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Vertebrate Predation in *Cebus capucinus:* Meat Eating in a Neotropical Monkey

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Abstract. A long-term study of two groups of white-faced capuchins *(Cebus capucinus)* in Santa Rosa National Park in Costa Rica provides evidence of unusually high levels of vertebrate predation compared to those reported in other field studies of *Cebus.* The hunting techniques for different prey types are described, and several questions concerning vertebrate predation in primates are addressed. Why is there variation between individuals and between groups in the rate of predation? Why do males hunt more than females? Previous hypotheses to explain hunting in Old World primates are applied to this Neotropical example. Finally, I argue that successful vertebrate predation can readily arise in species like *Cebus,* which are characterized by opportunistic foraging patterns, manipulative and cognitive skills and well-developed techniques for locating and subduing invertebrate prey.

Introduction

Primatologists and anthropologists have long been interested in reports of predation by monkeys and apes, largely because of analogies drawn to the hunting behavior of early hominids [1–14]. When it was first discovered that chimpanzees and baboons hunt and eat meat, the research findings quickly made the headlines, and it is perhaps no coincidence that chimpanzees and baboons were also the two species most often used in models of early hominids. A related reason for the intense interest in primate predation is the widespread assumption that hunting in omnivorous monkeys and apes involves higher-order cognitive skills. In his review of primate predatory behavior, Rose [7] argued that the finding and processing of any prized, hidden or rare food item, such as animal prey or honeycomb or bird's eggs, requires a high degree of premeditation, persistence, flexibility, decision making and, in some cases, cooperation. Still, he saw predation as arising out of the general behavioral and cognitive traits of omnivorous, ground-dwelling, Old World primates.

More recently, modelers of early human life have de-emphasized hunting and instead developed models of how human gathering

or collecting might have arisen from primate foraging patterns [15]. Concurrently the interest in primate meat eating has declined. However, two recent reviews of the topic [1, 2] emphasize that vertebrate predation is widely reported across the primate order (although infrequently practised in any given species) and as such is a phenomenon that deserves careful scientific consideration. Apart from these reviews, almost all of the literature on primate predation consists of reports and theories exclusively related to Old World, terrestrial primates. It is generally held that Neotropical monkeys are not successful vertebrate predators, even though most callitrichids and all capuchin species have been reported to take the occasional bird or lizard [2, 16]. Occasional killing and eating of vertebrates has been reported in the South American *Cebus apella* and *Cebus olivaceus* 17–20]. In the present report I would like to present data on vertebrate predation by the Central American monkey, *C. capucinus* [21, 22], along with possible explanations for the variable rates of vertebrate predation found in this species.

Methods

Two groups of white-faced capuchins have been observed from 1984 to the present at Santa Rosa National Park in Costa Rica, as part of a larger, long-term project to track the population dynamics and individual life histories of the three species of monkeys in the park. In particular, during the field season of January to June 1986, I collected 363 h of focal data on the foraging and social behavior of the two groups and followed them on a regular daily basis. The present report is based on this 5-month period of intensive, daily data collection. In addition, these monkeys have often been seen to capture and eat vertebrate prey in the other 5 years of our study, so that we have nearly twice as many observations of meat eating as will be described in this report. Data from a third group of capuchins in the park, studied over a 3-year period by Chapman [23], will be referred to briefly for comparative purposes.

Santa Rosa consists of 10,800 ha of tropical dry forest and open pasture areas in a series of stepped plateaus from the foothills of volcanic mountains down to the Pacific coastal plain. Prior to the establishment of the park in 1970, some parts of the upper plateaus were cleared as cattle pasture and are only now reverting to woody vegetation. Capuchin groups are found throughout the park and seem better able to exploit young successional forest than are the spider and howling monkeys. Of the two study groups reported upon here, the one responsible for most of the vertebrate predation, group T, occupies a range in which the forest is estimated to be only 40 years old, whereas the other group. group S, occupies a forest known to be approximately 100 years old. The third group, group B, lives in a nearly pristine semievergreen forest. Ecological sampling of the home ranges of these groups [Chapman and Fedigan, in preparation] shows that the youngest of the forests exhibits the lowest food density at certain times of the year and also experiences longer periods of fruit scarcity. Thus, group T, in the 40-year-old forest, has the poorest access to fruit of the study groups, especially during the dry season.

