

SEASONAL VARIATION IN THE DIET OF RING-TAILED COATIS (*NASUA NASUA*) IN IGUAZU, ARGENTINA

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There is widespread evidence that feeding ecology can lead to differences in mammalian social systems. To understand how diet and ecology affect the social behavior of ring-tailed coatis (*Nasua nasua*), detailed measures of feeding behavior were recorded from 2 well-studied groups over a 2-year period. The proportion of fruit and invertebrates in the diet of ring-tailed coatis in Iguazu, Argentina, was very similar to that in diets of white-nosed coatis (*N. narica*) and ring-tailed coatis studied at field sites in Brazil. Consumption of vertebrates in Iguazu was exceptionally rare. The proportion of time spent foraging for invertebrates and fruit generally matched seasonal changes in the abundance these foods in the environment. During the winter, when invertebrate and fruit availability was low, coatis spent a large amount of time feeding on 2 exotic fruit species. The presence of exotic fruits provided coatis with food during the lean winter season and may have influenced the high reproduction and survivorship found in this population. Coatis spent about 44% of their fruit-foraging time exploiting pindo palm (*Syagrus romanzoffianum*) fruits and it appeared that this fruit species played a major role in shaping the ranging and feeding behavior of coati groups. The time spent foraging at fruit trees and the total number of fruits eaten varied depending on the species of tree. Coati groups spent an average of 2.5–12.5 min feeding on different species of fruit trees, and coati groups ate an average of 2.6–269.8 fruits per tree species. The quick depletion of fruit trees and high density of foraging individuals, especially when feeding on pindo, plays an important role in shaping the social system of coatis.

Key words: coati, fallback foods, foraging behavior, fruit depletion, Procyonidae, socioecology

Feeding ecology is an important variable that affects the biology of animals. Variables such as food-handling time, nutrient content, caloric energy, and depletion time can greatly influence animal behavior (Kamil et al. 1987; Krebs 1986). When groups of animals (as opposed to lone individuals) encounter food patches, food properties such as patch size, availability, and whether individuals have prior knowledge of the resource can lead to changes in individual and group behavior (Giraldeau and Caraco 2000). The size and distribution of different food types is a particularly important variable that can influence feeding competition (Dubois et al. 2003; Grant et al. 2002; Janson and van Schaik 1988; Sterck et al. 1997; van Schaik 1989; Vehrencamp 1983; Wrangham 1980). In general, food items that are small and quickly depleted lead to within-group scramble competition and large patchy food

resources can lead to within-group contest competition (Isbell and Young 2002). To understand how feeding ecology may shape the social structure of a species, it is important to record measures of food-depletion time and patch size. The purpose of this study was to provide detailed measures of the seasonal dietary patterns and use of fruit trees by groups of ring-tailed coatis (*Nasua nasua*) in Iguazu, Argentina. These measures are also useful for comparative studies with other coati populations and other mammalian species.

Coatis (*Nasua*) are medium-sized social mammals found throughout Central and South America (Gompper 1995). Coatis are generally described as omnivorous and have diets composed of fruit, ground-litter invertebrates, and occasional vertebrate prey (Alves-Costa et al. 2004; Gompper 1996; Kaufman 1962; Valenzuela 1998). Most previous work on coatis has focused on the white-nosed coati (*N. narica*), and little is known about the behavior and ecology of ring-tailed coatis. Recent work on ring-tailed coatis from 2 populations in Brazil has focused on ranging, seasonal dietary patterns, and seed dispersal, but detailed behavioral data were not collected (Alves-Costa et al. 2004; Alves-Costa and Eterovick 2007;

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Beisiegel 2001; Beisiegel and Mantovani 2006). In a study of diets of ring-tailed coatis in Mangabeiras Park, Brazil, Alves-Costa et al. (2004) found that coatis mostly ate insects, millipedes, spiders, and fruit. The proportion of millipedes and spiders in the diet increased during the wet season (October–March), which should have been the period of highest invertebrate abundance (Beisiegel and Mantovani 2006). Alves-Costa et al. (2004) found that the proportion of fecal samples that contained fruit seeds was inversely related to the presence of millipedes and insects. The authors hypothesized that coatis use fruit as a fallback food when millipede and insect abundance is low (Alves-Costa et al. 2004). Coatis typically respond to periods of low food abundance by traveling further, increasing their daily activity, ranging over a larger area, and by changing the food items consumed in accordance to their availability; thus, seasonal fluctuations in resource abundance can have major impacts on the behavior and biology of coatis (Valenzuela 1998; Valenzuela and Ceballos 2000).

In Iguazu, ring-tailed coatis were regularly observed fighting over food items. Because food size and distribution are likely to be important factors shaping their social behavior and dominance relationships, it is important to understand when and how different foods are consumed (Hirsch 2007a, 2007b). Agonism occurred during foraging on pindo (*Syagrus romanzoffianum*) fruit more often than any other activity; thus, understanding the manner in which coati groups utilize pindo may be particularly important to understanding the dominance and social system of this species (Hirsch 2007a). The presence of several introduced fruit species in Iguazu may have changed the typical socioecology of this coati population. In particular, the presence of additional fruit during the Argentine winter (June–September) may have provided a fallback food for coatis during the season of low fruit availability.

