

Dietary Differences between Neighboring *Cebus capucinus* Groups: Local Traditions, Food Availability or Responses to Food Profitability?

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Abstract. The feeding patterns of three neighboring groups of *Cebus capucinus* were documented over a 3-year period in Santa Rosa National Park, Costa Rica. We describe the diets of the three groups and examine whether dietary differences between groups could be attributed to environmental differences in food abundances, to differences in the profitability of what was available or to learned local traditions. Diets were variable among groups; group A primarily ate fruit (81.2% of feeding time) and spent little time eating insects (16.9%), while group C was more heavily reliant on insects (44.3%) and ate less fruit (53.0%). Group B had a diet that was somewhat intermediate (69.8% fruit, 29.0% insects). By measuring the densities of all major plant foods, we were able to determine that many of the dietary differences between groups could not be attributed to simple measures of food abundance, but we could not distinguish between the food profitability hypothesis and local tradition hypothesis.

Introduction

With the increasing number of primate field studies, there is a growing documentation of variation in behavioral patterns, particularly dietary patterns, among populations of the same species [1-6]. Currently, dietary differences between populations are explained either in terms of environmental variation in food abundance (typically presence/absence) or as learned behaviors that arise despite the environmental similarity

among groups (i.e. 'cultural differences or local traditions') [7-9].

It seems probable that many dietary differences between populations are a result of specific foods being absent from the home range of one population. However, some dietary differences seem to be independent of simple measures of food abundance [2, 6, 7, 10, 11]. For example, Richard [12] found that one population of *Propithecus verreauxi* fed extensively on the fruit of *Rothmannia decaryi*, whereas another population ignored

the fruit, even when it was abundant. In this case, it is possible to reject the hypothesis that group-specific foraging behaviors are related to differences in the presence or absence of food types. However, there are two other alternatives that should be considered: local traditions and food profitability. With respect to the food profitability argument it is necessary to consider not only if a food item is present, but if there are more profitable foods available (profitability being considered in terms of nutrients, energetics, toxins and availability). In the above example, the fruit of *R. decaryi* may not be important in determining the diet of one group of *P. verreauxi*, because another, more profitable, type of food shapes their diet. If this more profitable food were present in the home ranges of both *P. verreauxi* groups, neither group would possibly feed on the fruits of *R. decaryi*. Rejecting the profitability hypothesis requires knowing the profitability of all potential food items in each group's home range, which would require detailed analyses of nutrition, energetics and toxins. The complexity of performing such analyses may have introduced bias towards accepting the local tradition hypothesis as an explanation for dietary variability among populations that is not related to the presence or absence of food species.

The objective of this present study was to describe the diets of three neighboring groups of white-faced capuchin monkeys (*Cebus capucinus*). We examine the degree to which the observed variation among groups can be attributed to the presence or absence of specific food items within their home ranges. In addition, we attempt to examine the possibility that the residual variance among groups may be attributed to differences in the availability of other more profit-

able foods or to learned local traditions. To do this, we compare the general diets of the groups to the availability of their food resources and subsequently contrast their diets only in the area of home range overlap. Further, we use anecdotal evidence to examine the potential contribution of learned local traditions and food profitability in accounting for dietary variation among the three monkey groups.

Methods

Study Site and Group

Three neighboring groups of capuchin monkeys were studied during three field seasons, for a total of 20 months of observations. The study was conducted in Santa Rosa National Park, Costa Rica. This park is 10,800 ha in size and is situated 35 km northwest of Liberia, adjacent to the Pan-American highway. The primary type of forest vegetation found in the park is tropical dry forest, and throughout much of the dry season (December to late May) the majority of the nonriparian trees lose their leaves. The data for this study were collected between 1984 and 1986: group A from January to July 1984 and January to July 1985, and groups B and C between January and July 1986. Group A contained on average 26 individuals: 2-4 adult males, 9-10 adult females, 4-5 large immatures, 5-6 small immatures and 0-4 infants. Group B contained 16 individuals: 4 adult males, 3 adult females, 2 large immatures, 3 small immatures and 4 infants. Group C was composed of 26 individuals: 7 adult males, 6 adult females, 2 large immatures, 5 small immatures and 6 infants.

