Primates (2003) 44: 61–66
DOI 10.1007/s10329-002-0008-6

ORIGINAL ARTICLE

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Increase in tannin consumption by sifaka (*Propithecus verreauxi verreauxi*) females during the birth season: a case for self-medication in prosimians?

Received: 1 May 2002 / Accepted: 10 September 2002 / Published online: 20 November 2002

Abstract In this study we report preliminary data on the consumption of tannin-rich plants by sifakas (*Propithecus verreauxi verreauxi*) living in the Kirindy forest, western Madagascar. Sifakas spent most of their time feeding on only a few plant species. The tannin intake during the period between the pregnancy and birth season was significantly higher in pregnant females or females with lactating infants than in non-reproductive females and males. These periparturient females secured a larger proportion of condensed tannins by short feeding bouts on plants not included in the group's limited preferred food species. The measured increase in tannin intake is puzzling in light of the fact that tannins are commonly known for their protein-binding properties. Since protein demands are highest in pregnant and lactating females, possible medicinal benefits of tannin ingestion are considered. Tannin consumption is associated with an increase in body weight and stimulation of milk secretion. Veterinarians administer tannins as an astringent, anti-hemorrhagic and anti-abortive. Their high potential as an alternative anthelminthic has also recently been recognized. Thus, when viewed as self-medicating behavior, controlled increase in tannin intake could have multiple prophylactic advantages for females during the periparturient period. The high selectivity in their plant choice, and the presence of unusual feeding habits by a particular group of individuals (females with infants) limited in time (birth season), suggests that an increase in tannin ingestion may be a self-medicating behavior with multiple directly adaptive benefits to female reproduction.

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Keywords Self-medication · Condensed tannins · Sifaka females · Reproductive benefits

Introduction

The study of self-medication, or zoopharmacognosy, is a relatively new field in the discipline of animal behavior (see Huffman 2001; Engel 2002). Research on primate self-medication was first inspired by Janzen (1978) and gained momentum with the observation of chimpanzees in western Tanzania (Wrangham and Nishida 1983; Huffman and Seifu 1989) and baboons in Ethiopia (Philips-Conroy 1986) consuming plants of known medicinal value. Further detailed studies pointed to the control of internal parasite infection and/or relief from the related discomfort as a principle function of such behavior in the African great apes (e.g., Huffman et al. 1993, 1996; Wrangham 1995; Huffman and Caton 2001). Geophagy and charcoal ingestion, two variations of the same form of self-medication, are widely reported among apes and monkeys (Krishnamani and Mahaney 2000). Based on the excellent absorptive capacity of charcoal and clay, self-medication is proposed as a means of relieving gastric distress brought on by the ingestion of too much toxic plant material, intestinal parasite infection or a restricted diet etc. (e.g., Cooney and Struhsaker 1997; Wakibara et al. 2001). It has been proposed, for black lemurs and capuchins, that rubbing volatile insect or plant matter into the fur, controls infestation by ectoparasites (Baker 1996; Birkinshaw 1999; Valderrama et al. 2000). All of these behaviors are considered to enhance, in one way or another, the user's immediate wellbeing and thus increasing the user's chances of survival.

Little is known to date about the possibility of self-medication directly altering reproductive fitness. It has been suggested that secondary compounds in the primate diet can enhance or inhibit reproductive outcome. For example, although tentative, intriguing evidence has been presented to suggest that feeding on seasonally available plants with known phytoestrogens may mediate conception and estrous in chimpanzees, muriquis and vervets (Whitten 1983; Garey et al. 1992; Strier 1993; Wallis 1997). It has also been speculated that other secondary plant compounds present in commonly consumed foods induce facultative birth spacing and influence the sex of offspring in mantled howler monkeys (Glander 1980, 1994). The line between instances of a primarily nutritional and of a medicinal function can be difficult to draw from field observations alone. Pharmacological evidence and direct analyses suggest that a medicinal component does exist, particularly in highly seasonally ingested items of demonstrated pharmacological value (e.g., Huffman et al. 1998; Cousins and Huffman 2002).

From this brief overview, it seems likely that there is a reproduction-modulating component in the primate diet, but at present little is known about the possible effects of such a diet on reproduction and even less about the potential for self-medication in prosimians. The periparturition period is a critical time for females, and the alleviation of related problems via behavioral and biological adaptations are considered to be a high priority for reproduction and survival. From a dietary perspective, females are in need of increased amounts of protein for the maintenance of reproductive function, such as development of the uterus and mammary glands (e.g., Houdijk et al. 2001). The physiological prioritizing of protein and other nutrient resources to reproduction comes at a price, resulting in a drop in immunity to parasite infection during pregnancy and lactation (see Coop and Holmes 1996; Coop and Kryiazakis 1999; Houdijk et al. 2001).

