BRIEF REPORT

Diademed Sifakas (*Propithecus diadema*) Use Olfaction to Forage for the Inflorescences of Subterranean Parasitic Plants (Balanophoraceae: *Langsdorffia* sp., and Cytinaceae: *Cytinus* sp.)

> MITCHELL T. IRWIN^{1*}, FANOMEZANTSOA JEAN-LUC RAHARISON², HARISON RAKOTOARIMANANA³, EDMOND RAZANADRAKOTO³, EDMOND RANAIVOSON³, JUSTIN RAKOTOFANALA³, AND CHARLES RANDRIANARIMANANA³ ¹Interdepartmental Doctoral Program in Anthropological Sciences, Department of Anthropology, Stony Brook University, Stony Brook, New York ²Département de Biologie Animale, Ecologie-Environnement, Université d'Antananarivo, Antananarivo, Madagascar ³Tsinjoarivo Forest Fragments Project, Tsinjoarivo, Madagascar

> Primates usually locate food resources using visual cues and memory, yet

The potential for olfactory-guided (or olfactory-assisted) food location remains relatively unexplored. Here we report observations of wild *Propithecus diadema* that strongly suggest that olfaction is used to locate the inflorescences of two subterranean parasitic plant species (*Langsdorffia* sp. and *Cytinus* sp.). These valued but seasonal food resources are found obscured in leaf litter, and sifakas spend considerable time on the ground engaged in what appears to be olfactory exploration before they locate the inflorescences. Because they are visually obscured and occur within a substrate that is rarely used by sifakas, accidental discovery of these resources seems unlikely. Individuals may learn to exploit them by watching conspecifics. Am. J. Primatol. 69:471–476, 2007. © 2006 Wiley-Liss, Inc.

Key words: sensory ecology; olfaction; Propithecus diadema; Langsdorffia; Cytinus

INTRODUCTION

It is thought that, relative to other mammals, primates have greatly reduced their capacity for olfaction and rely more on visual and auditory acuity (although many prosimians and platyrrhines still use olfaction in social communication [Epple, 1986]). Most primates locate food mainly using vision and memory [Dominy et al., 2001; Garber & Hannon, 1993], although there are some exceptions. Aye-ayes (*Daubentonia madagascariensis*) locate larvae in dead trees

Contract grant sponsor: Margot Marsh Biodiversity Foundation; Contract grant sponsor: Primate Conservation, Inc.; Contract grant sponsor: IPPL; Contract grant sponsor: Stony Brook University; Contract grant sponsor: Earth and Space Foundation; Contract grant sponsor: NSERC.

*Correspondence to: Mitchell T. Irwin, Department of Biology, McGill University, 1205 Docteur Penfield Ave., Montreal, Quebec, Canada H3A 1B1. E-mail: mitchell.irwin@mail.mcgill.ca

Received 23 February 2006; revised 11 May 2006; revision accepted 12 May 2006

DOI 10.1002/ajp.20353

Published online 11 December 2006 in Wiley InterScience (www.interscience.wiley.com).

© 2006 Wiley-Liss, Inc.



472 / Irwin et al.

using auditory cues and/or olfaction [Erickson, 1998; Hladik, 1979; Petter et al., 1977], and lorisoids detect insects using olfaction [Hladik, 1979]. In addition, chimpanzees (*Pan troglodytes*) and spider monkeys (*Ateles*) use olfactory and tactile evaluation to gauge fruit ripeness [Dominy et al., 2001].

It has been suggested that primates' olfactory sensitivity is comparable to that of other mammals, and that their reputation as visual creatures may have impeded the progress of research investigating olfaction [Epple, 1986; Laska et al., 2000]. Indeed, some captive primates use odors to locate hidden food [Bolen & Green, 1997; Hübener & Laska, 1998]. While olfaction may play a larger role in foraging than has been presumed, there is still only limited evidence of olfactionassisted food location in wild primates.

Here we report the apparent use of olfaction by a wild population of *Propithecus diadema* in Madagascar to locate a hidden food resource, the inflorescences of two subterranean parasitic plants (*Langsdorffia* sp. [Balanophoraceae] and *Cytinus* sp. [Cytinaceae]; Fig. 1). These plants parasitize the roots of trees or vines, and consist of rhizomes and large, fleshy inflorescences [Kuijt, 1969]. They are inconspicuously colored (unlike some species in the same families), and remain obscured underground and within leaf litter (except for mature inflorescences, which emerge from the ground). Inflorescences have a strong sweet smell (even to humans) when they are split open.

MATERIALS AND METHODS

We followed four habituated *Propithecus diadema* groups at Tsinjoarivo, eastern Madagascar (19°41′ S, 47°48′ E; 1400–1650 m) from January to December 2003 [Irwin, 2006]. Two study groups were located at Vatateza, a continuous forest site, and two inhabited Mahatsinjo, a fragmented forest site (Table I). Data were collected during all-day focal-animal follows, including instantaneous activity data (5-min interval) and continuous recording of feeding bouts (defined as uninterrupted time spent feeding on a single species with no more than a 10-sec break in consumption). Data were collected by the authors and field assistants during 651 focal-animal days, for 6,464 observation hours (spread roughly evenly among months). Animals were collared for individual recognition.