METHODS AND MATERIALS

Study site.—This study was conducted in Iguazu National Park (25°40'S, 54°26'W), Argentina, between August 2002 and September 2004 (for details about the field site see Brown and Zunino [1990] and Di Bitetti [2001a, 2001b]). This area of Atlantic Coastal Forest is dominated by 2nd-growth forest and has a high density of fleshy-fruit trees (3–5/ha). The forest areas used by the coatis were not homogeneous. Some areas were composed of mature primary-growth forest, whereas others were altered by humans for the convenience of tourists and park employees. Coatis would occasionally travel through areas with mowed grass to reach fruit trees, but did not typically search for ground-litter invertebrates in these areas. The coati groups appeared to spend most of their time foraging in secondary forest. Coati groups would regularly travel on and below steep 80-m cliffs where they were not easily observed (Hirsch 2007c). The coatis also regularly traveled and foraged on a series of small islands along the Iguazu River.

Fruit abundance in the study area was determined using previously published data that indicated that ripe fleshy fruits were much less common during the cold winter months of

June–September (Di Bitetti 2001a). Fruit abundance was based on the average number of grams of dry fruit per hectare per day, averaged by month. Although measures of fruit abundance were not taken concurrently with the behavioral data, seasonal patterns of fruit abundance are similar across years and these data should have been an excellent proxy for available resource abundance during the period of coati behavioral sampling. Iguazu, Argentina, does not have clearly defined wet and dry seasons similar to those at sites where ring-tailed coatis have been studied in Brazil (Alves-Costa et al. 2004; Beisiegel and Mantovani 2006). Iguazu has the traditional 4 seasons found in temperate and subtropical climates, with peaks of rain during May and October (Di Bitetti 2001a).

The fruit species targeted by Di Bitetti (2001a) were observed being consumed by sympatric capuchin monkeys (*Cebus apella*), a species with a fruit component of their diet roughly similar to that of coatis. All fruits seen eaten by coatis also were eaten by capuchin monkeys; thus, using the abundance of fruit species eaten by capuchins should be a useful measure of fruit available for coatis. Several fruit species consumed by capuchins were not observed being eaten by coatis. Because most of these fruits were not common, it was assumed that these discrepancies were in large part due to the shorter time period of the coati study (2.5 years for this study of coatis compared to 10 years for Di Bitetti's [2001a] study of capuchins). Di Bitetti (2001a) sampled fruit trees in an area that was within the home range of all 4 observed coati groups, and immediately north of a set of large waterfalls that are a major tourist attraction. Large numbers of introduced fruit species were present in some areas of the park, especially near the waterfalls. Several exotic species were introduced into the study area before the park was granted protected status (1937). One invasive species, *Hovenia dulcis*, was commonly found in disturbed areas, and was found in high-density clusters in some areas near the waterfalls (>5 trees/ha). Tangerine, grapefruit, and orange trees also were introduced in this time period, but were less common than *Hovenia*. Several *Eriobotrya japonica* and an exotic *Ficus* species were planted in the park as ornamentation, and these trees were concentrated in the waterfalls area of the park as well. Because fruit abundance was measured north of the waterfall area, the exotic species were generally not included in the data on fruit abundance (with the exception of some *Hovenia* trees).

The area near the waterfalls also contained restaurants, snack bars, and trash cans (Hirsch 2007c). The coatis were able to enter many of the trash cans, and would eat discarded foods when available. I was not able to ascertain the exact behavior of the coatis when they were not being followed, but when I was present I was able to prevent coatis from directly feeding on human foods. The number of tourists typically increased during the peak winter months of June–August.

Study species and behavioral sampling.—The coati groups followed in this study ranged from 8 to 31 individuals (Hirsch 2007c). One to 3 adult females per group were fitted with radiocollars to facilitate locating the groups. Coatis were captured using Tomahawk or similar traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin), anesthetized, and fitted with

radiocollars (M2210; Advanced Telemetry Systems, Inc., Isanti, Minnesota) or given multicolored plastic ear tags (Rototags, Dalton Co., Oxfordshire, United Kingdom) for individual identification. All trapping and handling methods were carried out in accordance with guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). Ear tags were placed on juveniles older than 4 months of age, and all group members could be individually recognized after this age. Groups of coatis were usually habituated within 2–3 weeks. Habituated coatis would allow observers to silently walk within 2 m of a focal animal without disturbance. Feeding data were recording using individual focal samples and group-scan samples. Individual focal samples were taken from all 4 age–sex classes: adult males (>24 months of age), adult females (>24 months of age), subadults (between 12 and 24 months of age), and juveniles (between 2 and 12 months of age).