Results

During the 1986 field season, I observed 21 attempted predation episodes, 17 of which were successful and resulted in capture and consumption of at least 19 vertebrate prey. The vast majority of predation (91%) was seen in study group T (table 1), which exhibited 1 hunting attempt for every 12 h of observation and 1 successful capture of 1 or more prey for every 15 h of observation. This rate is nearly equal to that of the Gilgil baboons at the height of their hunting period [9], a rate reported to be the highest known for monkeys. The other study group of capuchins, group S, had a much lower rate, only 1 attempt for every 37 h and 1 suc-

Table 1. Vertebrate predation by group T from January to June 1986: participation by age/sex class and types of prey taken

	Lizards	Adult birds	Eggs, nest-lings	Bats	Squir-rels	Coatis	Incidents in which each age/sex class participated, %	Age/sex class ever seen to participate, %
Adult males (n = 7)								
Chase	3	–	–	–	6	–	100	86
Capture	3	1	–	–	3	2	88	71
Consume	3	1	2	–	5	4	88	100
Adult females (n = 6)								
Chase	–	–	–	–	2	–	38	33
Capture	–	–	–	–	–	–	12	0
Consume	–	–	1	–	2	1	29	50
Juveniles (n = 7)								
Chase	–	–	–	–	1	–	50	29
Capture	–	1	–	2	–	–	12	29
Consume	–	3	–	2	5	5	35	100
Total incidents	3	2	3	1	6	2	17	
Carcasses	3	2	?	2	4	6		

Total group size including infants = 26.

cess for every 74 h of observation. Our less intensive and more incidental observations made over the other years of the study suggest that group T consistently hunts and eats more vertebrate prey than the other groups of capuchins followed in the park. However, the killing and eating of vertebrates is a widespread behavioral trait at our study site (and, according to the literature, at all sites where capuchins have been studied). It is likely that some attempts occurred in my study groups which I failed to see, even during the intensive 5-month period. Some predation episodes, such as the relay chasing of squirrels by several monkeys, create a major disturbance in the foraging progression, whereas other incidents, such as single monkeys pouncing on a lizard, can go almost unnoticed in a widely dispersed foraging group.

The types of vertebrate prey taken at Santa Rosa include Iguanidae (lizards), Aves (adult parrots and jays as well as eggs and nestlings of many species), Sciuridae (squirrels), Chiroptera (bats) and Procyonidae (coatis). All of these animals, except the latter two types, are also reported to be preyed upon by *C. capucinus* on Barro Colorado Island, the other site at which this monkey species has been most intensively studied [24, 25]. Coati pups and young squirrels, as well as bird's eggs and nestlings, are removed from nests, which are regularly searched during the nesting seasons. Adult squirrels are always carefully scrutinized when encoun-

tered, and if found in a vulnerable location, they are chased, sometimes by several group members, and often captured when they fall to the ground. Such relay chasing, in which one or more individuals pursue the prey until another takes over, has been described for baboons and chimpanzees. Capuchins occasionally appear to surround a squirrel in a tree, cutting off its escape routes and forcing (or knocking) it to the ground (4 out of the 6 squirrel hunts reported in this paper were relay chases). Chases of both squirrels and lizards (10 out of 21 incidents reported here) are variable in duration, lasting from approximately 30 s up to 5 min. Adult female white-crowned parrots are captured by reaching into holes in trees and removing them, apparently as they sit defensively on their clutches of eggs. Magpie jays harass capuchin monkeys boldly and have been seen literally to be snatched from the air or branch when they come too close.

