

## Massive Destruction of *Symphonia globulifera* (Clusiaceae) Flowers by Central American Spider Monkeys (*Ateles geoffroyi*)<sup>1</sup>

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### ABSTRACT

Although more than 39 primate species have been described as nectar feeders, no studies have documented the negative affect this behavior may have on the reproductive success of the plants they consume. Here we report, for the first time, massive flower destruction of the tropical tree *Symphonia globulifera* by the frugivorous spider monkey, *Ateles geoffroyi*, and document the detrimental effect this behavior has on fruit set. Foraging behavior was collected from one troop of *A. geoffroyi* during 460 contact hours from June 1999 to May 2000 in the tropical humid forest at the Refugio de Vida Silvestre Punta Rio Claro (8°39'N, 83°44'E) in the Osa Peninsula in Southwestern Costa Rica. Detailed phenological data were collected from ten *S. globulifera* trees that the monkeys fed upon and ten trees that were outside of their home range, but in the Refugio. From July to September 1999 *S. globulifera* was the most important species consumed, representing from 86 to 100 percent of the total feeding time each month. Monkey foraging on *S. globulifera* flowers was destructive, detaching the flowers completely from the branches in 80 percent of the foraging bouts, and leaving flowers without petals and with damaged reproductive parts in 20 percent of the bouts. None of the ten trees where the monkeys were foraging set fruit, but seven of ten trees outside of their home range set fruit in November and December 1999. These results suggest that some primates may play an important role in floral herbivory in tropical forests and the subsequent reduction in reproductive success. Future studies should focus on evaluating the long-term effect this foraging behavior may have on the population structure of this species and evaluate the effect of primate floral herbivory on the reproductive success of other plant species.

### RESUMEN

Aunque se han descrito más de 39 especies de primates como consumidoras de néctar, ningún estudio ha documentado el efecto negativo que tiene este comportamiento alimentario en el éxito reproductivo de las plantas que son consumidas por los primates. En este estudio documentamos, por primera vez, la destrucción masiva de flores del árbol *Symphonia globulifera* por el mono araña (*Ateles geoffroyi*) y su efecto en el establecimiento de frutos. Se estudió el comportamiento de forrajeo de una tropa de *A. geoffroyi* durante 460 horas de observación durante los meses de junio 1999 hasta mayo 2000 en un bosque tropical húmedo en el Refugio de Vida Silvestre Punta Rio Claro en la Península de Osa, en el suroeste de Costa Rica (8°39'N, 83°44'E). Se colectaron datos fenológicos detallados de diez individuos de *S. globulifera* de los cuales las flores fueron depredadas por los monos araña, y 10 individuos que se encontraron afuera de su área hogareña, pero dentro de la Refugio. Desde julio hasta setiembre de 1999 *S. globulifera* fue la especie más importante en la dieta de *A. geoffroyi*, representando entre el 86 y el 100 por ciento del total de tiempo de la dieta en este periodo. El comportamiento alimenticio de las flores fue destructivo, removiendo completamente las flores de las ramas en un 80 porcentaje de los eventos alimenticios y dejando las flores sin pétalos en un 20 porcentaje. Ninguno de los 10 árboles que fueron visitados por los monos produjo frutos, mientras que 7 de los 10 árboles que se encontraron fuera del área de forrajeo de los monos lo hicieron durante noviembre y diciembre del 1999. Estos resultados sugieren que algunas especies de primates pueden jugar un papel importante en la herbivoría floral en bosques tropicales, reduciendo el éxito reproductivo de las especies afectadas. Futuros estudios deben enfocar en evaluar los efectos de largo plazo de este comportamiento alimenticio sobre la estructura de la población de esta especie y evaluar el efecto de herbívoro de flores sobre el éxito reproductivo de otras especies de plantas.

*Key words:* *Ateles geoffroyi*; Costa Rica; flower predation; foraging behavior; fruit set; lowland rainforest; Osa Peninsula; spider monkeys; *Symphonia globulifera*.