Individual focal samples were taken on known individuals from 2 groups (PQ and PSG) from August 2002 until October 2004 (2 other tagged and collared groups were not used in this study). Focal samples were 10 s in duration, and the same individual was not resampled within 10 min. During the focal sample, I recorded a variety of behavioral variables (month, time of day, group speed, group size, age–sex class, number of neighbors within 3 m of the focal individual, and within-group spatial position measured from front to back of the group), and the number of food items ingested (for further behavioral sampling methods see Hirsch [2007c]). Short focal samples were used because many of the associated variables recorded during the focal samples changed frequently and rapidly. Individuals were selected opportunistically. Because of poor overall visibility in the dense forest, it was not feasible to select individuals based on a predetermined order. When individuals were feeding on fruit, I recorded the total number of fruits eaten during the sample (to the nearest one-fourth fruit). Coatis ate 1 fruit per bite for 4 of the 6 most common fruits (*Cecropia* and *Hovenia* being the exceptions). *Hovenia* fruits were sufficiently large so that I was able to see the proportion of an individual fruit that the coati consumed during the sample (coatis typically bit off one-fourth to one-half of a *Hovenia* fruit per bite). When coatis ate *Cecropia*, it was difficult to determine the percentage of fruit eaten, but it was possible to count the number of bites taken by the individual. These bites were converted into number of fruits by estimating that it took a coati 12 bites to eat an entire *Cecropia* fruit. When coatis ate invertebrates extracted from soil or the leaf litter, I was only able to see the ingested item in a small percentage of cases. When I was able to determine the type of invertebrate, I recorded this information. In several cases, I was not able to see the item, but heard a distinctive crunching sound when the coati was chewing the prey item. In these cases, it was assumed that the prey item had a thick exoskeleton, and was likely an arthropod. In some cases, the coati rolled a prey item in its paws before ingesting, which is typically an indication that the prey had irritating morphological features such as spines or was covered with a noxious substance (Gompper and Decker 1998). An analysis of fecal samples could have provided a better method

to determine the abundance of different types of arthropods in the coati diet (e.g., Alves-Costa et al. 2004; Valenzuela 1998). On the other hand, the common occurrence of bright orange pindo seeds in some feces made them far more visible than “typical” scat samples. The use of fecal sampling methods in the Iguazu study population would probably have biased the results.

Data on monthly diet patterns was taken from 15-min group-scan samples. During these scans the percentage of individuals searching for food or feeding was recorded. If more than two-thirds of the group were foraging, this was classified as a foraging scan. The relative proportion of individuals searching for or feeding on fruit, invertebrates, or trash was recorded. If some individuals in the group were not visible, the percentage of individuals foraging on each food type was based on the individuals seen at the time of the scan. Scans were only recorded when two-thirds or more of the group was visible. If any fruit trees were located inside the group spread, the number of trees of each species was recorded.

Fruit tree depletion times and the amount of fruit eaten per tree were calculated using tree focal samples. When I was able to arrive at a fruit tree before the group, the number of coatis feeding and searching for fruit was recorded every minute for the duration of the time that the coatis fed at the tree. Before the start of the sample, a timer was set to beep once every minute. The tree focal sample started with the 1st beep after the arrival of the coatis and at each beep, the number of individuals feeding and searching for fruit was recorded. From these tree focal samples it was possible to determine the average depletion time for different species of fruit trees and the amount of total feeding at the fruit tree in “coati minutes” (the sum of time that all coatis in the group spent feeding on a tree). By multiplying the number of coati minutes times the average number of fruits eaten during the 10-s feeding samples (multiplied by 6 to equal 1 min), it was possible to estimate the average total number of fruits eaten from a tree during a visit by a coati group. These values were then averaged for major fruit species. Although the coati group may have left the fruit tree before eating every available fruit, it appeared that the number of uneaten fruits left after a group visited was typically low. Approximately 80% of tree focal samples were recorded during 2004; thus, the average group size during most tree focal samples was between 25 and 30 individuals (the exact percent of samples recorded by year varied depending on the fruit species).

Statistical analyses.—Ten-second focal samples were used to test the relationship between feeding success (defined as the presence of food ingestion during a focal sample) and a variety of behavioral factors. Two generalized linear models were constructed with fruit or invertebrate feeding success as the dependent variable, and several other potentially confounding variables were entered into the models (month, time of day, group speed, group size, age–sex class, number of neighbors within 3 m of the focal individual, and within-group spatial position measured from front to back of the group). Because coatis rarely ate more than 1 invertebrate during the 10-s samples ($n = 52$), feeding success was defined as consuming at