Our monthly records indicate that more prey is taken during the dry season, but to this finding should be added the information that we do more intensive work during the dry season, which is also the season when several of the prey species produce most of their young. Most prey are consumed while still alive, and most or all of the flesh is eaten. Although the 'craniocervical killing' bite has been described as being widespread in primates [8], I have only seen it performed once, by a male capuchin when the adult squirrel that he was trying to subdue bit him several times.

As can be seen from table 1, adult males account for significantly more of the chases ($\chi^2 = 129.2$; $p \leq 0.001$), captures ($\chi^2 = 116.8$; $p \leq 0.001$) and consumption ($\chi^2 = 80.3$; $p \leq 0.01$) of vertebrate prey than expected from their proportional representation in the group. Adult males are responsible for most of the capturing, especially of mobile prey, although females and juveniles of both sexes sometimes join in the chase and often in the meat consumption. Tolerated scrounging of larger prey (such as coati pups and squirrels) occurs, and pieces of carcass are dropped to the ground or left on a branch by the original owner and are then retrieved and eaten by the other group members. Processing of the food, such as the removal of feathers and larger bones, may occur over a lengthy period, during which time other individuals approach and gain partial access to the carcass. Younger and subordinate individuals attempt to touch, sniff and lick the prey. Dominant individuals, particularly the alpha male, often threaten and attempt to intimidate the possessor of a carcass into giving it up, but this attempted intimidation is not always successful.

The type of vertebrate predation seen in *Cebus* is *not* similar to the stalking pursuit of game described for chimpanzees and human hunters. The South American *C. apella* have been characterized as 'destructive foragers' [26]. Similarly, when *C. capucinus* move through the forest in a foraging progression, the prevailing image is of a collective beating of the bush by human hunters, or – more in keeping with Terborgh's [26] depiction – the impression could be described as that of an 'invading army'. Branches crash to the ground under the deliberate pounding of the monkeys' hind limbs, large pieces of bark are stripped from the trees and dropped, debris showers from palms and tangled vines as the foragers penetrate them in the search for food, rocks and leaf litter are noisily turned over on the forest floor, arms are thrust into every possible crevice and sudden pounces are made onto exposed, fleeing prey, whether vertebrate or invertebrate.

Discussion

This is the first extended description and examination of successful predation by a Neotropical monkey on a variety of vertebrate species. Capuchins in group T preyed often on vertebrates, more often than other groups of capuchins living nearby and more often than has generally been described in the literature. Three questions arise from these results. First, why is predation more frequent in this group than in others, or, more generally, why is vertebrate predation so labile a characteristic? Second, why do males hunt more than females? And finally, what characteristics of *Cebus* behavioral ecology facilitate successful vertebrate predation?

We can begin with the first question: Why is vertebrate predation unevenly present in omnivorous primates? In the several reviews and specific descriptions of primate predation available in the literature, at least three types of explanations have been offered repeatedly for the facultative occurrence of this behavior in Old World primates, particularly in baboons and chimpanzees. The possible application of these explanations to the Neotropical case of capuchins will be explored here briefly, although these hypotheses are not easily testable.

One category of explanations, which we might refer to as ecological hypotheses, has been proposed by researchers like Strum [10] and Teleki [13]. These investigators argue that primate predation occurs when certain necessary environmental conditions are present: primarily, that there are abundant and suitable prey species and, more importantly, that the larger, competing carnivores have been recently reduced in numbers. At both Gombe and Gilgil, the sites where predation by Old World primates has been observed most often, the large terrestrial carnivores have been largely eliminated in recent times. Teleki [13, 14] has argued that chimpanzees, because of their highly flexible behavior, have been able to expand into this presently unoccupied carnivore niche. However, at other sites where predation is reported, such as Amboseli [27] and Santa Rosa, there is little evidence for recent or extreme reductions in the number of carnivores. Santa Rosa has five species of cats, all of which we have seen, four of them in the home ranges of our study groups. Further there is a large mustelid species in the park, and abundant coyotes and boa constrictors, all of which fill the role of vertebrate predators. There is also no evidence to suggest that a population explosion of the prey species (coatis, parrots or squirrels) has occurred in the areas where the monkeys hunt them. While there is no doubt that suitable and relatively available prey is a necessary condition for hunting, the 'niche expansion' hypothesis does not appear to account for the pattern of vertebrate predation reported in this study.