ANIMALS THAT FEED UPON FLOWERS CAN REDUCE THE REPRODUCTIVE success of plants either through direct destruction of potential gametes or by negatively affecting pollinator visits (Heithaus *et al.* 1982, Cunningham 1995, Krupnick & Weis 1999, Krupnick *et al.* 1999, Mothershead & Marquis 2000, Malo *et al.* 2001, Canela & Sazima 2003, but see Lowenburg 1994). Among vertebrates, several primates have been described as nectar feeders, including at least nine species of lemurs from Madagascar, 20 species of platyrrhines from the Neotropics, and ten species of primates from the Paleotropics (Sussman & Raven 1978, Lucas & Corlett 1991, Ferrari & Strier 1992, Kress *et al.* 1994, Peres 1994, Stoner 1996, Dominy 2001, Lima & Ferrari 2003). The

importance of this component to the diet and the number of species exploited varies greatly among primate species. For example, *Cercopithecus ascanius* in western Uganda consumed flowers of 12 spp. (Dominy 2001) while *Ateles paniscus* in Surinam consumed flowers of 33 spp. (van Roosmalen 1985).

In spite of the importance that flowers may have in the diet of many primates, few studies document the consequences of this feeding behavior in terms of the reproductive success (*i.e.*, fruit set) of the affected plants. Kress *et al.* (1994) demonstrated that the ruffed lemur (*Varecia variegata*) serves as a pollinator of the traveler's tree (*Ravenala madagascariensis*) and several studies have speculated that primates may be important pollinators of some tree species (Janson *et al.* 1981, Ferrari & Strier 1992), but no studies have quantified the potential negative effect flower-feeding primates may have on fruit set. Part of this lack of interest may

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reflect the view that flowers are only exploited as a food resource by frugivorous primates when few fruit are available (Garber 1988, Ferrari & Strier 1992, van Schaik *et al.* 1993, Peres 1994).

*Symphonia globulifera* L. f. (Clusiaceae), a tropical tree with a wide distribution across America, Africa, and Madagascar, deserves special attention because it has already been identified as a resource for a number of primates in several locations. In the Amazon, the nectar of *S. globulifera* is consumed by the brown capuchin monkey (*Cebus apella*), the common woolly monkey (*Lagothrix lagotricha*), tamarins (*Saguinus mystax* y *S. fuscicollis*), and the common squirrel monkey (*Saimari sciureus*; Garber 1988, Peres 1994, Lima & Ferrari 2003). In Kibale (western Uganda), *S. globulifera* flowers are consumed by the red-tailed monkey (*Cercopithecus ascanius*) and the red colobus (*Piliocolobus badius*; Dominy 2001). All these instances have generally been explained as a behavior induced by fruit shortage. In spite of these observations, little is known about the potential effect that such feeding behavior may have on fruit set in *S. globulifera*. Here, we describe the massive use and destruction of *S. globulifera* flowers by Central American spider monkeys (*A. Geoffroyi*) while foraging for nectar, and document the destructive effect of this behavior on fruit set.

## METHODS

**STUDY SITE AND SPECIES.**—The study was conducted at the Refugio de Vida Silvestre Punta Río Claro (8°39'N, 83°44'E) in the Osa Peninsula in southwestern Costa Rica. The vegetation in this area is classified as tropical humid forest (Holdridge *et al.* 1971). The mean annual rainfall is 3000 mm, with a marked dry season from December to April (Hartshorn 1983). The refuge encompasses an area of approximately 700 ha including 450 ha of mature forest, 200 ha of forest in advanced regeneration or mature forest that has been selectively logged, with the rest being open area or pasture. This site is located 5 km from the 52,000 ha Parque Nacional Corcovado with similar flora and fauna.