When faced with such biologically mediated challenges at critical times, flexible behavioral adaptations are likely to play an increasingly important role (e.g., Huffman and Caton 2001). From the perspective of self-medication, we are interested in the possible role of plant secondary compounds in directly and indirectly overcoming the challenges of reproduction by females. Focusing on peculiar dietary changes offers an interesting area of investigation.

In this paper we take advantage of preliminary data on tannin content in the plant-food diet of a population of sifaka (*Propithecus verreauxi verreauxi*) living in the Kirindy forest, western Madagascar, to test the hypothesis that tannin consumption has a self-medicating function beneficial to pregnant and lactating females.

Methods

Study area

Kirindy is a primary dry deciduous forest of about 100,000 km^2 in the central-western part of Madagascar. The field camp is located at roughly 44° ± 9′E, 20°3′S, at an altitude of 30 m above sea level. The research area, CS7, is a locality in the southern part of Conoco road, 7 km from the main road. The surface area is about 40 ha, 2 km east of the main camp. The climate is characterized by a long dry season (April–November) and a short wet season (December–March). The mean annual rainfall is 800 mm, mostly in the rainy season. The temperature shows contrasting daily highs and lows (7–25°C) during the dry season, but is relatively stable (25–30°C) during the wet season.

Study groups

Since the beginning of 1995, we have placed color-fabric collars on all members of eight sifaka study groups living in CS7. We followed four neighboring groups during 8 months, from May 1995 to August 1998. Environmental changes (e.g., river flooding) and variations in group composition (e.g., death of an individual) took place during the study period, causing some modification of the study groups.

Three adults (3 years or older) from each group were observed 3 days per month, from dawn to dusk, using focal animal sampling. One of the females, Alice, was technically a sub-adult, but she gave birth to her first infant at the age of 2.5 and is included in the analyses. Hourly turnover of the focal animal allowed us to have, at the end of every monthly cycle, a full day of observation per individual. In total, 27 subjects, belonging to three categories (males, reproductively active females, and reproductively inactive females), were observed. The monthly observations were grouped into four periods corresponding to a female's reproductive state: the mating season; the pregnancy period; the birth season; and the lactation period. The number of individuals observed per period is given in Table 1.

Plant samples and chemical analyses

During behavioral observations, plants eaten by sifakas were marked and every part not eaten was collected immediately after the animal left the spot or within 1–2 days later, depending on circumstances. Plant identification was performed by a Malagasy plant expert at the Centre de Formation Professionelle Forestale, Morondava. Each sample was sun- or oven-dried and stored in a closed plastic bag until chemical analysis could be performed in the laboratory. Plant food specimens were analyzed in two different test runs at the following institutions and times: Deutsches Primatenzentrum (DPZ), Gottingen, Germany, July 1996; Zoology Department, University of Hamburg (ZDU), Germany, October 1998. The extraction technique used was the same at both laboratories, but the dilution of suspension was different.

Each plant sample was first pulverized in a grinder, then kept overnight in an oven at +60°C to dry. An aliquot from each dried sample (50 mg) was suspended in 50% methanol/water (at DPZ) or 100% methanol (at ZDU). After 24 h, 0.5 ml of the suspension was diluted with 4.5 ml of 50% or 100% methanol. An aliquot (2.5 ml) of the suspension was mixed with 2.5 ml of the reagent and kept in a boiling water bath for 2 h.

From this aliquot, condensed-tannin content was photometrically evaluated by measuring light absorption at 540 nm, using the following formula: % tannin = (absorbency×4,500)/milligrams of dried sample. The amount of plant material ingested by each sifaka was evaluated by multiplying the percentage of each item ingested (dry-weight unit) by the time spent (seconds) feeding on any given plant/plant part. The data were pooled by month in order to smooth out random fluctuations.

Statistical analysis

In comparing average levels of condensed tannins consumed in the three categories (males, pregnant/lactating females, and reproductively inactive females), we used the non-parametric Kruskal–Wallis analysis of variance. Owing to the small sample size, we selected the level of significance of $\alpha = 0.1$ (see Hays 1991, p. 1029).

