# FLORIVORY, NECTARIVORY, AND POLLINATION – A REVIEW OF PRIMATE-FLOWER INTERACTIONS

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*Abstract.* Due to their principally arboreal way of life, primates can potentially interact with flowers from a broad diversity of tropical and subtropical plants. In fact the consumption of flowers and/or nectar has been reported for many primate species, but the role in primate diets is generally underestimated. Also, evidence has been provided for the role of some primate species as pollinators. This paper aims at reviewing information on the interactions between primates and flowers and to examine factors like body mass and dietary strategy as determinants for the type of interaction, i.e. whether entire flowers or nectar are consumed. I also review the available evidence for pollination by primates and the consequences of flower predation for subsequent fruit set. I conclude that (a) the contribution of flowers and/or nectar to primate diets can be substantial, at least seasonally, and therefore (b) primate-flower interactions (flower predation, pollination) are more prevalent and may have larger impact on affected plants than previously thought. *Accepted 27 January 2011.*

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## INTRODUCTION

Pollination is a critical step in the plant reproductive process, affecting not only the reproductive success of individual plants but also gene flow and thus plant population dynamics. Many angiosperms and some cycads and gnetales depend on animals for pollination and have evolved adaptations, including the offering of nectar as a nutritious reward, to attract flower visitors and to enhance pollination (Pellmyr 2002). In turn, many animals have evolved adaptations for the exploitation of nectar, feeding on flowers non-destructively while simultaneously transferring pollen from one flower to another (Pellmyr 2002). However, other animals may exploit nectar without pollen transfer ("nectar stealing"), may destroy flowers to obtain nectar, or may consume entire flowers ("florivory"). Such feeding strategies can potentially have a negative impact on plant reproductive success.

Primates are mainly tropical animals (Martin 1990) that by virtue of their principally arboreal way of life may interact with flowers from a diverse spectrum of flowering plants. In fact an increasing number of field studies has documented the exploitation of flowers and flower parts by primates. However,

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evidence for pollination by primates is still mainly anecdotal and scattered throughout the primatological, botanical, and ecological literature. A role for primates in pollination has been specifically suggested for Madagascar, where flower-visiting bats (which are important pollinators in many other regions) are very rare (Sussman & Raven 1978). Since Sussman and Raven's work, additional information has emerged that suggests that some primate species indeed may act as pollinators. So far, no systematic attempt has been made to synthesize these findings and to identify factors influencing the type of interaction between primates and flowers. In this paper I therefore aim at reviewing the current knowledge on primate-flower interactions, specifically addressing the following questions:

(1) How important are flowers and nectars in primate diets?

(2) Do body size (body mass) and dietary strategies influence florivory and nectarivory in primates?

(3) Do any primates possess morphological adaptations for nectarivory (e.g. longer tongues, specific tongue surface structures)?

(4) What is the evidence for pollination by primates?

(5) What impact does primate exploitation of flowers and nectar have on plants? More specifically, do florivory and pollination by primates impact the seed set?

Nectar is a source of readily available energy in the form of simple carbohydrates and proteins (Nicolson & Thornburg 2007). Nectar is generally offered in relatively small amounts per flower, but both amount and quality of nectar may be tuned to the energetic demands of pollinators (Nicolson 2007). Nevertheless, due to the usually small amounts of nectar per flower it may not pay for large animals to feed selectively on nectar. On the other hand, petals and other structural components of flowers mainly consist of structural carbohydrates that require bacterial breakdown to make the energy available. Since this bacterial breakdown requires space in the gastrointestinal tract (Chivers & Hladik 1980), smaller animals may be constrained in the exploitation of structural carbohydrates (but see Foley & Cork 1992). With regard to the influence of body mass and dietary strategies, I therefore make the following predictions:

(a) Feeding on nectar is more prevalent in small-bodied primates, while larger primates are more likely to consume whole flowers.
(b) Frugivorous-faunivorous primates are more likely to feed on nectar, while folivorous and frugivorous-folivorous primates are more likely to feed on whole flowers.

These two predictions are not completely independent of each other, since there is a strong link between body mass and dietary strategy, with smaller species tending towards frugivory-faunivory, and larger species towards frugivory-folivory and folivory (Terborgh 1992).