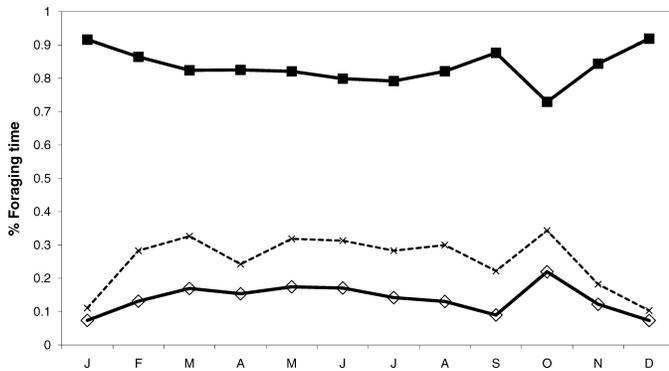


FIG. 1.—Diet of coatis (*Nasua nasua*) at Iguazu, Argentina, 2002–2004, by month. Values indicate the percentage of scan samples in which the group was foraging for invertebrates (black squares) or fruit (open diamonds). The presence of fruit within the group is indicated by the dashed line.

least 1 food item within the 10-s sample. An unequal sample size was recorded for each age–sex class because of differences in the number of individuals in each age–sex class and opportunistic sampling (adult males $n = 238$, adult females $n = 1,902$, subadults $n = 835$, and juveniles $n = 1,499$). To test for non-linear seasonal patterns, both the month (represented by numbers 1–12), and month squared were entered as variables in these models. To determine whether feeding behavior was related to food abundance, monthly fruit and invertebrate abundance values were taken from a previous study and regressed against the percentage of fruit foraging scans per month (Di Bitetti 2001b). All statistics were done in the JMP 3.2 statistical package (SAS Institute Inc., Cary, North Carolina), with the exception of the generalized linear models, which were conducted in STATISTICA 5.5 (Statsoft, Tulsa, Oklahoma).

RESULTS

Coatis primarily ate fruit and ground-litter invertebrates. Coatis spent between 69.7% and 97.5% of their monthly feeding time foraging for ground-litter invertebrates ($n = 4,648$ feeding scan samples). The amount of time spent foraging for invertebrates was highest during the summer months of November–February, which also was the period when in-

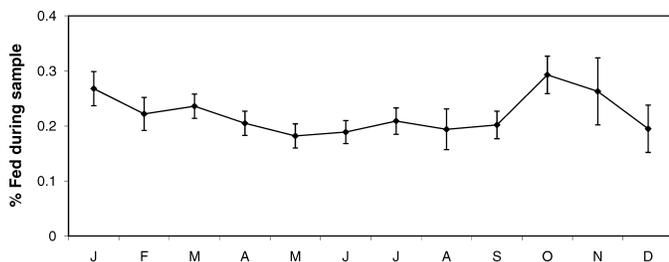


FIG. 2.—Invertebrate feeding success of coatis (*Nasua nasua*) at Iguazu, Argentina, 2002–2004, by month. Values represent the percentage of scan samples in which at least 1 invertebrate was eaten, summarized by month.

TABLE 1.—Results of generalized linear model for factors affecting the food intake of coatis (*Nasua nasua*) searching for ground-litter invertebrates in Iguazu, Argentina, 2002–2004. $n = 3,429$, $\chi^2 = 23.739$, $df = 10$, $P = 0.008$. All P -values are 2-tailed.

Variable	<i>df.</i>	Estimate	<i>SE</i>	<i>P</i> -value
Month	1	−0.195	0.067	0.004
Month ²	1	0.014	0.005	0.007
Time of day	1	0.000	0.000	0.402
Group speed	1	−0.129	0.076	0.088
Group size	1	−0.019	0.006	0.003
Age–sex	3			
Adult female		0.000	—	—
Adult male		0.106	0.140	0.448
Subadult		−0.128	0.096	0.181
Juvenile		0.045	0.085	0.591
Neighbor density	1	0.031	0.023	0.187
Spatial position (front to back)	1	0.000	0.028	0.994

vertebrate abundance was the highest (Fig. 1; Di Bitetti 2001b). The feeding success rate on invertebrates was higher during these months as well (Fig. 2; Table 1). Even though it appeared that coatis spent more time foraging for invertebrates during the season of greatest invertebrate abundance, there was no significant relationship between invertebrate abundance and the monthly percent of time spent foraging for invertebrates ($n = 10$, $R^2 = 0.008$, 1-tailed $P = 0.404$). Coatis had lower foraging success when their group size and speed increased (generalized linear models, group-size slope = -0.019 , $P = 0.003$, group-speed slope = -0.129 , 1-tailed $P = 0.044$).

It was possible to observe or infer the type of invertebrate consumed in 11.5% of the invertebrate feeding samples (77 of 671). In 54.5% of these cases, I observed the coatis eating annelid worms ($n = 42$). During 26.0% of these samples, I heard a distinctive crunching sound indicating the consumption of an exoskeleton ($n = 20$). Coatis were observed rolling the prey item between their paws before consuming the item during 11.7% of the samples ($n = 9$), and it was likely that the coatis were consuming millipedes and tarantulas during these samples (Alves-Costa et al. 2004). Coatis also were observed eating formicid larvae ($n = 3$), scarabaeid larvae ($n = 2$), and an individual orthopteran during the focal samples ($n = 1$).

