

Spider Monkey Foodways

Overview

Spiders inhabit the same or similar ecosystems as howler, though different niches within those ecosystems, and weigh about the same size as them--even though they are way more slender and long with enormously long legs, arms and tails so that they look like spiders. They are so arboreal that they cannot even walk over the ground in any way--and thus rarely come to the ground.

DIET

When available, ripe fruit is greatly preferred, and they are known specifically for spreading fruits seeds across the jungle through their scat (wisc.edu)--thus showing the unique and symbiotic relationship they have with fruit trees: plants make their fruits nutritious so that spiders will eat them and then help them reproduce--which in turn helps the spider by providing food for their own future generations. They feed on fruits about seventy percent of the time; otherwise, they eat leaves twenty one percent of the time, and flowers at seven percent of the time; and other plants and insects at about three percent. When necessary, they feed on rougher fallback foods such as bark, roots and bulbs.

When looking at total feeding time, which isn't the same as total nutrition, fruits account for an average of 67% of total feeding time, followed by leaves (21%), flowers (7.1%), and other plant parts and insects (2.6%) (González Zamora 2009). Link et al. found that the brown spider monkey ate fruit 93.4% of the time (Link 2011). This was in Ecuadorian spider monkeys. Milton writes that their diet is 72% fruit, 22% leaves, and 6% flowers (Milton 2006); I'm sure these differences relate to different habitats and species of spider monkeys studied.

Source: Cawthon Lang KA. 2007 April 10. Primate Factsheets: Black spider monkey (*Ateles paniscus*) Behavior. <http://pin.primate.wisc.edu/factsheets/entry/black_spider_monkey/behav>. Accessed 2018 June 17

When fruit is harder to find, the Spiders, unlike the Howlers, will make extra effort to track down this food. Otherwise, they will also eat nuts and leaves, flowers and insects and, when necessary, will concentrate on fallback foods, such as honey, insects (this is mentioned above), bark, roots, bulbs and rotting trees (wisc.edu; Milton 2006, Gonzalez Zamora 2009). Spiders can also sustain themselves for extended periods of time on only one or two fruits in conjunction with some nuts--although they will eat as many as one hundred and fifty different plant species (Over 165 plant species. In fact, 165 plant species contribute to 80% of their total feeding time across all spider monkey species. However, within spider monkey species, they typically feed on about 24 species of foods. So, less diversity within a given species of spider monkeys in a given territory. Gonzalez Zamora 2009.). Overall, fruit usually accounts for somewhere between 70 and 90 percent of their total nutrition.

SENSING

They seem to have some unique adaptations, separating them from other primates, that allow them to smell their fruit better: they can distinguish between ripe and unripe fruit better (All monkeys have this ability) by detecting various molecules detecting ripeness even when many other compounds are also present. In other words, they can focus on many different compounds suggesting the ripeness of fruit amidst many other odors. Finally, regardless of their type of color vision (dichromatic vs. trichromatic) spider monkeys smell fruits that are difficult to distinguish from background leaves more often than those fruits that are easy to distinguish visually in the forest. Additionally, they were less likely to eat fruits that they smelled first, suggesting that they use their sense of smell to distinguish between edible and inedible fruits when their vision is insufficient to give them that information (Hiramatsu 2009). Interesting evolutionary side-note on fruit odor: Nevo et al. found that only plant species whose seeds are specifically distributed by primates demonstrate a significant change in their odor profile upon ripening. In contrast, plant species whose seeds are distributed by birds do not change their odor profile upon ripening. They suggest that these odor changes in the species that primates distribute the seeds evolved to increase the plant's reproductive success. (Nevo 2016).

We also do not know much conclusive about their sense of smell, other than that one study suggests they have special abilities to smell distinctions between ripe and unripe fruit (Other monkeys have this ability, I wouldn't suggest that it's unique to spider monkeys. More notes on olfaction below) (Nevo 2015).

HEARING

Spider monkeys likely hear for the same reason as other monkeys, not to find their food, but to hear others in their group. Spider monkeys and many other new world monkeys hear better at high frequencies than old world monkeys--but whether new world monkeys communicate at higher frequencies is not known. (Apparently, New World monkeys actually hear better at higher frequencies than do Old World monkeys and humans.