## METHODS

To address the questions posed in the Introduction, I performed intensive literature surveys in the database PrimateLit (http://primatelit.library.wisc.edu) which covers the primate literature published since 1940, including non-referenced publications and "gray literature" (e.g. theses). I also searched in the ISI Web of Knowledge. I used the following key words in the literature search: [nectar* or flower] for PrimateLit; [(nectar* or flower) and primate*] for ISI Web of Knowledge. I also scanned the primatological literature for data on primate diets and the quantitative contribution of flowers and/or nectar to diets. Information published before April 2010 is considered in this review. I do not pretend that my literature search is exhaustive; older natural history literature in particular (before 1940) may not be well represented. Nevertheless, I am confident that the review by and large represents the current state of information.

From the references, I extracted the following information:

(a) Type of flower exploitation and flower handling, i.e., only nectar consumed, entire flowers consumed or both (only nectar from some plant species and entire flowers from other plant species consumed).
(b) Proportion of flowers or nectar in the overall diet and maximum proportion in a specific period of the year (season or month).
(c) Information on potential morphological adaptations for nectarivory.
(d) Evidence or clues for primate pollination.
(e) Evidence or clues for negative impacts of florivory on fruit set.

Most studies that reported the consumption of flowers and/or nectar did not explicitly describe flower handling. Therefore I assumed florivory when only flowers were mentioned as dietary items, nectarivory when only nectar was mentioned. A number of studies quoted "flowers/nectar" as a dietary item, and others reported that flowers from some plant species and nectar from other plant species was consumed. I categorized these cases as "both" (i.e., florivory and nectarivory). The proportion of flowers and/or nectar in the diet is reported here both for overall (annual or across-season) diets and as seasonal maximum (proportion in a limited period, i.e. month or season).

Body mass data were taken from Smith & Jungers (1997). I used female body mass and created the following body mass categories for analyses: < 0.5 kg, 0.5-1 kg, 1-5 kg, 5-10 kg, ≥ 10 kg. Primate species for which no body mass information was available were allocated to the body mass category of their closest relatives. Information on the dietary category was extracted from the specific literature on each species. I defined the following categories: folivores (feeding principally on leaves); frugivores-folivores (feeding principally on fruit pulp and/or seeds, complemented with leaves); frugivores-faunivores (feeding principally on fruit pulp and/or seeds, complementing this with animal prey); and exudativores (feeding principally on exudates [gum, latex, sap]). I calculated distributions of the number of species over body mass and dietary categories. The distribution over body mass was compared with an expected distribution of the type of flower exploitation (with the null hypothesis that this is indepen-

dent of body mass) using a χ²-test in Statistica 9.0. Distributions over dietary categories were compared with an *r* x *c* contingency test in SsS 2.0. Pair-wise comparisons were performed by partitioning the contingency table and performing a χ²-test, or when the conditions for the χ²-test were not met the extended Fisher-test. The significance level was set at 0.05, and for pair-wise comparisons at 0.0083 (0.05 divided by the number of comparisons). All statistical comparisons were performed with counts, but in the figures percentages are shown.

I generally used the scientific primate names as provided in the source, except where recent taxonomic revisions have resulted in a change of name.

## RESULTS & DISCUSSION

*The importance of flowers and nectar in primate diets.* I found reports on the exploitation of flowers and/or nectar by 165 species from all primate families except the Tarsiidae[1] (Online Appendix 1). The majority of studies reports flower consumption (68%, N = 113), fewer primate species consume nectar (17%, N = 28) or both flowers and nectar (15%, N = 24).

The contribution that flowers and/or nectar make to the overall diet is highly diverse between and within primate genera and species (Online Appendix 1). For the majority of species, flowers and/or nectar contribute <10% of food intake. However, there are also a few species where flowers and/or nectar are the most important food resource either overall or seasonally. For slow lorises, *Nycticebus coucang*, nectar from the palm *Eugeissona tristis* is the most frequently consumed food resource (Wiens *et al.* 2006). Flowers of *Domohonea perrieri* (Euphorbiaceae) are the single most important food item in the diet of diademed sifakas, *Propithecus diadema* (Powzyk & Mowry 2003). For several primate species, flowers and/or nectar may account for up to 84% of seasonal food intake, generally during periods of fruit scarcity (e.g. Terborgh 1983). Nectar is actually considered a fallback resource for some primate species (Terborgh & Stern 1987, Hemingway & Bynum 2005). This may also hold true for flowers (see seasonal maxima reported in Oline Appendix 1).