*Symphonia globulifera* L. f. (Clusiaceae) is distributed across tropical America, Africa, and Madagascar (Gentry 1993). In the Osa Peninsula, it is one of the most common tree species (Hartshorn 1983, Thomsen 1997), with reproducing trees ranging in height from 3 to 35 m (Quesada *et al.* 1997). This variability is typical of the species in the Neotropics, where it can sometimes reach the canopy but is often in the understory (Gill *et al.* 1998). Its axillary inflorescences contain groups of between 1 and 17 flowers of which 1 to 3 may be open in an inflorescence at any given time. These flowers are bright red, odorless, and face upward (Gill *et al.* 1998). Its fruits are yellowish-brown ovoid drupes 2–3 cm in diameter (Quesada *et al.* 1997), and have been described as bat-dispersed (Steyermark *et al.* 1998).

*Ateles Geoffroyi* is one of four species in the spider monkey genus, formerly found from Tamaulipas and Jalisco, Mexico in the north, south along both coasts to Oaxaca, and through Central America to southeastern Panama (Reid 1997). The diet generally consists of 57–77 percent fruit, 7–14 percent young leaves, and 2–10 percent flowers, but other items like seeds also have been reported (Cant 1977, Chapman 1987).

**DATA COLLECTION.**—The foraging behavior of one troop of *A. Geoffroyi* containing 30 individuals was studied from June 1999 through

May 2000. Data were collected using 2-min focal animal continuous observations to obtain information on food consumption and handling behavior (Altmann 1974). For flower consumption bouts, we established two categories of handling: (a) detached—when flowers were detached from inflorescences to consume nectar; and (b) non-detached—when flowers remained attached to the inflorescences after feeding on nectar. All individuals feeding on flowers were identified by sex and age-class and focal animals were randomly changed after each 2-min observation. Only data from adults were included in the analysis because of the infrequent observations on juveniles. Data were collected 2 d per week from 0600 to 1800 h. During some of the focal events, we timed and counted the number of flowers consumed by spider monkeys to estimate foraging rate. We also noted if other potential pollinators or flower predators visited the tree when the spider monkeys were feeding. Additionally, we conducted *ad libitum* observations to describe flower-foraging behavior.

The frequency of visits of spider monkeys to trees during the day were divided into four time periods: (a) early morning from 0600 to 0900 h; (b) late morning from 0901 to 1200 h; (c) early afternoon from 1201 to 1500 h; and (d) late afternoon from 1501 to 1800 h. We used these divisions to determine the potential effect that monkeys may have in preempting perching bird visitation. Birds have been described as the main pollinators of this species in Peru (Gill *et al.* 1998) where they were most active foraging in *S. globulifera* trees in the early morning and early afternoon. A Kruskal–Wallis test was used to determine if spider monkeys visited *S. globulifera* more intensively during one of the four time periods during the day.

The importance of flowers, young leaves, and fruits in the diet each month was calculated as the percent time devoted to consuming each item in relation to the overall feeding time on all food items each month. We calculated the monthly importance of *S. globulifera* flowers in the diet of spider monkeys as percent time devoted to consuming this species in relation to total feeding time on flowers. The overall importance of each flower species in the diet was calculated as the percent time devoted to consuming each species in relation to the overall feeding time on flowers. The importance of flowers compared to young leaves or fruit in the diet of *A. Geoffroyi* during the flowering season of *S. globulifera* was evaluated using a Kruskal–Wallis test.

We also determined the effect of monkey flower feeding on fruit set by marking ten trees of *S. globulifera* visited by spider monkeys and ten trees outside of their home range but within the Refugio, where we never saw them forage. We followed their phenology from July 1999 to May 2000. Individual tree crowns were inspected using 10 × 42 binoculars every 2 weeks to quantify the presence of buds, flowers, and fruits. Each of these three items were ranked from 0 to 4 based on the amount of crown coverage: 0 when reproductive structures were not present; 1 when they occupied 1–25 percent; 2 when they covered 26–50 percent; 3 when they covered 51–75 percent; and 4 when >75 percent was occupied by the item. We estimated flower availability every 2 weeks using an index of availability calculated as (100 × sum of abundance score)/number of trees scanned (Peres 1994). A monthly value of this index was calculated for each item by summing the value for the two periods in each month. Following Quesada *et al.* (1997), we expected trees to bear fruit during November or December of 1999.