Coatis were rarely observed eating vertebrates. Vertebrates (order Anura) were consumed during 2 scan samples ($<0.01\%$). Frogs were the most commonly observed vertebrate prey. Fourteen frogs were either seen or heard being consumed during 32 months of study, based on opportunistic data collection. When frogs were captured, the frogs often emitted loud screams that attracted other coatis. When conspecifics approached the possessor of the frog, there were often aggressive fights for control of the carcass. Other than frogs, coatis were observed consuming a dead bird ($n = 1$) and turtle eggs buried in the ground ($n = 1$). Although coatis were seen chasing rabbits and small lizards, they were never observed catching or consuming these vertebrates. With the exception of a monthly spike in foraging on trash in the PQ group during

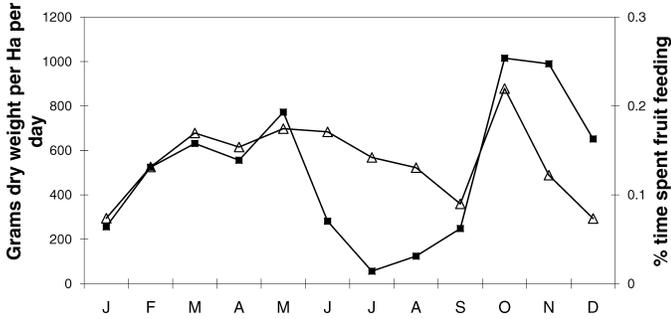


FIG. 3.—Availability of fruit in Iguazu, Argentina (black squares [from Di Bitetti 2001a]) compared to the percent of time spent foraging for fruit by coatis (*Nasua nasua*) per month, 2002–2004 (open triangles).

September 2003, the groups consistently spent <5% of their monthly foraging time searching for human foods.

Most noninvertebrate foraging time was spent searching for or consuming fruit. Trees containing ripe fruit were found within the group spread during 6.3–39.9% of the scan samples by month (Fig. 1). Group spread was defined here as the area inside the minimum convex polygon of all individuals in the group. In many cases, only a fraction of the group was actually feeding on or searching for fruit when a fruit tree was present within the group spread. When coatis were foraging for fruit, an average of 1.45 trees occurred within the group spread ($n = 826$). In general, fruit foraging was lowest during the summer months of November–February, when invertebrate foraging was highest (Fig. 1). The level of fruit foraging appeared to be closely linked to the availability of fruit but the correlation was not significant for all months ($n = 12$, $R^2 = 0.154$, 1-tailed $P = 0.104$). During June–August, there was a major discrepancy between the amount of fruit-foraging scans and fruit availability (Fig. 3). During June and July, the coatis spent large portions of time feeding on *Hovenia* fruits (Fig. 4). Because Di Bitetti (2001a, 2001b) censused an area immediately north of the waterfall area, he likely recorded far fewer *Hovenia* trees in his samples than were commonly available for the coatis in and near the waterfall area. Excluding these winter months from this analysis is probably a more accurate reflection of the amount of fruit available to coatis. When values from June to August were excluded from the sample, fruit availability and the percentage of time spent foraging for fruit were significantly correlated ($n = 9$, $R^2 = 0.424$, 1-tailed $P = 0.029$).

Twenty-nine fruit species were observed being consumed by coatis during the scan samples (Table 2). Although coatis were observed eating some additional species not recorded during the scan samples, these were rare occurrences. All of these additional species also were present in the diet of sympatric capuchin monkeys (Di Bitetti 2001a). Pindo trees were the major fruit source for coatis and more than 43% of fruit foraging scan samples contained pindo trees. The next most commonly eaten fruit was the exotic species *H. dulcis*. Fruits of *Hovenia* were ripe during the winter months when the

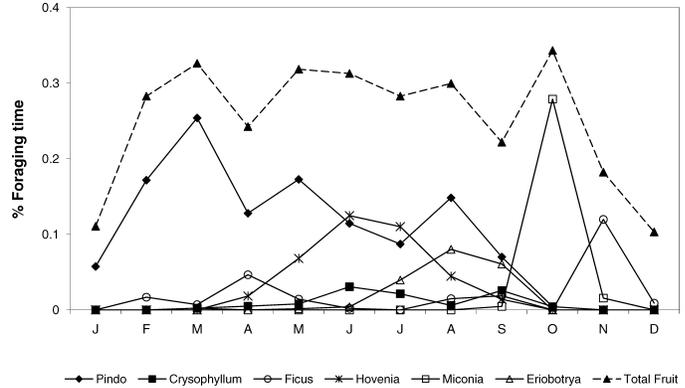


FIG. 4.—The percentage of foraging scan samples in which the 6 major fruit species were observed inside the group spread of coatis (*Nasua nasua*) at Iguazu, Argentina, 2002–2004. Total fruit values were calculated using all fruit species.

availability of other fruits was low. The abundance of invertebrates and invertebrate foraging success of the coatis also was lowest during these winter months. Consumption of exotic fruit species made up a significant portion of the coatis' fruit-foraging time throughout the year (27.9%), but this

TABLE 2.—List of all plant species observed being consumed during group scan samples. Percent values per fruit species were calculated from the total number of scans when fruit was observed inside the group spread. Species with an asterisk (*) indicate exotic species, which represented 27.94% of fruit foraging scan samples.