There can be considerable inter-annual variation in the exploitation of flowers and nectars. Nectar accounted for 43% of plant feeding in golden lion tamarins, *Leontopithecus rosalia*, in one year, but no nectar was consumed in the previous year (Dietz *et al.* 1997). In tamarins, *Saguinus fuscicollis* and *Saguinus mystax*, nectar accounted for 4.4% and 8.0% respectively of the diet in one year, and <0.5% in both species in the following year (Smith 1997, Knogge & Heymann 2003). For red colobus monkeys, *Colobus badius*, flowers are a negligible component of the diet in most years, but may account for up to 15% of feeding records in some years (Struhsaker 2010). Such variation is most likely to be related to availability of nectars/flowers and their profitability in comparison to alternative resources.

Apart from seasonal variation in flower consumption, there may also be diurnal variation. Mantled howler monkeys, *Alouatta palliata*, feed preferentially on the flowers of *Pithecelobium saman* (Fabaceae) at flower opening times, which has been interpreted as a strategy to maximize nutrient or energy intake (Jones 1983).

A bizarre case of florivory has been observed in *P. diadema,* which feed on the inflorescences of underground parasitic plants from the genera *Langsdorffia* (Balanophoraceae) and *Cytinus* (Cytinaceae) (Irwin 2007). The inflorescences are visually obscured and detected by the sifakas through intensive olfactory search.

*The influence of body size and dietary strategy on florivory and nectarivory.* Primates below 1 kg body mass are more likely to include nectar in their diet than medium-sized and large primates (χ² = 27.8, df = 4, p < 0.001), while primates above 5 kg body mass are more likely to consume entire flowers (χ² = 39.9, df = 4, p < 0.001; Fig. 1). Primates with a body mass between 1.0 and 5.0 kg tend to include both nectar and flowers in their diet, but the difference between observed and expected distribution is not significant (χ² = 7.7, df = 4, p > 0.05).

The distributions of florivory, nectarivory or both differ significantly between dietary categories (χ² = 61.7, df = 6, p < 0.001; Fig. 2). Folivorous and frugivorous-folivorous primates mainly feed on flowers, while the proportion of nectar consumers is highest in frugivorous-faunivorous primates; among exudativorous primates the proportions of flower and nectar consumers are almost equal. For detailed statistical comparisons see Online Appendix 2.

*Do primates possess morphological adaptations for nectarivory?* There is little evidence that primates possess morphological adaptations for nectarivory. Red-bellied lemurs, *Eulemur rubriventer*, which lick nectar

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1 The Tarsiidae, represented by the single genus *Tarsius*, are the only purely faunivorous primates.

TABLE 1. Reports of pollination by primates

| Plant family / species | Primate species | Flower handling | Evidence or signs of pollination | Region | Reference |
|---|---|---|---|---|---|
| Asphodelaceae<br>*Aloe ferox* | *Chlorocebus aethiops* | | faces covered with pollen | South Africa | Skead 1967 |
| Capparaceae<br>*Crateva greveana* | *Phaner furcifer* | flowers licked | sequential feeding at different flowers | Madagascar | Sussman & Raven 1978 |
| Celastraceae<br>*Brexia madagascariensis* | *Eulemur fulvus* | nectar licked from open flowers; no damage to flowers | sequential feeding in several plants | Madagascar | Birkinshaw 2002 |
| Clusiaceae<br>*Symphonia nectarifera* | lemurs | | regular visits | Madagascar | Jumelle & Perrier de la Bâthie 1910 quoted in Sussman & Raven 1978 |
| Combretaceae<br>*Combretum fruticosum* | *Ateles chamek*<br>*Cebuella pygmaea*<br>*Cebus albifrons*<br>*Cebus apella*<br>*Saguinus fuscicollis*<br>*Saguinus imperator*<br>*Saimiri boliviensis* | nectar licked; moderate to heavy loss of distal portions of flowers | faces conspicuously tinted with pollen; abundant seed set by many plants that had been used; trap-line feeding | Peru | Janson *et al.* 1981 |
| Combretaceae<br>*Combretum lanceolatum* | *Cebus* sp. | "quite destructive" | face covered with pollen; sequential feeding on flowers from same and different plant individual | Brazil | Prance 1980 |
| Euphorbiaceae<br>*Mabea fistulifera* | *Brachyteles hypoxanthus*<br>*Callithrix flaviceps*<br>*Cebus apella* | nectar licked; minor damage to inflorescences | face covered with pollen | Brazil | Torres de Assumpção 1981, Ferrari & Strier 1992 |
| | *Leontopithecus chrysopygus* | nectar licked; no damage to inflorescences | face covered with pollen | Brazil | Passos & Kim 1999 |
| Euphorbiaceae<br>*Mabea* sp. | *Saguinus fuscicollis*<br>*Saguinus mystax* | nectar licked; no damage to inflorescences | pollen visible on facial hair; sequential feeding on flowers of same and different plant individual | Peru | Heymann, pers. obs. (see video in Supplementary Material) |