RESULTS

Sifakas ate whole immature inflorescences of *Langsdorffia* sp. and *Cytinus* sp. We observed 68 *Langsdorffia* feeding bouts and nine *Cytinus* bouts (Table I), and one to four inflorescences were consumed per bout. *Langsdorffia* was consumed by all study groups, while *Cytinus* was consumed by only three (however, *Cytinus* was found within the fourth group's home range). Consumption was highly seasonal, and observed feeding bouts occurred between July and October (the time of lowest fruit availability [Irwin, 2006]).

When foraging for inflorescences, the sifakas descended to the ground and moved slowly on all fours. They held their nose to the ground and moved it from side to side without digging or overturning the leaf litter. Searching continued until an inflorescence was found. The sifaka would then dig into the litter with its muzzle, locate the inflorescence, and pull it from the rhizome with its mouth (occasionally using a hand as well). During the search no other terrestrial activities (e.g., play or geophagy) were noted. The habituation of the study groups permitted observations to be made from a distance of $<5 \,\mathrm{m}$ for some bouts.



Fig. 1. Langsdorffia sp. (Balanophoraceae): (a) lateral view of inflorescence containing many small flowers, (b) longitudinal cross-section of inflorescence, (c) close-up (\times 3) of cross-section's lateral margin showing individual flowers under scales, (d) superior view of inflorescence, (e) lateral view of rhizome with developing inflorescences, and (f) superior view of the same rhizome. *Cytinus* sp. (Cytinaceae): (g) lateral view of inflorescence with a single flower (three of four bracts removed for illustration), (h) longitudinal cross-section of inflorescence (left bract removed), and (i) superior view of inflorescence (two bracts removed). Illustration: M. Irwin.

Instantaneous data show that locating inflorescences requires prolonged time spent on the ground. Focal-animal heights were well below typical levels for at least two samples (i.e., 5–10 min) before feeding bouts (Fig. 2). Animals also showed an elevated likelihood of being on the ground: 52% at one sample before feeding (<5 min before feeding) and 35% at the previous sample (5–10 min before feeding), which are both much higher than the average likelihood during July–October (1.66%). The height reduction may partly reflect the fact that



Fig. 2. Top: Boxplots of focal animal's height during 5-min instantaneous samples before and after Langsdorffia or Cytinus feeding at Mahatsinjo (box: 25th/75th percentiles, whiskers: 10th/90th percentiles). Bottom: Likelihood of being on the ground during instantaneous samples before and after Langsdorffia or Cytinus feeding at Mahatsinjo. Only data preceding an individual's first parasitic flower feeding bout of the day were included (n = 23 feeding events). Reference lines were derived from all instantaneous samples between July and October (n = 15,235).

	Langsdorffia sp.				Cytinus sp.			
Group	# Days	# Bouts	# Animals ^a	% Feeding time ^b	# Days	# Bouts	# Animals ^a	% Feeding time ^b
Continuous1	1	2	1/6	0.02	_	_	_	_
Continuous2	2	9	1/6	0.05	3	6	2/6	0.08
Fragment1	15	56	4/4	0.52	2	2	2/4	0.02
Fragment2	1	1	1/5	0.02	1	1	1/5	0.003

 TABLE I. Inclusion of Langsdorffia and Cytinus Flowers in Diet of Four

 Propithecus diadema Study Groups at Tsinjoarivo

^aNumber of animals in the group observed to eat the species, excluding infants/group size during months of *Langsdorffia* and *Cytinus* feeding.

^b% Feeding time derived from continuous feeding bout data over the annual cycle.

animals might incidentally detect inflorescences from lower heights, but this does not explain the time spent actually on the ground or the prolonged terrestrial searching.

These inflorescences appear to be valued food items, since they are one of very few items regularly observed to be the subject of food-related aggression. Dominant animals (or juveniles relying on a mother's protection) were observed to steal inflorescences from other animals. Inflorescences are large and are consumed slowly (*Langsdorffia*: mean = 3.6 min., SD = 2.4, range = 0.1–11.2; *Cytinus*: mean = 3.8 min., SD = 2.6, range = 0.8–8.7).

DISCUSSION

The observations described here strongly suggest that sifakas use olfaction, rather than vision, to locate *Langsdorffia* and *Cytinus* inflorescences. The animals tended to spend several minutes on the ground before they located the inflorescences, during which time they appeared to actively smell broad areas of leaf litter. Further research will be necessary to better assess the role of olfaction in the location and evaluation of food resources by sifakas and other wild primates. Previous studies reported that at least two other sifaka populations feed on Langsdorffia inflorescences. *Propithecus diadema* at Mantadia [Powzyk, 1997], and *P. edwardsi* at Ranomafana [Hemingway 1995; P. Wright, personal communication] (recorded by Hemingway as "mushroom"/"fungas").