Family	Genus and species	% of scans
Annonaceae	<i>Rollinia emarginata</i>	0.32
Araceae	<i>Philodendron bipinnatifidum</i>	0.08
Bromeliaceae	<i>Pseudananas sagenarius</i>	0.16
Caricaceae	<i>Carica papaya</i> *	0.40
Lauraceae	<i>Nectandra</i>	1.83
Leguminosae	<i>Inga</i>	0.24
Melastomataceae	<i>Ossaea</i>	0.24
Melastomataceae	<i>Miconia pusilliflora</i>	5.65
Moraceae	<i>Cecropia pachystachia</i>	0.80
Moraceae	<i>Maclura tinctora</i>	1.59
Moraceae	<i>Ficus</i>	6.68
Moraceae	<i>Ficus</i> *	0.16
Moraceae	<i>Morus alba</i>	0.16
Moraceae	<i>Sorocea bonplandii</i>	0.32
Myrtaceae	Unknown genera	1.27
Myrtaceae	<i>Eugenia involucrata</i>	0.08
Myrtaceae	<i>Eugenia</i>	0.64
Myrtaceae	<i>Psidium guajaba</i>	2.23
Palmae	<i>Syagrus romanzoffianum</i>	43.76
Phytolaccaeae	<i>Tricostigma octandrum</i>	0.08
Piperaceae	<i>Piper</i>	0.88
Rhamnaceae	<i>Hovenia dulcis</i> *	16.15
Rosaceae	<i>Eriobotrya japonica</i> *	6.37
Rutaceae	<i>Citrus tangerine</i> *	3.42
Rutaceae	<i>Citrus orange</i> *	0.80
Rutaceae	<i>Citrus grapefruit</i> *	0.64
Sapindaceae	<i>Allophylus edulis</i>	0.48
Sapotaceae	<i>Cryosophyllum gonocarpum</i>	4.06
Unknown	Small, round, red berries	0.56

TABLE 3.—Average depletion time and fruit intake for 6 common fruit species. The depletion time was the average number of minutes that the group spent feeding on a fruit tree. A coati minute is the total sum of time spent feeding, multiplied by the number of individuals feeding. Feeding rates represent the average number of individual fruits consumed by 1 coati (*Nasua nasua*) in 1 min. The number of coati minutes was multiplied by the feeding rate to determine the average number of fruits per tree that the coatis ate when they visited. The number of fruits per tree according to this latter calculation may have been less than the total number of available fruits.

Fruit genus	Depletion time	Coati minutes	Feeding rate	No. fruits per tree	<i>n</i>
<i>Cryosophyllum</i>	7.24	30.55	2.91	89.02	42
<i>Cecropia</i>	2.49	5.04	0.52	2.64	37
<i>Ficus</i>	11.4	48.25	5.59	269.81	20
<i>Hovenia</i>	9.68	29.07	2.67	77.50	41
<i>Eriobotrya</i>	12.52	50.19	3.31	166.13	27
<i>Syagrus</i> (pindo)	5.69	22.65	4.36	98.80	438

increased during the winter months of June–August (51.9% exotics).

The average depletion time of fruit trees varied by species. Some species such as *Cecropia* only contained 1–4 ripe fruits at a time, and the coati groups consumed these very quickly (average 2.5 min). Other species such as *Ficus* and *Eriobotrya* took an average of 11.4–12.5 min respectively to be depleted of fruit (Table 3). The calculated amount of fruit eaten per fruit tree visit roughly matched calculations of fruit-tree productivity in Iguazu; thus, I concluded that these estimates are biologically realistic. An entire coati group was typically not observed foraging in the same tree at the same time, except when a group fed in large *Ficus* trees. The mean number of individuals that foraged in a fruit tree per minute was calculated by dividing the number of coati minutes by the depletion time. For most tree species, approximately 4 individuals simultaneously foraged at the same tree during any given minute. This value was lower for *Hovenia* and *Cecropia* (averages of 3.0 and 2.0 individuals, respectively).