| Plant family / species | Primate species | Flower handling | Evidence or signs of pollination | Region | Reference |
|---|---|---|---|---|---|
| Fabaceae *Daniellia pynaertii* | *Allenopithecus nigroviridis* *Cercopithecus ascanius* *Cercopithecus wolfi* *Lophocebus aterrimus* | nectar licked; no damage to flowers; monkeys never seen to eat any other part of the flower | sequential feeding on flowers of same and different plant individual; fruit set positively associated with patterns of monkey visits | Zaire | Gautier-Hion & Maisels 1994 |
| Fabaceae *Eperua falcata* | *Cebus apella* *Saimiri sciureus* | nectar licked; no damage to flowers | | Surinam | Mori *et al.* 1978 |
| Fabaceae *Inga edulis* | *Aotus lemurinus* | no damage to flowers | face covered with pollen; sequential feeding at different flowers | Colombia | Marín Gómez 2008 |
| Fabaceae *Parkia bicolor* | *Perodicticus potto* (*Galago* sp.) | nectar licked | face, necks, hands dusted with pollen | Cameroon | Grünmeier 1990 |
| Fabaceae *Parkia madagascariensis* | *Eulemur macaco* | nectar licked | | Madagascar | Colquhoun 1993, Birkinshaw & Colquhoun 1998 |
| Fabaceae *Strongylodon craveniae* | *Cheirogaleus major* *Eulemur fulvus* *Eulemur rubriventer* *Microcebus rufus* | depending on primate species, nectar feeding is never, rarely, or largely destructive | animals come in contact with styles and anthers (depending on species systematically or haphazardly) | Madagascar | Nilsson *et al.* 1993 |
| Fabaceae *Strongylodon* sp. | *Cheirogaleus major* | nectar licked; no damage to flowers | sequential feeding on several flowers of same plant | Madagascar | Wright & Martin 1995 |
| | *Eulemur fulvus* *Eulemur rubriventer* | nectar licked; no damage to flowers | face covered with pollen; sequential feeding in different plant individuals | Madagascar | Overdorff 1992 |
| Malvaceae *Adansonia digitata* | *Otolemur garnettii* | | face covered with pollen; sequential feeding at different flowers | Kenya | Coe & Isaac 1965 |
| Malvaceae *Adansonia perrieri* *Adansonia rubrostipa* *Adansonia za* | *Cheirogaleus medius* *Phaner furcifer* | | | Madagascar | Baum 2003 |
| Malvaceae *Adansonia* sp. | *Phaner furcifer* | flowers licked | sequential feeding at different flowers | Madagascar | Sussman & Raven 1978 |

| Plant family / species | Primate species | Flower handling | Evidence or signs of pollination | Region | Reference |
|---|---|---|---|---|---|
| Malvaceae<br>*Ceiba pentandra* | *Microcebus murinus*<br>*Eulemur mongoz* | nectar licked; no damage to flowers | | Madagascar[2] | Sussman & Tattersall 1976, Sussman 1978 |
| | *Ateles chamek*<br>*Cebus apella*<br>*Saimiri boliviensis* | no damage to flowers | faces conspicuously tinted with pollen | Peru | Janson *et al.* 1981 |
| Malvaceae<br>*Ochroma pyramidale* | *Cebus capucinus* | no damage to flowers | pollen on face; sequential feeding at flowers of same and other plant individuals | Panama | Oppenheimer 1977 |
| Malvaceae<br>*Quararibea cordata* | *Ateles chamek*<br>*Cebuella pygmaea*<br>*Cebus albifrons*<br>*Cebus apella*<br>*Saguinus fuscicollis*<br>*Saguinus imperator*<br>*Saimiri boliviensis* | nectar licked; some flowers may be damaged, but flowers borne in great excess | faces conspicuously tinted with pollen; trap-line feeding | Peru | Janson *et al.* 1981 |
| Passifloraceae<br>*Passiflora adenopoda* | *Saimiri oerstedii* | reproductive flower structures left intact | face covered with pollen | Costa Rica | Happel 1983 |
| Strelitziaceae<br>*Ravenala madagascariensis* | *Eulemur macaco* | | | Madagascar | Birkinshaw & Colquhoun 1998 |
| | *Varecia variegata* | nectar licked; no damage to flowers | fur covered with pollen; sequential feeding on flowers from same and different plant individuals | Madagascar | Kress *et al.* 1994 |
| Strelitziaceae<br>*Strelitzia nicolai* | *Otolemur crassicaudatus* | nectar licked; no damage to flowers | face and hands covered with pollen | Africa | Frost & Frost 1981 |