The three groups used different sections of forest near the park's administration area (fig. 1). The areas differ in their history of human intervention. Group A used two types of habitat. The first was a section of nearly pristine semi-evergreen forest, although the area has been selectively logged for species such as mahogany (*Swietenia macrophylla*). The trees in this area maintain their leaves throughout much of the dry season or drop them for only a short period of time. This area is dominated by such trees as *Hymenaea courbaril*, *Manilkara chicle* and *Quercus oleoides*. The second area used by group A was an old successional

area, estimated to be between 75 and 100 years of age [D.H. Janzen, pers. commun.]. When this area was cleared for pasture, a number of large trees were left standing. Trees such as *Leuhea speciosa*, *Bursera speciosa* and *Spondias mombin* are common. Group B had a home range adjacent to that of group A. It contained old successional habitat similar to that described for Group A. Group C occupied a second section of successional forest estimated to be 40 years old. In this area trees such as *L. speciosa*, *Bursera simaruba* and *Simaruba glauca* are common. Here again, many large trees, such as *Ficus* spp., were left standing. In this area, the diversity of large trees used by the capuchin monkeys was relatively low. During the dry season, when many trees lose their leaves, there may be relatively little food available for the capuchin monkeys (Chapman, unpubl. data).

Behavioral and Ecological Data

Data on dietary patterns and feeding techniques were collected using a focal animal sampling regime, with a 10-min session length. If the focal animal was lost from view prior to the end of the session, the test was terminated, and the data were discarded. When possible, the selection of the subject for the focal animal session was based on a fixed rotation between identifiable individuals. When this was not possible, because of the dispersion of the group, the focal animal was chosen based on a rotation between age/sex classes. The percentage of foraging time devoted to a specific plant item was calculated as the total time spent eating that item divided by the total amount of continuous observation time that the monkeys were seen to feed. By simultaneously observing groups B and C, we ensured that both observers used the same procedures and classified food items using the same criteria.

To determine the relative abundances of the plant species used by any of the three groups, grids with a 10×10 m cell size were established in representative sections of each of the group's home ranges, and the location and size of each food tree in these grids were determined. The size of a tree was represented as the diameter of the tree measured at breast height (DBH). DBH has been shown to fairly accurately predict the reproductive capacity of fruiting individuals for a number of tropical tree species [13]. Because the capuchin monkeys rarely used very small trees, only trees which had a DBH greater than 5 cm were considered. The exception to this is the use of *Acacia col-*

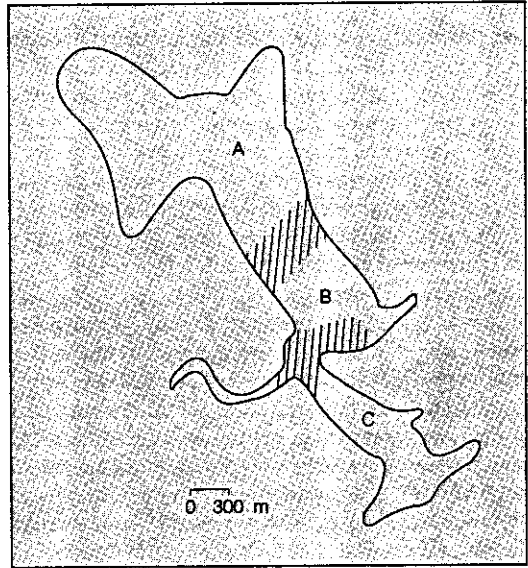


Fig. 1. A map of the home ranges of the three white-faced capuchin (*C. capucinus*) groups studied in Santa Rosa National Park, Costa Rica. The hatched areas depict home range overlap between adjacent groups.

linsii trees for ants (usually *Pseudomyrmex belti*) [14] and fruit. Capuchin monkeys often fed in very small trees of this species. Thus, all *A. collinsii* trees which had reached 1 m in height were considered. We assume that DBH is related to the number of ants available on a tree. As the ants on this tree sting, the DBH for *A. collinsii* trees was estimated. Group A was the subject of an intensive foraging study [15, 16], thus the habitat used by this group was studied more thoroughly than that used by groups B and C. Three permanent 4-ha grids were established within group A's home range. Each grid was 200×200 m in size and consisted of 400 cells, each 10×10 m in size (total area sampled = 12 ha). Corners of the cells were marked with individually labelled steel posts. These grids were sampled approximately every 3 weeks, to identify the size, location and phenology of plants used by the capuchins (see 15, 16 for further details of this sampling regime). For groups B and C, 5 grids were established to sample the habitats present in the home ranges of the groups. However, unlike the sampling regime used for group A, the grids were tempo-