DISCUSSION

Ring-tailed coatis in Iguazu had diets similar to those of other previously studied coati populations (Alves-Costa et al. 2004; Gompper 1996; Kaufman 1962; Valenzuela 1998). Many of the same fruit species eaten in Iguazu also were found in ring-tailed coati scats in Mangebeiras Park, Brazil (Alves-Costa and Eterovick 2007). Despite these similarities, the major fruit species consumed by ring-tailed coatis in Iguazu were quite different from those consumed in Brazil. Of the 10 most commonly eaten fruits in Iguazu, only 2 genera overlapped with the 10 most commonly fruit seeds found in Brazilian coati scats (*Ficus* and *Miconia*—Alves-Costa and Eterovick 2007). The most commonly eaten fruit species in Iguazu (pindo [*S. romanzoffianum*]) was not found in coati scats in Brazil, although coatis were observed consuming this species (Alves-Costa and Eterovick 2007). The most common fruit species

found in scats in Mangebeiras Park (*Guazuma ulmifolia*) did not occur in Iguazu. Although the proportion of fruit in the diet of ring-tailed coatis in Iguazu and Brazil was similar, different plant species compositions in the 2 study areas likely led to the differences observed in the commonly eaten fruit species.

On average, coatis spent just over 80% of their feeding time foraging for ground-litter invertebrates. The seasonal and monthly variation in diet appeared to be driven by resource abundance, especially of ripe fruit (Alves-Costa et al. 2004; Valenzuela 1998). Coatis spent more time foraging for fruit during months with higher fruit availability. Seasonal changes in foraging patterns and directed travel behavior were consistent with the hypothesis that fruit is the preferred food resource of coatis in this population (Hirsch 2007c). Because sympatric capuchin monkeys typically spend more time foraging for insects in the winter due to low fruit availability, coatis could be expected do the same. This pattern was not observed. Instead, coatis ate large quantities of exotic fruit species during the lean winter months (especially *H. dulcis* and *E. japonica*). These 2 fruit species were most commonly found in the waterfall area of the park, and the presence of these trees probably enticed the coati groups to use these areas more frequently during the winter season. These exotic species probably served as fallback foods during the lean winter months, and their availability was likely a major factor contributing to high reproduction and survivorship in this coati population (Hirsch 2007c). Ring-tailed coatis in other locations also eat exotic fruit species, and it appears that coatis easily adapt to eating new and introduced food resources (Alves-Costa and Eterovick 2007; Kaufmann 1962).

Fruit tree depletion times ranged from 2.5 to 12.5 min per tree. In some cases, only 1 or 2 individual coatis would feed at a fruit tree, while the rest of the group would forage for invertebrates or use other fruit trees. This was particularly common during feeding on *Cecropia*. In a few cases, all or most of the group would feed at a large *Ficus* or *Eriobotrya* tree. When feeding on larger fruit trees, all or most of the group members spent time feeding at the tree, although the entire group did not arrive at and leave the fruit tree during the same minute. When feeding on pindo, coati behavior was particularly variable. In some cases, only 1 or 2 individuals would feed at a tree, in other cases, most or all of the group would feed at the pindo tree. This variability was likely the result of different quantities of fruit available. In many cases, coatis visited relatively unproductive pindo trees, or visited the same tree multiple times per day (in some cases 4 or 5 times per day). The circuitous nature of coati travel patterns led groups to use the same areas multiple times per day. Thus, even if a fruit tree had recently been visited, when the group passed by the same tree later in the day, some individuals would typically visit the tree to forage. When a large, productive pindo had not been recently visited, it typically contained enough fruit so that 10–15 individuals were able to simultaneously forage underneath (plus an additional 1–5 individuals in the tree). One implication of this is that coatis often fed at small clumped food resources, which typically results in high levels of within-group contest competition (Dubois et al. 2003; Grant et al. 2002;

Isbell and Young 2002; Janson and van Schaik 1988; Sterck et al. 1997; van Schaik 1989).

Coatis spent a large amount of time foraging for pindo fruits, and they did so more than sympatric capuchin monkeys. Capuchins typically visited pindo fruits during $\leq 5\%$ of their visits to fruit trees (April–January), with a seasonal peak of 38% of their visits during February–May (C. H. Janson, University of Montana, pers. comm.). Coatis spent 30% of their fruit-foraging time at pindo trees (April–January), with a seasonal peak of 60% of fruit-foraging time during February–May. This is a major difference in use of fruit by 2 sympatric frugivorous mammal species. It appears that coatis specialized on pindo fruits, whereas capuchins foraged more often in larger fruit trees, which resulted in slower fruit tree depletion times. This specialization on smaller, more quickly depleted fruit resources may have led to different patterns of feeding competition between the 2 species (Hirsch 2007a; Janson 1984).

When foraging for ground-litter invertebrates, coatis ate approximately 1 item every 40 s. In general it was not possible to determine what type of invertebrate was consumed. Of the items that were visible, annelid worms made up more than one-half of these items. This result may have been influenced by sampling bias. Because of the long shape of the worms, it was probably easier to see annelid worms compared to other smaller items that the coatis swallowed directly. Although annelid worms have been observed to be eaten by white-nosed coatis (Kaufman 1962), no previous study has reported that annelid worms comprised a large component of the invertebrate portion of the diet of coatis. Failure to record annelids in diets may have been due to the use of fecal sampling in other studies, because soft tissue parts may not have been visible in feces. Feeding on annelids was particularly noticeable in areas near the waterfalls, which were damp and mossy year-round because of water sprayed from the falls. It appeared that the coatis preferentially ranged in areas with high densities of annelids, but additional studies are needed to confirm this.