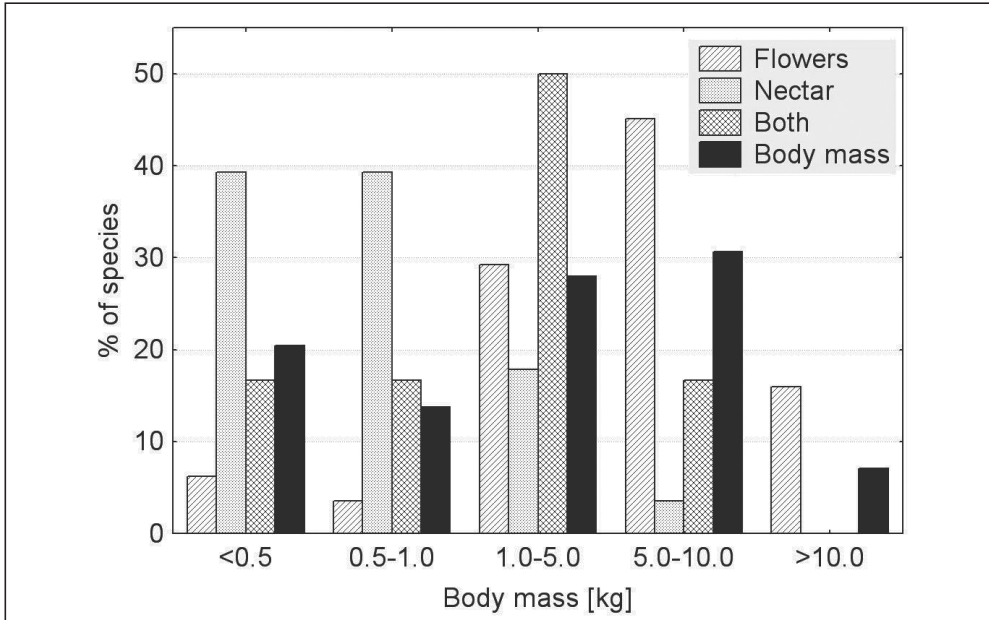2 *Ceiba pentandra* is not autochthonous to Madagascar but has been introduced

FIG. 1. Distribution of the consumption of flowers (hatched bars), nectar (stippled bars), or both (cross-hatched bars) over body mass categories; black bars indicate the expected distribution (based on the distribution of body mass).
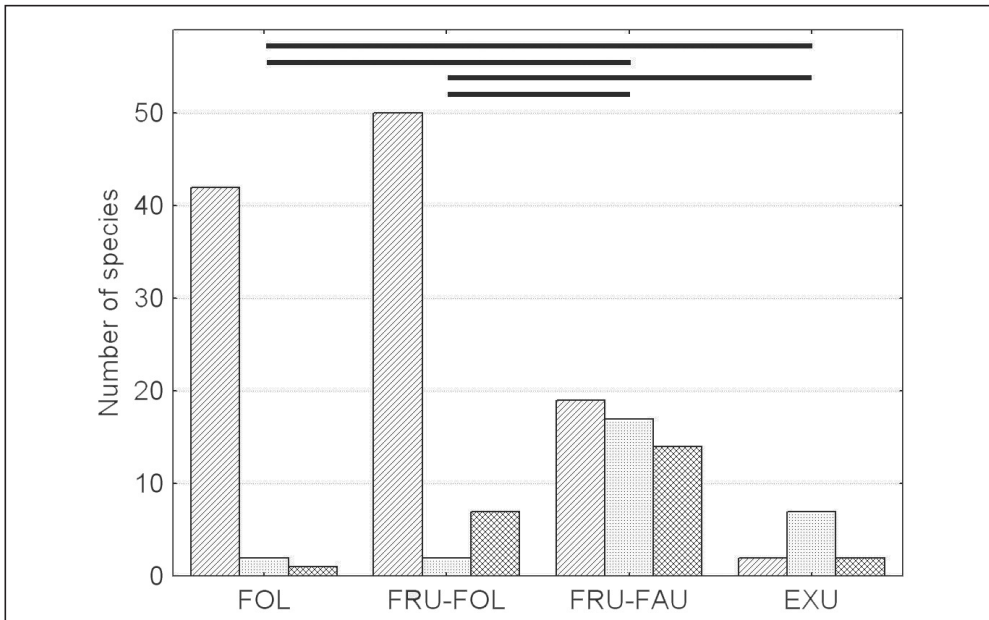