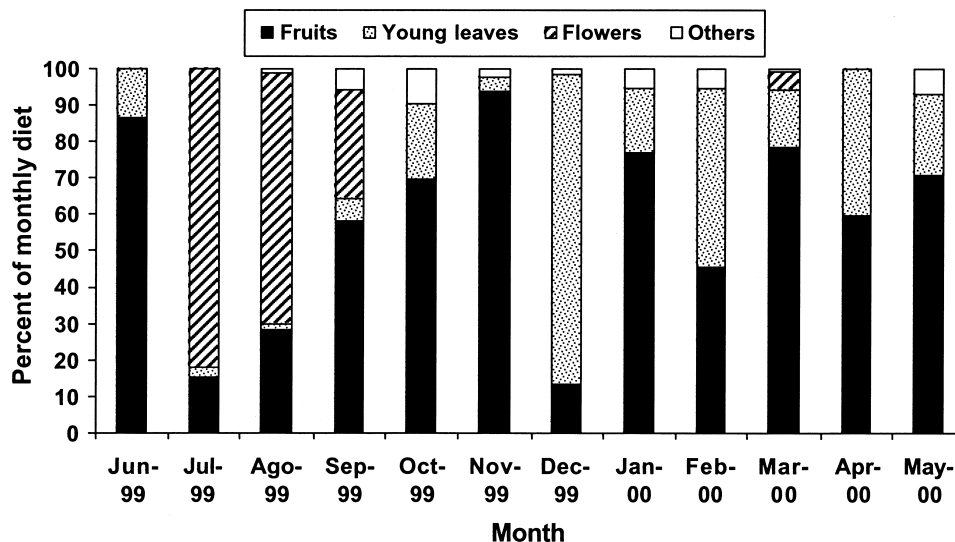


FIGURE 1. Monthly percentage of plant items included in the diet of spider monkeys (*A. geoffroyi*) from June 1999 to May 2000 in a tropical humid forest in Costa Rica. Black solid bars represent fruits, black dot-filled bars represent young leaves, diagonal line-filled bars represent nectar from flowers and white solid bars represent other items. Percentages are based on 1490 min of focal observation.

## RESULTS

Spider monkey foraging behavior was collected during 460 contact hours from June 1999 to May 2000. Observations were made for approximately 7 h per day (range 4–11 h). Overall, the monkeys spent 60 percent of their feeding time consuming fruits, 26 percent on flowers, and 14 percent on young leaves. Consumption of flowers of different species took place mostly from July to September in 1999 and during March 2000 (when flowers were consumed in small quantities (5.17%; Fig. 1). From July to September 1999, flowers were the most important plant item in the monkeys' diet ( $H = 6.49$ ,  $P = 0.04$ ,  $df = 2$ ; Fig. 1); during this period, spider monkeys were observed feeding in *S. globulifera* during 14 days. From July to September 1999 *S. globulifera* was not only the most important species in the diet, representing from 86 to 100 percent of the total feeding time each month, but also represented 92 percent of the total time feeding on flowers. Monkeys were observed feeding in 79 different trees of *S. globulifera* (average DBH,  $52.5 \pm 22.3$  cm and average height,  $20.8 \pm 6.3$  m) and were often observed visiting the same tree. Foraging in these trees varied throughout the day with most activity in the morning, especially late morning, and less in the afternoon; however, this difference was not significant ( $H = 3.0$ ,  $P = 0.392$ ,  $df = 3$ ). During 321 min of flower-feeding bouts of spider monkeys in *S. globulifera*, we did not observe any other potential pollinators or flower predators. White-faced capuchin monkeys (*Cebus capucinus*) were occasionally observed feeding on *S. globulifera* flowers, but never when spider monkeys were there. In contrast, during the phenology observations of the ten control trees, we observed several perching birds including the red-legged honeycreeper (*Cyanerpes cyaneus*), the blue dacnis (*Dacnis cayana*), and several species of tanagers (*Tangara* spp.) foraging in the flowers.