Source: "Primate Sensory Capabilities and Communication Signals: Implications." *Primate Sensory Capabilities and Communication Signals: Implications for Care and Use in the Laboratory*,
www.nc3rs.org.uk/primate-sensory-capabilities-and-communication-signals-implications-care-and-use-laboratory.

VISION

Spider monkeys' ability to detect unripe from ripe fruit is very nuanced, in that they are able to detect unripe from ripe fruit via multiple olfactory compounds marking fruit ripeness, not just one compound. Additionally, they can identify ripe fruit even when the odor signal is accompanied by a lot of 'noise' (scents that don't indicate ripeness vs. non ripeness (Nevo 2015). Spider monkeys also use their sense of smell more often when fruits are unripe. When fruits are ripe, they use their sense of touch and taste more often (Pablo-Rodriguez 2015). They also typically use their sense of vision most often with familiar foods, and use other senses, like smell and

touch, more often with novel foods. This study also found that, compared to squirrel monkeys, spider monkeys rely more on olfactory cues versus tactile cues when examining novel foods (Laska 2007).

Like many other new world monkeys, spiders have both dichromatic, mostly the males, while some of the females have trichromatic vision--which is due, it seems, to the mechanics of genetics. However, we can nonetheless see the advantages of some spiders having better vision than others: just one primate with better color vision can identify fruit better than others and lead the others to fruit; and these others, too, thus receive the benefit of this vision without having to use the nutrition to support the trait. At the same time, spiders have unique adaptation in their dichromatic vision that allows them to distinguish fruit from leaves, thus evidently giving them the usual advantage of having their vision evolved to their specific food. Overall, there are actually 6 possible color vision phenotypes in new world monkeys due to polymorphisms in the opsin genes.

(Data don't support this speculation from the notes above. Due to the fact that color vision is inherited via the X-chromosome, differences in color vision between males and females is due to the fact that males only have one X chromosome, so if they inherit an X chromosome with an odd mutation, then their vision will be different from all females except those who inherit the same mutation from both parents, which is less likely. This is why rates of color-blindness are much higher in males than females, because it's much less likely that both parents will have the mutation AND that the female child will inherit both mutations. There are more notes on color vision in spider monkeys below).

Source: Blakeslee, Barbara, and Gerald H. Jacobs. "Color Vision in the Spider Monkey (Ateles)." *Folia Primatologica*, vol. 38, no. 1-2, S. Karger AG, 1982, pp. 86-98. Crossref, doi:10.1159/000156045.

Color vision in spider monkeys: Spider monkeys have a unique mutation in their color vision that improves their ability to distinguish fruits from leaves in the forest. This mutation is unique to spider monkeys in particular, not just to New World monkeys (Matsumoto 2014). However, many spider monkeys are dichromats instead of trichromats. This is more common among males than females, for the reasons listed above. Overall, there are actually 6 possible color vision phenotypes in new world monkeys due to polymorphisms in the opsin genes (Riba-Hernandez 2004).

TASTE

SWEET

Interestingly, spiders taste sweetness as sucrose at about the same level as humans, perhaps showing their preference for sweetness. Like all primates, spiders detect sucrose better but, unlike most primates, they also detect starch in the form of a carbohydrate called polycose, perhaps because some of their fruits contain greater amounts of starch than sucrose--but perhaps also to taste their fallback foods when fruit is scarce.

When squirrel spider monkeys and humans were tested, they showed the same order of preference and it is surmised that this may be common amongst all or most primates. (Laska 1998)

In a related study, Laska et al. found that spider monkeys can detect the flavor of starch (tested using polycose), but they detect sucrose better. Interestingly, they found that macaques likely have specialized taste receptors for starch and that their taste responsiveness is actually more similar to rats than to other primates (Laska 2001).

AMINO ACIDS

Spiders, like baboons, detect the same as lower levels than some other comparable primates, such as macaques and squirrel monkeys. Spiders, like other primates as well as humans, also taste amino acids as typically correlating to sweet, sour, umami or bitter and they taste them, strangely enough, as humans: they detect them at similar levels as ourselves and show the same preference. For example, they show significant preferences for glycine, proline, alanine, serine, glutamic acid, aspartic acid, and lysine. They reject tryptophan, tyrosine, valine, cysteine, and isoleucine, and are indifferent to the remaining amino acids tested.