FIG. 2. Distribution of the consumption of nectar (hatched bars), flowers (stippled bars), or both (cross-hatched bars) over dietary categories. FOL: folivores, FRU-FOL: frugivores-folivores, FRU-FAU: frugivores-faunivores, EXU: exudativores. Horizontal bars indicate significant differences between distributions.

from flowers, possess a brush-like tongue tip, in contrast to rufous lemurs, *Eulemur fulvus*, which consume entire flowers (Overdorff 1992). An "extraordinary long tongue" has been suggested as evidence for nectarivory in the hairy-eared dwarf lemur, *Allocebus trichotis* (Meier & Albignac 1991), but neither was tongue length quantified nor were data presented on the importance of nectar in the diet of this Malagasy primate. Callitrichids (marmosets and tamarins) can double the length of their tongue when protruding it out of the mouth (Heymann & von der Lage 2009). However, since flowers exploited for nectar by callitrichids present nectar relatively openly, this is unlikely to represent a specific adaptation for nectarivory. A comparative study on cranial shape in fruit, nectar and exudate feeders from the orders Marsupialia, Chiroptera, and Primates did not reveal any evidence for specific adaptations in primates (Dumont 1997). However, Muchlinski (2002) found that in *Eulemur macaco* and *Varecia variegata*, two lemur species with a high percentage of nectar in the diet, snouts are longer than predicted from the allometric relationship with body mass, analogous to lengthened snouts in nectarivorous bats (Howell & Hodgkin 1976). Additionally, Muchlinski (2004) reported structural modifications of the hair (divaricate scales) in a few seasonally nectar-feeding lemurs. These modifications were interpreted as structures that may aid in pollination, although they more likely evolved for the collection of pollen that is subsequently groomed out of the fur and consumed (Howell & Hodgkin 1976).

*Evidence for primate pollination.* Apart from non-destructive handling of flowers (at least the reproductive parts must remain intact), additional criteria have to be fulfilled to unequivocally consider a flower visitor as a pollinator: demonstration of picking up pollen at one flower and depositing it on the stigma of another, and subsequent seed production (Carthew & Goldingay 1997). Additionally, less rigid criteria can be used as supportive clues. Consistency of visits to flowers of the same plant species, visitors' dependency on nectar as a source of energy (at least during some period of the year), and morphological structures of the flower allowing access only to certain visitors can qualify these visitors as potential pollinators (Kress 1993).

Unequivocal evidence for pollen deposition and for lack of fruit set can only be obtained through experimental work (e.g. exclusion experiments, label-

ing of pollen), but such experimentation is inherently difficult with primates. Therefore evidence for primate pollination is mainly indirect, based on flower handling style, appearance of pollen in the face and fur, and sequential visits to different flowers and individuals of the same plant species. Available information is summarized in Table 1. A number of studies report non-destructive feeding at flowers, leaving at least the reproductive part intact, pollen adhesion to primate faces and fur, and subsequent visits to flowers of the same or different plant individuals. Only one study reports a positive association between primate visits to flowers and subsequent fruit set (Gautier-Hion & Maisels 1994), suggesting a definite role of primates as pollinators.