Results

Sifakas spent more than 97% of their feeding time concentrated on a few plant species. The Malagasy

Table 1 Distribution of observations (x) made on study subjects, by month and sex over reproductive class of individuals between 1995 and 1998 in the Kirindy forest, western Madagascar. *F+I* Reproductively active females, *F–I* reproductively inactive females, *M* males, – not observed. Total observation time 2,592 h (27 individuals × 12 h/month × 8 months)

Subject	Class	Mating season		Pregnancy		Birth season		Lactation	
		Feb	Mar	May	Jun	Jul	Aug	Oct	Nov
Vienna	F–I	x	x	x	x	x	x	x	x
Linz	M	x	x	x	x	x	x	x	x
Bregenz	M	x	x	x	x	x	x	x	x
Bonn	M	x	x	–	–	–	–	–	–
Colonia	F+I	x	x	–	–	–	–	x	x
Fulda	F+I	x	x	–	–	–	–	x	x
Jever	M	–	–	–	–	–	–	x	x
Tamatave	F–I	x	–	–	–	–	–	–	–
Tana	F+I	x	–	–	–	–	–	–	–
Tulear	M	x	–	–	–	–	–	–	–
Milano	M	–	–	x	x	x	x	–	–
Napoli	M	–	–	x	x	x	x	–	–
Roma	F+I	–	–	x	x	x	x	–	–
Alice [a]	F+I	x	x	x	x	x	x	x	x
Darwin	M	x	x	–	–	–	x	–	–
Adelaide	F–I	x	x	–	–	–	x	–	–
Canberra	F–I	–	–	x	x	x	–	–	–
Sydney	M	–	–	x	x	x	–	x	x
Berlin	M	–	–	–	–	–	–	x	x
Atlanta [b]	F+I	–	–	x	x	x	–	x	–
Boston	M	–	–	x	x	x	–	–	–
Dallas [c]	F–I	–	–	x	x	x	–	x	x
Juneau	M	–	–	–	–	–	–	x	x
Philadel	F+I	–	–	–	–	–	–	–	x
Geneva	F+I	–	–	–	–	–	x	–	–
Pisa	F–I	–	–	–	–	–	x	–	–
Pinky	M	–	–	–	–	–	x	–	–

[a] Alice belongs to F+I in August only
[b] Atlanta belongs to F+I in October
[c] Dallas belongs to F+I in October and November

names, species, family, and percentage tannin ingested from these plants are given in Table 2.

The yearly intake of tannins by females with infants did not differ significantly from that of females without infants and that of males (Kruskal–Wallis test: $H_2=0.82$, $n=27$, $P=0.66$). However, the increase in tannin intake from the pregnancy season to the birth season was significantly higher in females with infants than in the other two categories (Kruskal–Wallis test: $H_2=4.74$, $n=12$, $P=0.09$).

Monthly variation in the plant's percentage of condensed tannin explains the overall increase in tannin consumption for all three categories, since the peak in concentration is in the birth season (Fig. 1). Nevertheless, females with infants secured a larger proportion of condensed tannins by short feeding bouts on plants not included in the preferred species list of the group (Table 2). The peculiar choice of plant by females in this category was confirmed by the overall significantly lower number of plants consumed during the birth season in comparison with females without infants and males (Kruskal–Wallis test: $H_2=6.7$, $n=17$, $P=0.05$).

Discussion

During pregnancy and lactation, energy and protein requirements may increase between two- and ten-fold (Blaxter 1989; Jessops 1997). Protein requirements are expected to be considerably higher at this time than any other period of a female's life. Ideally therefore, periparturient females should adapt their dietary habits to meet the increased demand for metabolizable proteins in order to maintain reproductive function. This is supported by the findings of Sauther (1994) for female ringtailed lemur at Beza Mahafaly and by Vasey (2000, 2002) for female ruffed lemur and brown lemur at Andranobe, Madagascar. Pregnant and lactating females minimized foraging costs and ate more young leaves high in protein and low in fiber than non-lactating females and adult males in the group.

At Kirindy, sifaka are highly selective in their plant-food choice, both in the sense of positive (feeding on rare plants) and negative (excluding abundant plants) selection (Carrai 1999). A significant trend of increased ingestion of tannins by periparturient females, compared to other adult females and males, was demonstrated in the present study. One of the plants with relatively high tannin content was eaten exclusively by periparturient females (fihamy, scientific name unknown), and a second one (kily, *Tamarindus indica*) was eaten by periparturient females, but not by non-pregnant females, whereas males consumed it in significantly lower amounts (Table 2). Furthermore, in the birth season, fihamy leaves were found to have very little nutritional content. Fats and carbohydrates were below the analytical sensitivity of the technique applied, and proteins were present in an extremely low amount (Carrai 1999).