These unusual food items raise interesting questions about what motivates animals to search in certain areas. Unlike most sifaka foods, *Langsdorffia* and *Cytinus* inflorescences are visually obscured and located in a substrate (leaf litter) that is not normally used during locomotion (geophagy occurs only where soil is exposed). It is therefore hard to imagine that these resources are discovered accidentally. Individuals may learn how to locate them by watching other group members. If so, this foraging would fit the definition of a behavior transmitted through "public information" [Danchin et al., 2004]. Clearly, more research is needed on two fronts: First, experiments could clarify exactly how sifakas find inflorescences, by concealing real or model flowers and/or scent within leaf litter. Second, given that sifaka home ranges are stable over time [Wright, 1995], it would be interesting to investigate the year-to-year reliability of these foods, and whether individuals anticipate the presence and location of inflorescences based on past years' experience.

476 / Irwin et al.

ACKNOWLEDGMENTS

We thank the government of the Democratic Republic of Madagascar, and the Direction des Eaux et Forêts for research authorization. The methods used were approved by Stony Brook University IACUC (#2002–1169). Funding was provided by the Margot Marsh Biodiversity Foundation, Primate Conservation, Inc., International Primate Protection League, Stony Brook University, Earth and Space Foundation, and an NSERC postdoctoral fellowship to M.T.I. For research facilitation we thank P. Wright, B. Andriamihaja, Malagasy Institute for the Conservation of Tropical Environments (MICET), and the Institute for the Conservation of Tropical Environments (ICTE) (L. Donovan and F. van Berkum). For data collection assistance, we thank P. Rasabo, J.-C. Rakotoniaina, K. Parks, T. Anderson, N. Melaschenko, J. Lapoint, E. Hatton, J. Mitchell, J. Anderson, J. Tardi, and M. Ali. We also thank K. Glander and K. Samonds for assistance during several stages of the study. Comments from C. van Schaik, B. Hirsch, D. Nickrent, P. Rasabo, K. Samonds, N. Dominy, P. Wright, C. Chapman, and two reviewers improved this manuscript.

REFERENCES

- Bolen R, Green SM. 1997. Use of olfactory cues in foraging by owl monkeys (*Aotus nancymai*) and capuchin monkeys (*Cebus apella*), J Comp Psychol 111:152–158.
- Danchin É, Giraldeau L-A, Valone TJ, Wagner RH. 2004. Public information: from nosy neighbors to cultural evolution. Science 305: 487–491.
- Dominy NJ, Lucas PW, Osorio D, Yamashita N. 2001. The sensory ecology of primate food perception. Evol Anthropol 10:171–186.
- Epple G. 1986. Communication by chemical signals. In: Mitchell G, Erwin J, editors. Comparative primate biology. Vol. 2A. Behavior, conservation and ecology. New York: Alan R. Liss. p 531–580.
- Erickson CJ. 1998. Cues for prey location by aye-ayes (*Daubentonia madagascariensis*). Folia Primatol 69(Suppl 1):35–40.
- Garber PA, Hannon B. 1993. Modeling monkeys: a comparison of computer-generated and naturally occurring foraging patterns in two species of neotropical primates. Int J Primatol 14:827–852.
- Hemingway CA. 1995. Feeding and reproductive strategies of the Milne-Edwards' sifaka, *Propithecus diadema edwardsi*. Ph.D. dissertation, Duke University, Durham, NC. 352p.
- Hladik CM. 1979. Diet and ecology of prosimians. In: Doyle GA, Martin RD, editors. The study of prosimian behavior. New York: Academic Press. p 307-357.

- Hübener F, Laska M. 1998. Assessing olfactory performance in an Old World primate, *Macaca nemestrina*. Physiol Behav 64: 521–527.
- Irwin MT. 2006. Ecological impacts of forest fragmentation on diademed sifakas (*Propithecus diadema*) at Tsinjoarivo, eastern Madagascar: implications for conservation in fragmented landscapes. Ph.D. dissertation, Stony Brook University, Stony Brook, NY. 410p.
- Kuijt J. 1969. The biology of parasitic flowering plants. Berkeley: University of California Press. 246 p.
- Laska M, Seibt Â, Weber A. 2000. 'Microsmatic' primates revisited: olfactory sensitivity in the squirrel monkey. Chem Senses 25: 47–53.
- Petter J-J, Albignac R, Rumpler Y. 1977. Faune de Madagascar 44: Mammifères Lémuriens (Primates Prosimiens). Paris: ORSTROM/CNRS. 513p.
- Powzyk JA. 1997. The socio-ecology of two sympatric indriids: Propithecus diadema diadema and Indri indri, a comparison of feeding strategies and their possible repercussions on species-specific behaviors. Ph.D. dissertation, Duke University, Durham, NC. 307p.
- Wright PC. 1995. Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. Int J Primatol 16:835–854.