A second set of hypotheses, which we might characterize as social explanations, has also been proposed. Teleki [13] suggested that individuals in possession of a prey item increase their social status. Although this explanation may hold true for chimpanzees, Harding [4] and Hausfater [27] reported that the most frequent social behaviors surrounding predation in baboons are agonism and harrassment directed at the possessor and redirected to surrounding individuals. This is also the case in capuchins at Santa Rosa. Another hypothesis suggested by Strum [9] is that, once hunting originates in a particular group or individual, the prac-

tice may spread and be maintained through social tradition. Characterizing predation as a learned, protocultural behavior may help to explain its differential maintenance and its changing pattern over time. As noted by Strum and Mitchell [12], social facilitation and observational learning (or stimulus enhancement) as well as psychological and social factors that inhibit or encourage predatory behavior must all play a role. But we are still left with the question of why the capturing of vertebrates to eat would become a fixed cultural tradition in some groups and not in others, if it occurs opportunistically and sporadically in all groups. Would a social tradition develop simply fortuitously and with a momentum of its own? Or does it continue to be based, at least in part, on adaptive behaviors and therefore differ between groups when the behavior pattern itself is differentially advantageous? As Strum [9] has argued, it seems most likely that predation is maintained as a social tradition when certain necessary and sufficient environmental conditions come together, and the behavior may vanish just as rapidly when these conditions shift.

The third type of explanation which I will consider here briefly pertains to bioenergetics and nutrition. It has been argued in the past that animal flesh is a superior, even necessary [28] source of high-quality protein, or micronutrients such as vitamin B_{12} [27], and that animal protein in comparison to plant protein is more digestible, of greater nutrient value and a more balanced source of amino acids [3]. However, plant matter and insects rather than meat supply most of the dietary protein for omnivorous primates such as baboons and capuchins [27, 29]. It seems more appropriate to develop a general energetic hypothesis pertaining to the relative availability of different foods and their cost/benefit ratios, in order to address variation in the occurrence of meat eating.

Several primatologists [3, 12, 30] have argued that animal matter may be selected by an omnivore when the energy yield for meat, per unit of foraging time, is higher than the energy yield from plant food. According to this argument, in some situations meat offers a general energetic as well as specific nutritional value. Capuchins are generalist feeders, and therefore differential food availability has a major impact on how their diet varies over time and space. As noted by Robinson [pers. commun.], animals will take food items that give them a net benefit, and they may have to choose between food items (filling up with fruit may preclude hunting vertebrates, for instance). Thus, we would expect that high rates of vertebrate predation would occur when a set of circumstances arises such that the ease of obtaining vertebrate protein reaches levels where the net energy yield per unit of foraging time is greater than for other food types. Such conditions might come together in a regenerating tropical dry forest, especially during the extended dry season at Santa Rosa.

How would these three types of explanations apply to the very high rates of predation seen in group T of capuchins at Santa Rosa? Rather than being mutually exclusive explanations, some elements of several of these hypotheses can be combined to build a more complete picture of why this behavior is exhibited in certain individuals and groups and not by others. I suggest that hunting in group T first arose opportunistically out of the general form of insectivory displayed by this species, in which crevices and other hiding areas are regularly searched such that vertebrates are occasionally

flushed out along with invertebrates. In this respect, the foraging style of the white-faced capuchin is compatible with vertebrate predation. Secondly, of our well-known groups of capuchins, group T lives in the most marginal habitat in terms of fruit availability, especially during the dry season, and has a much larger proportion of insects in its diet than either of our other two groups (45% as compared to 28 and 18%). Presumably, group T is in a situation where the energy yield for any animal food, invertebrate or vertebrate, relative to plant food makes predation a worthwhile pursuit. Carnivory, in this case, may be seen as a response to lowered fruit availability in a recolonizing forest. It may also be that vertebrate predation becomes more worthwhile toward the end of the dry season when insects as well as fruit are declining in abundance. This suggested seasonal change in the bioenergetic equation is supported by the fact that the late dry season is also the primary nesting period for three of the common prey species – parrots, squirrels and coatis [31]. The availability and ease of capturing vertebrate prey may be increasing at the same time that alternative food sources in the diet of group T are least abundant.