rary and were not sampled every 3 weeks. These grids were sampled once near the end of the study and encompassed 1.8 ha and 1.6 ha for groups B and C, respectively. Instances occurred where a group used a plant species which did not occur in the grid and for which we estimated the density to be 0. In such instances, the sampling of the grids indicates that the density of this plant was low, not that the plant was absent from the group's home range. With group A, we determined the phenological cycles of the plant species over a 4-year period. These data indicated that most of the plant species used by the capuchin monkeys synchronized the production of fruit so that individuals in the population fruited at the same time (a notable exception was *Ficus* spp.). Few species fruited on a biannual or multiannual basis. Thus, by sampling the availability of food to groups B and C at the end of the study, we believe that the estimates of the presence of trees closely represent the presence of food resources and that between-year differences in availability were not great.

Data Analysis

Comparisons of the diets of the groups were made on two levels. First, we compared the overall diets throughout their home ranges for all groups and related the observed patterns to the availability of the food resources in the ecological sampling grids. This analysis is limited on two levels: first, the abundances of plants in the grids are assumed to represent the abundance of the trees throughout the group's home ranges, and secondly, groups were studied in different years. To eliminate these two shortcomings, we also compared the foraging patterns of two groups studied in the same year (B, C) in areas of known home range overlap and analyzed the patterns only when both groups were known to use the same area in the same month. With this analysis it is known that both groups had access to the same food resources. In the statistical analysis of percentage data, feeding time was arcsine transformed.

Results

In total, 534 h of focal animal data were recorded on the three neighboring groups (171 h of observations for group A by C.A.C. and 363 h of observations for groups B and C

by L.M.F.). During these observations the group spent on average 37.6% of the time feeding (total observed feeding time: A = 49 h, B = 54 h, C = 98 h).

For comparative purposes, the diets of primates are classically depicted in terms of major dietary categories (fig. 2). For all three groups, fruit was the predominant component of their diets, and only rarely were leaves or flowers eaten. However, the proportion of each group's feeding time that was devoted to eating insects differed by as much as 27.4%. Similarly, members of group C spent 2.5% of their feeding time eating vertebrate prey, such as squirrels (*Sciurus variegatoides*), lizards, bird's eggs and adult birds. In contrast, individuals from group A rarely ate vertebrate prey. Comparing the amount of time spent feeding on fruit and insects (the component of their diet that on average represented 98% of a group's diet and which was most accurately sampled), diet was not independent of group ($\chi^2 = 182.3$; $p \leq 0.001$).

Sampling of the environmental grids provided estimates of the density and size of most plant species used by the capuchins (table 1). Because the average size of the trees available to the groups differed by as much as 35%, plant density may not accurately represent food availability. Thus, in addition to presenting the density of the major food trees for each of the groups, table 1 provides an estimate of the total size (relative abundance) of each major food plant species on a per hectare basis (cm DBH/ha = weighted density). We present the use of plants on which any of the groups fed for more than 1% of their foraging time. This resulted in a comparison of 20 plant items. Density estimates were available for 16 of these species.

The use of plant foods fell into one of four categories, each of which has specific impli-