The consumption of vertebrates by coatis in Iguazu was exceptionally rare ($<0.01\%$ of foraging time). Previous studies of coatis have found vertebrate remains in 0–15% of fecal samples; thus, coatis in Iguazu fell on the low end of vertebrate consumption compared to other populations (e.g., Valenzuela 1998). The use of fecal samples generally results in similar patterns when compared to corresponding behavioral data in coatis and other mammals (Dickman and Huang 1988; Gompper 1996; Valenzuela 1998). On the other hand, fecal studies commonly underestimate or are unable to detect the presence of soft-bodied organisms in the diet. There is also a danger of misclassifying a scat if the researcher did not observe the feces being produced. Because raccoons (*Procyon*) are the most likely organisms to produce scats that appear similar to coatis, if any misclassification of scats occurs, this would result in an overestimate of vertebrate prey in the coati diet. Behavioral sampling also may lead to biases, especially if certain types of foods are difficult to observe being eaten and make up a small percentage of the diet. For example, Alves-Costa et al. (2004) found remnants of birds in 4.4% of scat samples (all vertebrates = 9.3% of scats). If coatis in Iguazu ate

birds and bird eggs while high in the canopy, this would have been very difficult to observe and could have resulted in an underestimation of vertebrate prey in the diet. Even if there was some degree of underestimation of vertebrate consumption in this study, the extraordinarily rare occurrence of vertebrate consumption observed ($n = 16$ during 2.5 years of study) indicates that coatis in Iguazu likely consume less vertebrate prey than ring-tailed coatis in Brazil (Alves-Costa et al. 2004).

In summary, the diet of coatis in Iguazu was similar to that of other studied populations. Coatis mostly ate fruit and ground-litter invertebrates, and vertebrate consumption was rare. In Iguazu, coatis appeared to eat large amounts of annelid worms, a pattern not recorded in other study sites. Higher levels of fruit feeding coincided with periods of increased fruit availability, and it appeared that fruit abundance was a more important factor driving seasonal feeding patterns than invertebrate abundance. During the winter, when most natural fruit species do not produce fruit, the coatis extensively exploited 2 exotic fruit species, *Hovenia* and *Eriobotrya*. The presence of exotic trees in the park may have benefited the coati groups during the winter, when both invertebrate and natural fruit availability was low. It is not entirely certain if the availability of these foods during the resource-scarce season led to an increase in the reproductive rate and survivorship of the coatis in Iguazu, but it appears highly likely (e.g., Hirsch 2007c). Coatis generally exploited small, quickly depleted fruit trees in comparison to sympatric capuchin monkeys. Specifically, coatis utilized pindo fruit trees far more often than did capuchins. How differences in use of fruit trees between these 2 sympatric mammal species specifically affects differences in ranging behavior, nutrition, feeding competition, and socioecology is not fully known. More-detailed comparative studies are needed to demonstrate how and why these ecological differences may have affected behavior.

RESUMEN

Exista amplia evidencia que la ecología de alimentación es responsable de las diferencias en los sistemas sociales de los mamíferos. Para entender como la alimentación y ecología afectan el comportamiento social de los coatíes de cola anillada (*Nasua nasua*), se recolectó datos de comportamiento de alimentación en dos grupos durante un período de dos años. La proporción de frutos y invertebrados en la dieta de los coatíes en Iguazú, Argentina era muy similar a la dieta de los coatíes de nariz (*Nasua narica*), y coatíes de cola anillada estudiados en Brasil. El consumo de vertebrados en Iguazu fue muy raro. La proporción de tiempo que los coatíes pasaron forrajeando por frutos y invertebrados, en general fue directamente proporcional a la abundancia de estos en el ambiente. Durante el invierno, cuando la cantidad de invertebrados y frutos era menor y los coatíes pasaron mucho tiempo comiendo 2 especies de frutos exóticos. La presencia de frutos exóticos proveía de alimento a los coatíes durante el invierno, época de baja abundancia de comida, y estas especies exóticas pudieran influir en la reproducción y mortalidad de los coatíes de esta población. El 44% de los frutos que los coatíes

comieron fue pindo (*Syagrus romanzoffianum*), ésta especie de fruto es muy importante con respecto al comportamiento social, y los movimientos de los grupos de coatíes. El tiempo que los coatíes pasaron en un árbol, y el número total de frutos que se comen depende de la especie de fruto. Los grupos de coatíes pasaron entre 2.5–12.5 min comiendo distintas especies de frutos, y comieron entre 2.6–269.8 frutos de cada árbol. El tiempo que un grupo de coatíes comen juntos los frutos en un árbol, y la densidad de coatíes cuando están comiendo frutos generan cambios en el sistema social de los coatíes.

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