Lepidoptera are found in affine species of the same genus and of affine genera, the latter being known to be pollinated by these insects. In contrast, *D. pynaertii* flowers typically meet the pollination syndrome currently defined for attracting large mammals: notably conspicuousness and open morphology of the flowers, nectar colour and abundance. These characteristics suggest that coadaptation between monkeys and plant or at least one-sided adaptation has operated.

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Introduction

In a recent book on the reproductive ecology of tropical forest plants, seven chapters dealt with plant-pollinator interactions (Bawa and Hadley 1991). None of them were devoted to African forests and there was almost no reference to pollination by mammals, bats excepted. Sussman and Raven (1978) previously reviewed pollination systems involving non-flying mammals and concluded that such systems concerned small-sized nocturnal species including rodents, marsupials and prosimians; these systems were considered to have a relict status and to have developed in the more ancient mammal taxa in regions where bats are not abundant. The importance of marsupials in pollination has been confirmed for Proteaceous plants in Australia (e.g. Turner 1982; Goldingay et al. 1991). In continental Africa, indirect evidence of pollination by primates again involved prosimians in the case of *Perodicticus potto* and an unidentified *Galago* licking *Parkia* flowers (Mimosaceae; Grünmeier 1990); these studies confirmed previous observations of Coe and Isaac (1975) of *Galago crassicaudatus* licking baobab flowers.

Since the review quoted above, nectar-feeding by simian primates and the possibility of pollination have also been documented. Studies in New World tropical forests (Prance 1980; Janson et al. 1981; Torres de Assumpção 1981; Terborgh 1983; Garber 1988) confirmed Oppenheimer’s (1968) initial observations on *Cebus* monkeys and showed that flowers of several plant species were to some extent visited by several primate species. Depending on the plant species, monkeys were described as causing little damage to flowers (Janson et al. 1981; Torres de Assumpção 1981) or as being highly destructive (Garber 1988). Consequently, they have been regarded either as
possible pollinators or as non-pollinators. Data are few for Old World monkeys: one Cercopithecus nictitans has been filmed licking nectar of Pentadesma butyracea in Cameroon (Aglad 1982); recently, a TV film on Tiwai Island (Gordon 1992), showed a C. mona campbelli licking the nectar of Pentaclethra sp. and a C. diana licking the nectar of a species we identified as Daniellia sp.

During a study of primate feeding ecology in Zaire, we observed that four monkey species visited flowering trees of a species of Caesalpinioideae (Leguminosae), Daniellia pynaertii De Wild. (1910). We soon realized that they were not consuming flowers but licking their nectar. While continuing to analyse the monkeys' diets by regularly following monkey troops, we carried out extensive observations of D. pynaertii trees and their visitors with the following aims: (1) to investigate the nature and the importance of relations between monkeys and flowers; (2) to check, using all the currently used criteria, whether the monkey behaviour (e.g. patterns of visits to flowering trees, pollen transfer, impact on the reproductive activity of the flower) was likely to lead to pollination; (3) to characterize the pollination syndrome from the floral biology; and (4) finally, to decide whether coadaptation between monkeys and plant could have operated.

Methods

Study site and subjects. The work was carried out at Bositima (01°15'S; 22°00'E) in the Salonga National Park, Zaire. The study area was located within a meander of the Lonela River that is covered by tropical rain forests growing on sandy, hydromorphic, patchily inundated soils. Study subjects included both D. pynaertii trees and the monkey community. D. pynaertii is a centro-guinean species, known to occur in mature forests on hydromorphic soils in Central Africa (Evrard 1968). This species is heliophilous, and its emergence trees have an open canopy with a flattened top. Flowering generally coincides with leaf fall (Tailfer 1989). These characteristics encouraged observations on visitors to the tree crowns.

The morphology of D. pynaertii flowers was described and flowering trees were analysed for possible antiherbivore chemicals, including alkaloids (Drageroff's solution), total phenolics (Folin-Denis assay), condensed tannins (proanthocyanidin method), free amides and amino acids (Yemm and Coking 1955). Fresh nectar was not collected separately, so the presence of lipids was tested on the nectar found on dried petals, using red Sudan III.