Although vertebrate predation may have begun opportunistically in group T, it is presently systematic in the group, and the practice may be maintained by continuing seasonal food availability patterns, by foraging success and perhaps by 'tradition' [12]. Today, all coati and squirrel nests and parrot nesting holes are regularly searched during the nesting seasons, even if this involves an adult male travelling some distance from the main body of the foraging group. These activities on the part of the adult males are closely watched by juveniles.

Why do adult females not participate more often in vertebrate predation? Although it recently has been reported that female chimpanzees and baboons hunt more than we had realized previously, it is still the case for most primates that males exhibit significantly more of this behavior. Robinson [20] and the present study both found that adult males account for approximately 90% of the vertebrate captures.

One fairly common explanation concerns sexual dimorphism in size and strength. Especially in a generalized feeder, such as an omnivorous primate, which has not evolved many specialized physical traits for carnivory, it may be that the larger body size of males is a significant advantage in capturing and subduing the prey and that the males' larger canines and stronger jaws can bite into and tear apart the carcass more readily [3, 12]. Female capuchins at Santa Rosa weigh 70% of male weight, and canine size is 77% of male size. Although capuchins would be large monkeys to be insectivores [26], they would also be small mammals to specialize in vertebrate predation, given the relative size of potential prey species. An adult male capuchin weighs only 3.25 kg on average, a size which does not make him much larger than a protective mother coati. I have seen two adult capuchins struggle to subdue an adult squirrel, and then experience difficulty biting into the carcass. So the 25–30% size advantage of male *Cebus* over females could be a factor in their willingness and ability to capture and subdue vertebrate prey. On the other hand, some juvenile and subadult male capuchins in group T are avid hunters and meat eaters, and are occasionally successful, even though they weigh no more than an adult female monkey.

Another possible explanantion for greater male participation is differential niche exploitation. It has been widely reported that chimpanzee males eat more meat and females more termites. In the present study, adult female capuchins did spend slightly more time foraging on insects than males (41% of foraging time vs. 35%), but the differences were not large. However, there were large differences in the average amount of time which males versus females spent foraging on the ground (17% of male foraging time is spent on the ground, versus 1% for females). Could this differential use of the ground be related to predation? It is not an obvious relationship, as most of the vertebrate prey species and their nests are arboreal, and yet the more successful hunters, the males, spend more time on the ground. It is true, however, that some prey, such as lizards and squirrels, were more successfully caught and subdued on the ground.

Fragaszy [17] reported for *C. olivaceus* that males spent more time on the ground and that they preferred animal foods and larger food packets, whereas females and juveniles favored buried or imbedded invertebrates. I also found that, even though both sexes spent similar amounts of time foraging on insects, males spent more of their time flushing insects on the ground, whereas females and juveniles did most of their insect foraging by biting into dead, hollow branches for encased larvae. One could hypothesize that the latter practice gives a lesser but more consistent return for energy invested than does a sweeping search through the leaf litter for larger, rarer prey. Robinson [20] found that *C. olivaceus* females had consistently more success feeding on invertebrates, while males spent more time looking for and attempting to capture relatively rare but 'high-quality' items such as vertebrate prey.

Dominance may also play a role in sex differences in predation. Adult females are usually subordinate to adult males in food priority, and agonism occurs over captured prey. Thus, females risk losing their prey to males after expending much energy to obtain it. On one occasion, I saw the alpha female of group T lose a squirrel in a tug-of-war with the alpha male, after she had done most of the work to chase it through the trees and run it to the ground. However, dominance, as determined by supplantation and agonistic signals, is not a straightforward determinant of access to a carcass. Two of the most frequent meat eaters in group T are old, postprime, subordinate males that often obtain and hold onto prey, even when they are threatened by younger, more dominant males.