Flowers of the Malagasy traveler's tree, *Ravenala madagascariensis* (Strelitziaceae), possess large flowers protected by tough bracts that have to be forcibly opened by animal visitors. Along with the observation of regular visits and the copious production of nectar, this led Kress (1993) and Kress *et al.* (1994) to suggest lemurs, particularly ruffed lemurs, *Varecia variegata*, as the primary pollinators of this plant species. However, a close coevolutionary relationship, as suggested by Kress (1993) and Kress *et al.* (1994) between *R. madagascariensis* and *V. variegata* is unlikely: the distributional ranges overlap only partially and *R. madagascariensis* may produce fruits in the absence of *V. variegata* (Jörg Ganzhorn, pers. comm.).

Most primates listed in Table 1 are small or medium-sized, and all reports of potential primate pollination come from the Neotropics, Madagascar, or Africa. Notably, there is no hint of pollination by Asian primates (Table 2). Since larger primates are more likely to consume entire flowers, the comparatively lower number of small and medium-sized primates, and high number of folivorous or frugivorous-folivorous primates in Asia compared with the other geographic regions (Kappeler & Heymann 1996), possibly accounts for this pattern. Also, this geographic pattern provides further arguments against the hypothesis put forward by Sussman and Raven (1978) that pollination by primates (and other non-flying mammals) has evolved where pollination by flying mammals, i.e. bats, is rare or absent, as in Madagascar (see also Janson *et al.* 1981).

*Impact of florivory.* Since the majority of primates consume entire flowers, negative impacts on fruit set are likely. Black-handed spider monkeys, *Ateles geoffroyi*, may massively destroy flowers of *Symphonia*

TABLE 2. Number of plant genera, and primate genera and species for which pollination has been suggested in different geographic regions

| Region | # plant genera | # primate genera | # primate species |
|---|---|---|---|
| Africa | 4 | 7 | 8 |
| America | 6 | 8 | 12 |
| Asia | - | - | - |
| Madagascar | 6 | 5 | 10 |

*globulifera* (Clusiaceae) and reduce fruit set in plant individuals located within spider monkey home-range areas when compared with plant individuals located elsewhere (Riba-Hernández & Stoner 2005). Flower consumption by chacma baboons, *Papio ursinus*, causes reduced fruit set in the succulent *Aloe marlothii* (Asphodelaceae) (Symes & Nicolson 2008). Mangabeys, *Cercocebus albigena*, may "virtually denude individual [*Milletia* and *Erythrina*] trees of flowers" so that practically no fruits are set (Waser 1977, p.195). Lion-tailed macaques, *Macaca silenus*, and Nilgiri langurs, *Semnopithecus johnii*, together with four small mammal species, account for 48-54% of destroyed flowers in *Cullenia exarillata* (Malvaceae [= Bombacaceae]) (Ganesh & Davidar 1997). Raju *et al.* (2005) noted that flower predation by bonnet macaques, *Macaca radiata*, and Hanuman langurs, *Semnopithecus entellus*, is detrimental to the reproductive success of *Bombax ceiba* (Bombacaceae), but did not provide quantitative evidence.

## CONCLUDING REMARKS

Of the currently recognized 390 primate species (IUCN/SSC Primate Specialist Group 2010), 165 have been observed to feed on flowers and/or nectar. It is quite likely that this feeding habit is found in most primates (except for the faunivorous tarsiers), but obviously varies considerably between species and even populations (see Online Appendix 1). My review revealed that flowers and/or nectar are of considerable importance in the diets of a number of primate species, at least seasonally. Reviewing the many publications on diet composition of primates, I found that for some species flowers and/or nectar actually rank second after fruit or leaves, making classification as frugivores-folivores or frugivores-faunivores inaccurate.

The importance of flowers and/or nectars in primate diets implies that primate-flower interactions are not uncommon and that there might be a considerable – and hitherto probably underestimated – impact of this interaction on the plant individual and population level. Most primates are flower predators, and may have a negative impact on the fitness of individual plants or local plant populations in years where flowers are particularly important in the diet. The few studies where long-term information on the diet of a primate population is available suggest that there is a strong inter-annual variation in florivory. This means that the potentially negative impact is not consistent and most likely not detrimental to the affected plants in the long run. Whether primate florivory may indirectly affect other flower visitors, and thus also affect ecosystem processes centered on animal-flower interactions, is completely unknown.