As noted before, nearly all amino acids are usually bound in larger molecules, like proteins, in most food, animal and plant--so there is some confusion around why we taste amino acids at all. But nonetheless fruits do contain some free amino acids in small concentrations that are nonetheless high enough for spiders to detect them--so scientists have theorized that spiders taste amino acids to detect them in fruit and use that detection to help them balance their intake of amino acids, especially since their diets are otherwise low in protein. We have at least several studies showing that rats balance their intake of amino acids through taste.

Nonetheless, this study does report that there are some free amino acids in tropical fleshy fruits that are in the millimolar range, which is low in concentration, based on this study, this range in concentration is high enough for the spider monkey to detect them. Therefore, the spider monkeys may potentially use the taste of free amino acids as gustatory cues that factor into their intake of different kinds of fruit in order to support the maintenance of amino acid balance. frugivorous, protein poor diet

With regard to MSG and sodium chloride (salt), Laska compared squirrel monkeys, macaques, baboons, and spider monkeys. They found that spider monkeys could taste MSG at very low concentrations (2mM) as could baboons, whereas macaques (50mM) and squirrel monkeys (300 mM) required much higher MSG concentrations to detect the flavor.

With regard to amino acids, one study examined spider monkeys' taste responses to the 20 proteinogenic amino acids. Their preferences for particular amino acids parallel those of humans.

The spider monkeys appear to have similar taste preferences and taste thresholds to the amino acids as do humans. They conclude that the taste responses of spider monkeys to proteinogenic amino acids may reflect an evolutionary adaptation to their frugivorous, protein-poor diet (Larsson 2014).

Off hand, this research and its potential implications are confusing, especially since individual amino acids are not taste stimuli that you would expect primates to have evolved to detect on their own. After all, the majority of the amino acids introduced into the mouth would be strung together as proteins, and would not begin to be broken down until they reach the stomach. Nonetheless, this study does report that there are some free amino acids in tropical fleshy fruits that are in the millimolar range, which is low in concentration, based on this study, this range in concentration is high enough for the spider monkey to detect them. Therefore, the spider monkeys may potentially use the taste of free amino acids as gustatory cues that factor into their intake of different kinds of fruit in order to support the maintenance of amino acid balance.

Another study not only found that the spider monkeys can detect free amino acids in concentrations present in fruit, but they can also discriminate between different kinds of amino acids, based upon the fact that they showed preference to some and aversion to others. Humans have also been shown to be able to discriminate between the different amino acids, each amino acid having its own particular set of taste qualities. Individual amino acids have been described as sweet (i.e. glycine), bitter (i.e. L-tryptophan), sweet-bitter (i.e. L-valine), obnoxious-sulphurous (i.e. L-cysteine), and meaty-salty-bitter (i.e. L-glutamic), for example. It seems as though the spider monkeys may perceive amino acids similarly as humans since they tended to reject the more bitter or unpleasant tasting amino acids (i.e. L-cysteine and L-tryptophan) and prefer the sweet-tasting (glycine, alanine, proline). This is not to suggest that both humans and spider monkeys' preference for or aversion to certain amino acids signifies differential nutritional value among the amino acids. Instead, it suggests that human taste perceptions of amino acids may be similar to spider monkeys. This may potentially be important since it has been shown that these preferences and aversions to the individual amino acids differ depending upon the species of nonhuman primate. The common marmoset, for example, was found to be indifferent to all of the 20 proteinogenic amino acids. This paper suggested that this might be reflective of the higher protein diet of the marmoset who is known to primarily feed on protein rich plant exudates and insects. This is in contrast to the spider monkey that feeds mainly on fruit, and thus consumes a low protein diet, and may therefore benefit from being able to detect and discriminate between amino acids in order to make dietary choices that support amino acid balance.

All that being said, these are just two examples that are based on associations (amino acid taste sensitivity and protein content of diet) that could or could not have any real true link.

So what is actually known at this point is:

- Individual amino acids have distinct taste qualities that allow them to be differentiated by spider monkeys, humans, and many other primates that have been tested.

- Individual amino acids can be detected at low concentrations, indicating that at least in fruit, free amino acids are in concentrations that can be detected and would contribute to the overall taste profile.
- Spider monkeys seem to perceive the taste of individual amino acids similarly to humans. Previous studies have shown that other nonhuman primates display similarities and differences in their responses to amino acids as compared to spider monkeys. Whether or not diet underlies these variations in taste perception of amino acids is not yet known, but has been proposed as a possibility.