Searching for, chasing and subduing vertebrate prey is probably a relatively costly and high-risk activity. It is high risk in terms of unpredictable returns and the physical dangers of falling from a tree and being bitten. Perhaps females, which are often pregnant or lactating and/or carrying an infant on their bodies, are less willing to risk the inconsistent returns and high energy expenditure rates of vertebrate predation, especially if they are going to be harassed when successful.

Size and strength dimorphism, differential use of the canopy and male dominance may all be relevant to sex differences in vertebrate predation in these monkeys, but the varying bioenergetic equations which result from the different reproductive patterns of males and females may be the most telling factor in whether an individual meets its nutritive and energetic needs by a low-expense, low-but-predictable return strategy,

or whether it gambles on a higher-risk activity such as vertebrate predation.

Finally, certain aspects of behavior common to *Cebus* species predispose these animals to being successful vertebrate predators. Like some species of Old World monkeys (such as vervets), capuchins are highly opportunistic, generalist feeders that readily exploit new food sources. In the case of capuchins, these new food sources are often discovered because of their manipulative, explorative approach to foraging. In laboratory studies, capuchins have demonstrated that they are clever problem solvers [32], being both persistent and flexible, as well as able to perform complex object manipulations [33], and to discover new ways to extract items by active exploration. Parker and Gibson [34, 35], in particular, have stressed the expertise of capuchins in processing and extracting embedded foods.

All of these characteristics – extractive foraging, exploration, manipulative and problem-solving abilities – would help ensure that capuchins are able to locate and process vertebrate prey items, but a final important factor facilitating the development and maintenance of successful vertebrate predation in these monkeys is their approach to the finding and subduing of invertebrate prey. Capuchins are accustomed to capturing and consuming prey such as wasps, stinging ants and scorpions, which have protected hiding places and noxious defense mechanisms. In other words, they are well equipped to solve the problems of exploiting foods which hide, run and fight back [36]. These well-developed techniques for locating and subduing invertebrate prey may also have played a role in the origin and maintenance of vertebrate hunting behavior by capuchins.

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References

1 Butynski TM: Vertebrate predation by primates: A review of hunting patterns and prey. J Hum Evol 1981;11:421–430.
2 Clarke AS: Animal foods in the diets of prosimians and New World primates; in Mitchell G, Erwin J (eds): Comparative Primate Biology. Vol 2b: Behavior, Cognition and Motivation. New York, Liss, 1987, pp 133–165.
3 Hamilton WJ, Busse CD: Primate carnivory and its significance to human diets. Bioscience 1978; 28:761–766.
4 Harding RSO: Meat eating and hunting in baboons; in Tuttle RH (ed): Socioecology and Psychology of Primates. The Hague, Mouton Publishers, 1975, pp 245–257.
5 Harding RSO: An order of omnivores: Nonhuman primate diets in the wild; in Harding RSO, Teleki G (eds): Omnivorous Primates. The Hague, Mouton Publishers, 1981, pp 191–214.
6 Harding RSO, Strum SC: The predatory baboons of Kekopey. Nat Hist 1976;85:46–53.
7 Rose MD: The roots of primate predatory behavior. J Hum Evol 1978;7:179–189.
8 Steklis HD, King GD: The craniocervical killing bite: Toward an ethology of primate predatory behavior. J Hum Evol 1978;7:567–581.
9 Strum SC: Primate predation: Interim report on the development of a tradition in a troop of olive baboons. Science 1975;187:755–757.
10 Strum SC: Processes and products of change: Baboon predatory behavior at Gilgil, Kenya; in Harding RSO, Teleki G (eds): Omnivorous Primates. New York, Columbia University Press, 1981, pp 255–302.
11 Strum SC: Baboon cues for eating meat. J Hum Evol 1983;12:327–336.