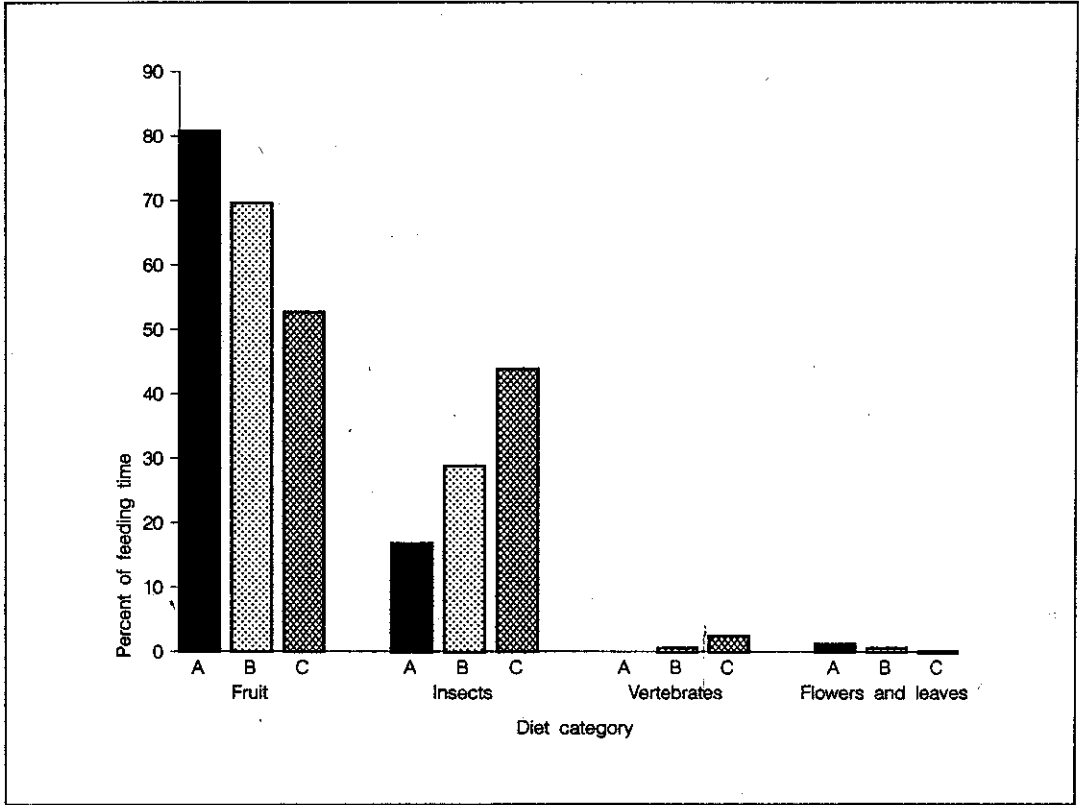


Fig. 2. The percentage of feeding time devoted to four different types of foods by three neighboring groups of *C. capucinus* in Santa Rosa National Park, Costa Rica. ■ = Group A (26 members); ▨ = group B (16); ▩ = group C (26); see text for group compositions. Comparisons between the amounts of time spent eating fruit and insects: $\chi^2 = 182.3$, $p \leq 0.001$.

cations for whether or not feeding differences between groups can be attributed to learned local traditions or simply to differences in availability. For the first two of these categories, use corresponded to availability (percent of feeding time vs. density: $r = 0.531$, $p = 0.042$, $n = 15$; percent of feeding time vs. weighted density: $r = 0.861$, $p \leq 0.001$, $n = 15$), but for the latter two, it did not (percent of feeding time vs. density: $r = 0.089$, $p = 0.622$, $n = 33$; percent of feeding time vs. weighted density: $r = 0.101$, $p =$

0.577 , $n = 33$). A plant item was placed in category 1 when it was only found in the home ranges of one (or two) groups which ate it and was not available in the other's home range(s); 19% of the plant items considered fell into this category (table 1). The second category involved instances where a plant item was used by all groups and the magnitude of use agreed with availability; 12.5% of the food items considered were placed in this category. Plant items were classified as category 3 when the plant was

present in all of the groups' home ranges, but only one (or two) of the groups fed on that item and at least one of the groups was never seen to eat it; 44% of the plant items considered fell into this category. Such differences in feeding patterns cannot be attributed to availability. The fourth category involved those cases where a plant item was used by all groups but the magnitude of its use did not correspond to the availability of the food; this category represented 25% of the

food items considered. It seems likely that learned differences in feeding patterns were one cause of such variation, but the case presented is not as strong as with category 3.