Taken in large amounts, tannins are known to affect plant palatability and to bind with important nutrients, such as protein and polysaccharides, and are typically considered to have a negative effect on food intake and

Table 2 Percentage of condensed tannins present in the plants eaten by males and females in the birth season (July and August). *F+I* Reproductive females, *F–I* non-reproductive females, *M* males; – not observed

Malagasy name	Species name	Family name	Mean % tannins ingested in the birth season		
			F+I	F–I	M
Alimboro	*Albizia bernieri* [b]	Mimosaceae	–	0.003	0.002
Alimboromalao	*Albizia* sp.	Mimosaceae	0.010	–	–
Amaninomby	*Terminalia bovini*	Combretaceae	–	0.024	0.005
Anakaraka [a]	*Cordyla madagascariensis*	Cesalpinaceae	0.029	0.086	0.314
Anatsiko	*Securinega seyrigii*	Euphorbiaceae	–	0.006	0.003
Arofy	*Commiphora guillaumini*	Burseraceae	–	0.003	0.001
Fihamy	Unknown	Unknown	0.138	–	–
Hazomboenga [a]	*Diospyros tropophylla*	Ebenaceae	–	0.328	0.243
Hompy	*Quivisianthe papinae*	Meliaceae	–	0.022	0.002
Kily	*Tamarindus indica*	Cesalpinaceae	0.606	–	0.254
Kironono [a]	*Capurodendron rubrocostatum*	Sapotaceae	–	–	0.027
Liana	Unknown	Unknown	0.442	0.215	0.142
Lopingo	*Diospyros perrieri* [b]	Ebenaceae	–	0.001	0.001
	Diospyros greveana [b]		–	–	–
Maintifototra	*Diospyros* sp.	Ebenaceae	–	0.030	0.015
Mamiaho [a]	*Baseonema acuminatum*	Asclepiadaceae	–	–	–
Manary	*Dalbergia* sp.	Fabaceae	–	–	0.027
Mandravasarotra [a]	*Desmodium ramosissimum*	Leguminosae	–	–	–
Manjakabenitany [a]	*Baudonia fluggeiformis*	Cesalpinaceae	0.056	0.053	0.035
Mapandry	*Cedrelopsis* sp.	Meliaceae	–	–	0.006
Mapilazy	Unknown	Unknown	0.015	–	–
Menambaho	*Foetidia asymetrica*	Lecythidaceae	–	0.006	–
Menavahitsy [a]	Unknown	Unknown	–	–	0.021
Namologna [a]	Foetidia retusa	Lecythidaceae	0.266	–	0.153
Nato	*Capurodendron perrieri*	Sapotaceae	–	–	0.002
Piropitsokala	*Rothmannia tropophylla*	Rubiaceae	–	0.022	0.076
Sarigoavy	*Bivinia jalberti*	Flacourtiaceae	–	–	0.020
Sarinato	*Foetidia* sp.	Lecythidaceae	–	0.005	–
Talinala	*Terminalia calcicola*	Combretaceae	–	–	0.001
Tanjaka	*Anakolosa pervillana*	Oleaceae	–	0.086	0.075
Tratramborondreo	*Colubrina decipiens*	Rhamnaceae	0.025	0.044	0.009
Tsingena	*Doratoxylon stipulatum*	Sapinaceae	–	0.007	–
Tsitake	*Rhus perrieri*	Anacardiaceae	0.001	–	–
Vahipindy [a]	*Alafia intermedia*	Apocynaceae	–	–	–
Vahipisaka	Unknown	Unknown	–	0.004	–
Valotsy	*Breonia perrieri*	Rubiaceae	0.001	–	–
Vohamea	*Dyospyros sakalavarum*	Ebenaceae	0.008	0.004	0.004

[a] Plants listed here accounted for more than 97% of sifaka feeding time
[b] Uncertain identification