When spider monkeys entered the tree crown, they searched visually for open flowers in the inflorescences and appeared to search systematically for open flowers in the entire crown before moving to a new tree.

In 80 percent of the total feeding time in *S. globulifera*, spider monkeys completely detached the flowers from the branch by biting with their front teeth. This was achieved by pulling the flowering branch to their mouth with their hands and then biting. Flowers were then manipulated with the mouth to extract the nectar. After the nectar was obtained, the monkeys spat out the flowers. On several occasions, spider monkeys broke the branches while attempting to pull them to their mouths, but they continued to forage in the same manner; this allowed us to make a closer inspection of the flowers that were not detached from the branch when they dropped the branch to the ground. Flowers that were not completely detached were left without petals and many had damaged reproductive parts with the tops bitten off the anthers and stigma. Since monkeys put flowers directly into their mouth to extract nectar, they did not accumulate any pollen on the fur surrounding their face, which makes it unlikely that they could have functioned as pollinators, even in the unlikely event that the reproductive structures were not damaged. Monkeys consumed flowers at a rate of  $0.4 \pm 0.3$  flowers/sec ( $N = 25$ ).

The majority of *S. globulifera* trees flowered from July to September 1999 at the study site, with the greatest abundance being in July (Fig. 2). The foraging time that monkeys dedicated to this resource appeared to follow flower availability until this resource disappeared from the area (Fig. 2). Even when fruits were more important in their diet, they continued to consume *S. globulifera* flowers while present. None of the ten trees where spider monkeys foraged produced fruits, while seven of the ten trees outside of their foraging area set fruit in November and December 1999.

## DISCUSSION

Our observations demonstrate that extensive foraging on *S. globulifera* flowers by *A. geoffroyi* resulted in no fruit set. Spider monkeys probably

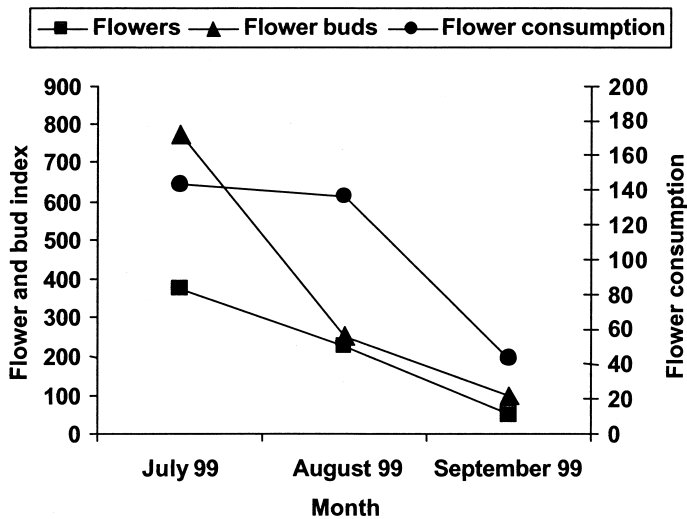


FIGURE 2. Reproductive phenology of ten trees of *S. globulifera* visited by spider monkeys (*A. Geoffroyi*) for their nectar and the total feeding time of spider monkeys on these flowers from July to September 1999. (▲) = flower buds, (■) = flowers, and (●) = total minutes of feeding time on *S. globulifera* flowers.

affected pollinator services, and thus fruit set, to *S. globulifera* both directly and indirectly. Directly, they destroyed or detached most open flowers, significantly destroying potentially fertilized ovules. Given that their flower consumption was so rapid, they may have depleted the total amount of open flowers for potential pollinators during a foraging bout. Indirectly, when flowers were not detached by monkeys, they were left without petals, often with damaged reproductive parts and presumably with less nectar. This flower-handling behavior may have had a two-fold effect: (i) reducing the floral advertising to pollinators and (ii) lowering the nectar reward to pollinators. Pristine flowers have petals that bulge outwards, creating a small chamber where nectar accumulates (Gill *et al.* 1998). Without petals, the flowers are either unable to maintain nectar to reward pollinators or may not be able to attract pollinators because of their reduced floral display (Cruzan *et al.* 1988, Anderson 1996, Krupnick *et al.* 1999).