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Field observations and methods of analysis. The flowering phenology of D. pynaertii was followed from July 1990 to October 1991, every second week, by: (1) surveying eight randomly chosen trees, and (2) scoring every flowering individual on a 1-m wide, 4.7-km long transect (including 2.2 km along the riverside and 2.5 km inland). Any tree whose canopy was above the transect was considered. Results of the transect are expressed as the mean monthly number of flowering trees per 100 m.

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Two types of observations on monkeys were made. First, the analysis of monkey diets was conducted over 8 months by following the monkey troops over a surface area of 3 km². During these observations (a total of about 1000 h), 6610 feeding records were obtained for the community (except C. (A.) nigroviridis) using the frequency method (Struhsaker 1975). Following Struhsaker, feeding records were distinguished as follows: (1) a different individual feeding on the same item; (2) the same individual feeding on a different item of the same species or on a different food species; (3) or the same individual feeding on the same food at least 30 min after any previous such observation. Results are expressed as the relative frequency of consumption of nectar relative to overall plant diet.

Second, detailed observations of monkeys and flowers were carried out from a fixed observation point on the opposite bank of the Lonela from the study area. Fourteen simultaneously flowering D. pynaertii trees, spread over 740 m of the river bank, were observed, using a telescope. Observations lasted 103 h (1–8 March 1991), which included 7 consecutive full days. Trees were scanned by one or the other observer from dawn until nightfall. All the diurnal visitors to the trees were noted. However, no observations were made during the night. Visits by monkeys to each tree were noted and records made of the timing of each visit. The species and the numbers of monkeys present were recorded. To analyse data, a "species-visit" to a flowering tree was scored from the moment when the first monkey of a given troop climbed into the tree up to the moment the last monkey of that troop left the tree. A "multi-species visit" involved several species in a mixed troop, feeding simultanea-ously. It was scored similarly. The number of "individual-visits" for a species-visit or a multi-species visit corresponded to the maximum number of monkeys seen together in the tree at any one time. It must be noted that monkeys were seen to feed most of the time when in a Daniellia tree.

During this observation period, each tree was scored every 2nd day according to the phenology of its flowers on a scale of 0–4; "4" meant that the whole canopy was in flower and "0" indicated no flowers. By pooling the scorings, a flowering index was obtained for every tree. Fruiting was scored every week over a period of 6 months following the blooming; scores were pooled to obtain a fruiting index. Finally, tree height and tree diameter at breast height (dbh) were measured.

To give a synthetic view of the interrelations between tree parameters and the patterns of monkey visits, a canonical correspondence analysis (Ter Braak 1986; Lebréton et al. 1988), also called correspondence analysis with instrumental variables (Lebréton et al. 1991), was carried out, using the BIOECON (1990) Program. This new method of analysis allows the simultaneous treatment of a number of dependent variables (those to be explained; in the present case, the fruiting index and the characteristics of monkey visits), and independent variables (explanatory variables: tree dbh and flowering index). In this work, the use of bivariate correla-tions is inappropriate in so far as the variables that characterize monkey visits are not independent of each other.

Results

The floral biology and the phenology of D. pynaertii trees

The large, pink-violet flowers of D. pynaertii are grouped in panicles and have an upright orientation. They form a highly conspicuous carpet above the flattened-top tree crowns. They have no obvious fragrance. Flowers have an open morphology. The receptacle is 0.5–0.8 cm long and its diameter is 4–5 mm. Corolla size is about 3 × 3 cm with five petals and four sepals (Fig. 1). The filaments of the ten exerted stamens may reach 4 cm in length. The ovary has a short style, which becomes accrescent at the end of the flowering period. At its base is exuded a large red-orange drop of nectar, 2–5 mm across, which lies in the cup formed by the perianth, at the base of the internal petals (Fig. 1). The flowers contained 3.4% total phenolics, 6.3% condensed tannins, some alkaloids and an unidentified amino-acid very close to proline. The nectar

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