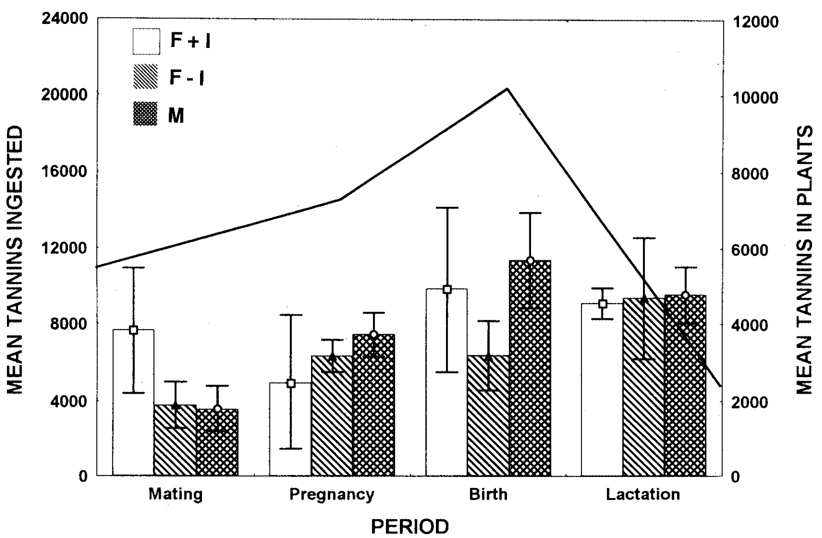

Fig. 1 Mean amount and SD of tannins ingested (mean tannin concentration × mean feeding time) over the four reproductive periods (mating, pregnancy, birth season, lactation) for the study subjects, by sex and reproductive state (*bars*, refer to left vertical axis) and the mean tannin concentration present in plants available in each period (*continuous line*, refer to right vertical axis). *F+I* Reproductively active females, *F–I* reproductively inactive females, *M* males. Values, based on all ingested plant species analyzed, are combined

digestibility (Glander 1982). While the level of tolerance to condensed tannins is not known in depth for lemurs, and particularly for *Propithecus v. verreauxi,* some data on avoidance by lemur species are available. According to Ganzhorn (1989) the tolerance of *P. v. coquereli* to condensed tannins should be relatively high, at least in terms of a lack of avoidance. The significant increased ingestion of tannins by periparturient sifakas is puzzling and led us to explore self-medication explanations for the selective ingestion of tannins by pregnant and lactating females and the role this foraging decision may play in overall health maintenance at this critical period.

Although it is difficult to obtain direct evidence for prophylactic effects of tannin consumption from field studies alone, a survey of the chemo-ecological, veterinary and pharmacological literature reveals a number of potentially beneficial and relevant properties that help to explain the observed increased intake of tannins by periparturient females. Tannin consumption is associated with increase in weight and the stimulation of milk secretion (e.g., Aerts et al. 1999; Barry and McNabb 1999). In veterinary practice, tannins are used for their astringent, anti-hemorrhagic and anti-abortive effects (Biagi and Speroni 1988). Recent work has also shown their high potential as an alternative anthelminthic (Athanasiadou et al. 2001). An increase in tannin intake therefore could have multiple prophylactic advantages during the periparturient period.

These properties of moderated tannin ingestion are consistent with the needs of pregnant and lactating females. Furthermore, the possible positive effect on reproductive fitness of this behavior for Kirindy sifaka females is supported by the fact that, in general, females here successfully give birth yearly, compared to every 2 years as noted in other sites (Richard et al. 1991). The benefit of increased tannin consumption by periparturient females at Kirindy is a hitherto unreported possible new form of self-medication enhancing female reproductive fitness. In the future, cross-site ecological and diet comparison should prove enlightening. The self-medication hypothesis advanced in this paper needs to be confirmed by further studies on this and other lemur species, as well as in other primate species. If confirmed by analogous or similar findings, our results will support the prediction that self-medication is widespread in primates (Huffman 2001) and furthermore that there are direct consequences of self-medication for increased reproductive fitness in females.

Acknowledgements Thanks are due to J. Ganzhorn and P. Kappeler for logistic facilities in Kirindy, laboratory use in Germany, useful suggestions in the set-up of the research project and stimulating discussions on sifaka socioecology. We are also grateful to A. Lunardini for significant contributions to the set-up of the research project on sifaka socioecology; R. Ralisoamalala for contribution to data collection; C. Rakotondrasoa, E. Rakotovao, R. Randriamarosoa for plant identification (Malagasy names); P. Meletti for plant taxonomy; A. Pagni and E. Bernardini for useful information on tannin effects; and E. Martinotti for valuable comments on a previous version of this manuscript. We wish to thank Drs. I. Kyriazakis and S. Athanasiadou for thoughtful discussions and information on tannins and to Dr. J. Caton for comments relating to the digestive tracts of sifakas.

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