The types of foods eaten by groups B and C in the area of home range overlap in the months that they shared the same areas was not independent of group ($\chi^2 = 175.6$, $p \leq 0.001$; fig. 3). This result similarly suggests that dietary differences are often not related to simple measures of food abundance, but it

Table 1. Use and availability of the foods used by the *Cebus* monkey groups studied in Santa Rosa National Park, Costa Rica

Plant/part	Group	Category	Percent of feeding time	Density/ha	Weighted density/ha
<i>Luehea candida</i> fruit	A	1	0.0	0.0	0.0
	B		5.8	5.6	255.6
	C		2.3	0.6	34.6
<i>Quercus oleoides</i> fruit	A	1	3.5	5.0	315.3
	B		0.1	0.0	0.0
	C		0.0	0.0	0.0
<i>Swartzia cubensis</i> fruit	A	1	1.7	0.1	6.1
	B		0.0	0.0	0.0
	C		0.0	0.0	0.0
<i>Ficus</i> spp. fruit	A	2	1.9	0.6	64.7
	B		4.4	1.1	77.8
	C		6.3	3.2	300.0
<i>Genipa americana</i> fruit	A	2	0.5	0.8	15.6
	B		0.2	0.6	16.7
	C		3.6	7.1	167.3
<i>Simaruba glauca</i> fruit	A	3	0.2	0.4	5.8
	B		0.0	11.7	192.8
	C		5.1	8.3	180.1
<i>Acacia collinsii</i> fruit	A	3	0.0	13.5	48.7
	B		0.1	27.8	84.7
	C		3.5	63.5	173.4
<i>Luehea speciosa</i> fruit	A	3	4.4	19.9	537.3
	B		0.0	40.6	1,498.3
	C		0.0	27.6	1,031.4

Table 1 (continued)

Plant/part	Group	Category	Percent of feeding time	Density/ha	Weighted density/ha
<i>Randia echinocarpa</i> fruit	A	3	0.0	1.6	15.3
	B		2.1	5.6	41.7
	C		0.1	1.9	25.6
<i>Sciadodendron excelsum</i> fruit	A	3	2.5	0.7	11.2
	B		0.0	1.1	47.2
	C		0.1	0.6	46.2
<i>Ficus</i> spp. leaves	A	3	2.4	0.6	64.7
	B		0.0	1.1	77.8
	C		0.0	3.2	300.0
<i>Dipterodendron costaricensis</i> fruit	A	3	1.3	2.5	43.8
	B		0.1	0.0	0.0
	C		0.0	0.6	0.1
<i>Sloanea terniflora</i> fruit	A	4	34.1	2.3	91.8
	B		14.7	0.0	0.0
	C		6.9	0.6	53.9
<i>Muntingia calabura</i> fruit	A	4	17.9	0.3	6.1
	B		0.6	0.6	6.1
	C		7.0	3.9	36.5
<i>Bursera simaruba</i> fruit	A	4	1.3	20.8	425.5
	B		26.6	38.3	812.8
	C		14.6	19.9	537.8
<i>Zuelania guidonia</i> fruit	A	4	1.7	0.8	20.8
	B		2.1	0.0	0.0
	C		0.6	5.3	12.8
<i>Karwinskia calderoni</i> fruit	A	-	0.0	-	-
	B		7.0	-	-
	C		0.4	-	-
<i>Guettarda macrosperma</i> fruit	A	-	0.0	-	-
	B		0.5	-	-
	C		1.1	-	-
<i>Hirtella racemosa</i> fruit	A	-	1.8	-	-
	B		0.0	-	-
	C		0.0	-	-
<i>Sterculia apetala</i> fruit	A	-	1.5	-	-
	B		0.0	-	-
	C		0.0	-	-

See text for a description of the categories and the weighting for density.

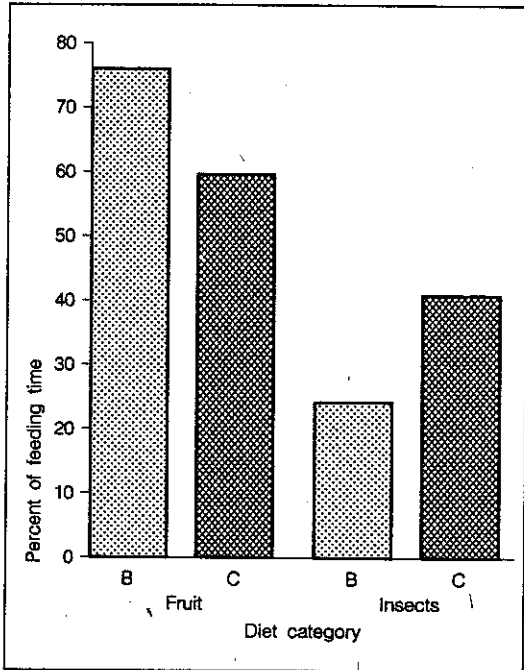


Fig. 3. The percentages of feeding time devoted to fruit and insects by the two neighboring groups B (▨) and C (▩) of *C. capucinus* in Santa Rosa National Park, Costa Rica, in the areas where the home ranges of the two groups overlapped ($\chi^2 = 175.6$, $p \leq 0.001$).

does not allow one to reject either the local tradition or the food profitability hypotheses.