*Symphonia globulifera* has been reported as part of the diet of many primates in the New and Old World; however, none of the species previously studied has shown as high a reliance on this plant species (van Roosmalen 1985, Ferrari & Strier 1992, Peres 1994, Dominy 2001, Lima & Ferrari 2003) as we found here for spider monkeys. Peres (1994) found that three species of Neotropical primates (*Cebus apella*, *Saguinus fuscicollis*, and *S. mystax*) used the nectar of *S. globulifera* flowers as a food resource during the dry season in *terra firme* forest in the Amazon. The two tamarin species used this resource intensively during the dry season of 1988, accounting for as much as 55 and 60 percent of monthly feeding time, respectively, but less so the following year (approximately 30 percent), while brown capuchin monkeys spent approximately 17 percent of monthly feeding time on *S. globulifera* nectar during both dry seasons. Similarly, Garber (1988) reported for these same species of tamarins, in the seasonally inundated tropical wet forest near Iquitos, Peru, that *S. globulifera* made up between 22 and 31 percent of the diet in July and August when fruit was scarce at this site. Consumption of *S. globulifera*

flowers also has been reported in the diet of black spider monkeys (*Ateles paniscus*) in Surinam; however, at this site it only comprised 0.05 percent of the total diet being consumed in August and September, representing 2.2 and 1.04 percent respectively, of the monthly diet (van Roosmalen 1985). Only Garber (1988) and van Roosmalen (1985) mention that this foraging appeared to be destructive to the flowers.

Several factors may have contributed to the high use of *S. globulifera* flowers for nectar by *A. Geoffroyi*. First, in the Osa Peninsula, *S. globulifera* is one of the most common trees, reaching density values of 20 stems/ha (Hartshorn 1983, Thomsen 1997). In addition, this tree produces "high red" flowers (Gill *et al.* 1998) that can be visually detected by spider monkeys regardless of their color vision capacities (Riba-Hernández *et al.* 2004). Finally, the flowers of *S. globulifera* produce large quantities (3.0–130  $\mu$ l) of hexose-rich nectar (Gill 1998) that make them an especially attractive resource for this large-bodied monogastric primate. Recently, it has been suggested that spider monkeys prefer hexose-rich fruits rather than sucrose-rich fruits (Riba-Hernandez *et al.* 2003). This factor may also influence the attractiveness of this species to spider monkeys. These characteristics together make *S. globulifera* a high-density, easily detectable, and energy-rich food source for *A. Geoffroyi*. Some other studies have concluded that primates utilize *S. globulifera* flowers as a food resource when fruit is scarce (Garber 1988, van Schaik *et al.* 1993, Peres 1994); however, in our study we cannot ascertain if feeding on *S. globulifera* flowers corresponds to a season of low fruit availability for *A. Geoffroyi*, or if they actually have a preference for this food resource, due to the above characteristics. Furthermore, it is not clear if the extensive use of *S. globulifera* flowers was an unusual event during the study period or if this pattern occurs more frequently.

In addition to Central America, *S. globulifera* also occurs in South America and Africa where it is used as a flower resource by primates. We suggest that further studies should be conducted throughout the distribution of *S. globulifera* to understand better the relationship between this tree species and the primates that consume its flowers. This information will allow us to assess the effects that different primates may have on the reproductive success of this species in different environments. Finally, since other species of *Ateles* have been described as swallowing entire flowers and destroying reproductive parts of several plant species (van Roosmalen 1985), more attention should be addressed to evaluate the effect this foraging behavior may have on the reproductive success of other plant species.

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