My review confirmed the predicted effect of body size and dietary strategy on the type of primate-flower interactions. These non-independent effects can be interpreted as the result of constraints imposed by body size on foraging efficiency in relation to the size, quality and availability of food resources (Richard 1985, Strier 2007). More interesting than the general trend for large primates feeding on entire flowers and small primates on nectar or both is the question of why several large primate species (e.g. *Ateles chamek*, *Brachyteles hypoxanthus*, *Lophocebus aterrimus*) feed on nectar of some plant species and even may serve as pollinators instead of consuming entire flowers. This is even more remarkable since related species are reported to eat entire flowers and have not been seen feeding on nectar only. Gautier-Hion and Maisels (1994) suggested that there must be a great energetic reward for large primates to feed on nectar only instead of consuming the flower. Additionally, protection of flowers by toxic compounds may restrict flower exploitation to nectar consumption (Gautier-Hion & Maisels 1994).

Another question is whether mutualistic or co-adaptive relationships between primate and plant species exist. A number of floral traits have been posited as part of a non-flying mammal pollination syndrome (Sussman & Raven 1978, Janson *et al.* 1981, Carthew & Goldingay 1997): robust flowers or inflorescences with at least partially fused and cuplike perianth, upright flower orientation, exerted stamina, visually conspicuous or strongly odorous flowers, and copious amount of nectar. While several of these traits are present in several plant species

for which pollination by primates has been postulated, other plant species do not conform. For instance, inflorescences of *Mabea fistulifera*, supposed to be pollinated by *B. hypoxanthus, Callithrix flaviceps* and *Cebus apella* (Torres de Assumpçao 1981, Ferrari & Strier 1992), are relatively fragile and presented in a hanging position. They do, however, produce large amounts of nectar (inflorescences of the related *Mabea occidentalis* produce 149 ± 50 mg sugar per night; Steiner 1981).

Given that potential primate pollinators vary in size (from ca. 30-65 g in *Microcebus* to *ca.* 8000 g in *Brachyteles*), activity pattern (nocturnal or diurnal), the relative role of different sensory systems in foraging and food selection (Dominy *et al.* 2006), and in color vision systems (Jacobs 2002), it is unlikely that plants (potentially) pollinated by primates converge on a small number of traits. As already stated by Carthew and Goldingay (1997) for non-flying mammals as pollinators, the variability in behavior and morphology will preclude the selection for specific traits. Nevertheless, the importance of nectar in the diet of a substantial number of primate species suggests that there are more cases of primate pollination than registered so far.

The legume *Daniellia pynaertii* remains the best documented case for primate pollination and co-adaptation. Apart from the correlation between primate flower visits and fruit set (see above), the contrast between floral traits of *D. pynaertii* and those of other species of the genus that are pollinated by butterflies provides tentative evidence for co-adaptations (Gautier-Hion & Maisels 1994).

One approach to evaluating the relevance of primate pollination, and whether it has an impact on plant reproductive traits, would be the comparison of fruit set in plant species between areas with potential primate pollinators and areas where these have recently gone extinct (expectation: fruit set higher in areas with primates, controlling for confounding factors), and the comparison of traits of a plant between areas with potential primate pollinators and areas where the same species has never interacted with primates (expectations: higher nectar production and more robust flowers in areas with primate pollinators). If expectations were met, this would actually provide a stronger case for a role of primates as pollinators. A similar comparative approach could be used to examine the impact of primate florivory on plant populations (see Riba-Hernández & Stoner 2005). Additionally, however, it will also be necessary in primate studies to report the type of interaction with flowers more precisely, and to provide good and quantitative natural history data that can form the basis for more quantifiable comparisons and tests of theoretical predictions. The contribution that flowers and nectar make to the diets of primates suggest that there is a high potential for primate-flower interactions. Understanding these interactions and their ecological and evolutionary implications will make a contribution to both primatology and tropical ecology.

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## SUPPLEMENTARY MATERIAL ON ECOTROPICA WEBSITE

Video: This video was recorded by Tobias Wommelsdorf in September 2010 at the Estación Biológica Quebrada Blanco (EBQB) in north-eastern Peru (4°21'S, 73°09'W) in the course of a field practical on primate behavior and ecology of the University of Göttingen. It first shows a saddle-back tamarin, *Saguinus fuscicollis*, feeding at a flower from a liana of the genus *Mabea* (Euphorbiaceae). Shortly after this tamarin has left, a moustached tamarin, *Saguinus mystax*, starts feeding on the same flower.
Appendix 1: Primate-flower database used in this study.
Appendix 2: Statistics to Fig. 2.

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