No major differences in feeding techniques were observed between the groups which could be attributed solely to 'cultural' traditions, even though elaborate feeding tactics are characteristics of capuchin monkey foraging patterns. All species in the genus *Cebus* are renowned for their ability to recognize sources of embedded food and for elaborate techniques to find, extract and prepare the food for consumption [17]. In the field, capuchins search for food by stripping bark from trees, breaking open dead branches,

rolling over stones, sifting through leaf litter on the forest floor and cracking open hard fruit on stones [17; Fedigan, unpubl. data].

Discussion

Given the extent of the variability that we have documented in the diet of neighboring capuchin monkey groups, how can this best be explained? The analysis of the feeding patterns of the three neighboring capuchin monkey groups in relation to food availability indicates that, in many cases, the selection of foods was not related to food availability. One possible explanation for the observed pattern is that food selection may be affected by learned group traditions. That is, individuals in the different groups may have learned to recognize different sets of plant items as food and only eat items in this set. The differences in diet between capuchin groups are similar in nature to documented differences between chimpanzee groups. With chimpanzees, these differences in diet are often considered to indicate learned group traditions [7, 18]. The extent to which these differences can be considered indicative of 'cultural' patterns depends on one's definition of culture, which is a difficult and complex issue [see 12, 18, 19 for insightful discussions of the issues involved in defining culture with reference to nonhuman primates].

The optimal foraging theory [20] presents an interesting alternative hypothesis which we have called the food profitability hypothesis. Consider the use of *A. collinsii* fruit. This plant is fairly common in the home ranges of all groups, but only group C ate the fruit of this plant to any degree. Members of group C ate this fruit in the dry season, when the young successional forest they used had

little other food available. In the home ranges of the other groups, different foods were available at the time when group C ate *A. collinsii* fruit. Thus, it is conceivable that groups A and B might have eaten this fruit if they had been placed in a similar situation in which little food other than that of *A. collinsii* was available. Such interpretations may account for a number of the foraging differences between groups. However, until the relative profitabilities of all the potential foods used by the capuchin monkeys are known, it is not possible to distinguish between those instances that involve learned tradition and those which do not. One observation provides support for an optimal diet interpretation. Over the 3 years of the study, 6 males were observed to move between groups. These males were usually observed daily following their immigration into the group, and evidence suggests that they quickly adopted the feeding pattern exhibited by their new group. Presumably, it would take these males some time to learn a new feeding pattern. However, we never observed these males eating foods that could be interpreted as inappropriate for their new group. Thus, it seems probable that these males were simply eating the most profitable foods available, which was also what the other animals in the group were eating. One must also consider the possibility that both optimal foraging and learned behavioral traditions contribute to the observed variability among groups.

The nature of the foraging differences between the capuchin monkey groups seems similar to those observed between chimpanzees studied at different locations [7, 8, 12, 18, 21], with the exception that we observed no differences in feeding techniques between groups. This may reflect the fact that we

studied differences between neighboring groups in which there were exchanges of members, whereas studies of cultural differences in chimpanzees documented variation between much more geographically isolated groups. Possibly, the degree of isolation between groups must be relatively great before changes in feeding techniques can develop. Alternatively, habitat differences between neighboring groups are probably smaller than between more distantly separated groups, and large habitat differences are possibly required for differences in feeding techniques to develop.

A number of researchers have documented that group size or composition can affect the foraging patterns of primates [22–25]. For instance, de Ruiter [23] demonstrated that large *C. olivaceus* groups tended to travel further than small groups and in periods of low food availability large groups foraged less on fruit. The members of the large groups appeared to compensate for this by foraging more on invertebrates, particularly terrestrial snails. The dietary differences observed between our capuchin groups in Santa Rosa do not appear to be a response to differences in group size. The groups with the most divergent diets (A, C) were of the same size and had similar compositions.

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