12 Strum SC, Mitchell W: Baboons: Baboon models and muddles; in Kinzey WG (ed): The Evolution of Human Behavior: Primate Models. New York, State University of New York Press, 1987, pp 87–104.
13 Teleki G: The Predatory Behavior of Wild Chimpanzees. Lewisburg, Bucknell University Press, 1973.
14 Teleki G: Primate subsistence patterns: Collector-predators and gatherer-hunters. J Hum Evol 1975; 4:125–184.
15 Zihlman AL: Women in evolution. 2. Subsistence and social organization among early hominids. Signs 1978;4:4–20.
16 Freese CH, Oppenheimer JR: The capuchin monkeys, genus *Cebus;* in Coimbra-Filho AF, Mittermeier RH (eds): Ecology and Behavior of Neotropical Primates. Rio de Janeiro, Academia Brasileira de Ciencias, 1981, vol 1, pp 331–390.
17 Fragaszy DM: Time budgets and foraging behavior in wedge-capped capuchins *(Cebus olivaceus):* Age and sex differences; in Taub DM, King FA (eds): Current Perspectives in Primate Social Dynamics. New York, Van Nostrand Reinhold, 1984, pp 159–174.
18 Izawa K: Frog-eating behavior of wild black-capped capuchin *(Cebus apella).* Primates 1978;19: 633–642.
19 Janson CH: Ecological and social consequences of food competition in brown capuchin monkeys; PhD diss University of Washington, 1985.
20 Robinson JG: Seasonal variation in use of time and space by the wedge-capped capuchin monkey. *Cebus olivaceus:* Implications for foraging theory. Smithson Contrib Zool 1986;431:1–60.
21 Newcomer MW, DeFarcy DD: White-faced capuchin *(Cebus capucinus)* predation on a nestling coati *(Nasua narica).* J Mammal 1985;66:185–186.
22 Freese CH: Food habits of white-faced capuchins *Cebus capucinus* L. (Primates: Cebidae) in Santa Rosa National Park, Costa Rica. Brenesia 1977; 10:43–56.
23 Chapman CA: Flexibility in diets of three species of Costa Rican primates. Folia Primatol 1987;49: 90–105.
24 Oppenheimer JR: Behavior and ecology of the white-faced monkey *Cebus capucinus* on Barro Colorado Island, Canal Zone; PhD diss University of Illinois, 1968.
25 Oppenheimer JR: *Cebus capucinus:* Home range, population dynamics and interspecific relationships; in Leigh Jr EG, Washington Rand AS, Windsor DM (eds): The Ecology of a Tropical Forest. Seasonal Rhythms and Long-term Changes. Washington, Smithsonian Institute, 1982, pp 253–272.
26 Terborgh J: Five New World Primates. A Study in Comparative Ecology. Princeton, Princeton University Press, 1983.
27 Hausfater G: Predatory behavior of yellow baboons. Behaviour 1976;56:44–68.
28 Dart PA: The carnivorous propensity of baboons. Symp Zool Soc Lond 1963;10:49–56.
29 Richard AF: Primates in Nature. New York, Freeman, 1985.
30 Gaulin SJC, Kurland JA: Primate predation and bioenergetics. Science 1976;191:314–315.
31 Janzen DH: Costa Rican Natural History. Chicago, University of Chicago Press, 1983.
32 Simons D, Holtkotter M: Cognitive processes in cebus monkeys *(Cebus apella)* when solving problem-box tasks. Folia Primatol 1986;46:149–163.
33 Westergaard GC, Fragaszy DM: Effects of manipulatable objects on the activity of captive capuchin monkeys *(Cebus apella).* Zoo Biol 1985;4: 317–327.
34 Gibson KR: Cognition, brain size and the extraction of embedded food resources; in Else J, Lee PC (eds): Primate Ontogeny, Cognition and Social Behavior. Cambridge, Cambridge University Press, 1986, pp 93–103.
35 Parker ST, Gibson KR: Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. J Hum Evol 1977;6:623–641.
36 Boinski S: Use of a club by a wild white-faced capuchin *(Cebus capucinus)* to attack a venomous snake *(Bothrops asper).* Am J Primatol 1988;14: 177–179.

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