Overall, I tend to think that if the taste of amino acids does play a role in food choice in order to achieve protein balance, it probably plays a much more minor one than the actual metabolic consequences of varying protein intake. That being said, this study referred to two studies in which taste is cited as having played a role in dietary choice in order to achieve amino acid balance in rats. Let me know if you would like for me to look further into these studies. Here are links to the abstracts of the two studies:

Source:

Gietzen, D.W., Aja, S.M. The Brain's Response to an Essential Amino Acid-Deficient Diet and the Circuitous Route to a Better Meal. *Mol Neurobiol* 46, 332–348 (2012).
<https://doi.org/10.1007/s12035-012-8283-8>

Leung, Philip M. B., et al. "Influence of Taste on Dietary Choice of Rats Fed Amino Acid Imbalanced or Deficient Diets." *Physiology & Behavior*, vol. 38, no. 2, Elsevier BV, Jan. 1986, pp. 255–264. Crossref, doi:10.1016/0031-9384(86)90161-7.

TERRITORY/LOCOMOTION

As mentioned, spiders inhabit prime, rich rainforest (whereas howlers will live in marginal terrain) and, rarely coming to the ground, live high in the trees, somewhere between eighty to one hundred feet. They inhabit much larger territories than howlers, about one square mile or more, perhaps ten times as large as the howlers.

To move through this terrain, they also locomote better and faster and more than howlers.

The home range size of spider monkeys is much larger than that of howler monkeys. One study found that their range is almost 1 square mile (.985), but their range could be larger than this, since that study included a geographical location that included areas, like granite formations and lowland forests, that black spider monkeys are unlikely to cross. Another study suggested a home range between 0.579 and 1.54 square miles. Additionally, they travel long distances daily to forage for food, anywhere from 0.311 to 3.11 miles (wisc.edu).

They have slender, light bodies and long limbs that allow them to swing from limb to limb, creating superb efficiency in their locomotion--while being able to casually hang from their tails to feed.

Spider monkeys prefer primary rainforests and living in the high rainforest areas that are not affected by seasonal flooding. They do not live in edge habitats, whereas howler monkeys will. They forage in the high canopy of the rainforest, anywhere from 82 to 98.4 feet high!

They use several forms of locomotion as mentioned on the section on primates in general: quadrupedalism, brachiation

Similar to the howler monkeys, spider monkeys have prehensile tails that help them cover large distances using less energy. They use several forms of locomotion, including walking on all fours (quadrupedalism), bipedalism, brachiation, clambering and also use long, prehensile tails as their fifth limb. Finally, similar to howler monkeys, spider monkeys use bridging to cross gaps in the forest, which they achieve by doing an incomplete leap to reach the support they're trying to get to, while still holding on to the original support with their hindlimbs and tail (Youlatos 2008). They also swing in between branches swinging between branches (brachiation), and also hanging or suspending from. When they leap, it is more of a horizontal movement, as 'leap' implies, whereas, dropping is more of a vertical movement (Youlatos 2008).

They can also walk bipedally, on their hindlimbs, sometimes using their forelimbs or tail for support, though they are very slow when moving this way. They can walk bipedally both on branches and on the ground (Youlatos 2008). Other categories of movement include clambering, where they are using their limbs to move across multiple, variably oriented supports, which is distinguished from quadrupedalism, when they're on one support (i.e. a branch). Below are some drawings from the Youlatos article of spider monkeys in different locomotor positions. Spider monkeys also don't have opposable thumbs!

Branches (suspensory locomotion), which they do most often when feeding. They typically sit or hang when eating (wisc.edu). Spider monkeys also leap or drop to cross gaps in the canopy.

The use of bridging for locomotion is specifically to help young spider monkeys cross gaps in the forest (wisc.edu)

CAPTURE

As primarily frugivores, and only secondarily folivores, spiders have adapted forms of capture designed for fruit--that is, using their long limbs, including their tail, to hang in all those positions already seen in our section on primate locomotion to pluck fruit from difficult places. Otherwise, since they mostly eat fruit, lower in toxins, and only small amounts of leaves, their diet is much lower--and they thus do not need to deal with them as much.

INGESTION

Another monkey species often found living in the same forests as *Cebus apella* is the spider monkey, *Ateles paniscus*. Spider monkeys are characterized by a low degree of manual

dexterity and small teeth, which are useless for cracking hard-shelled palm nuts. But spider monkeys specialize in soft fruits and tender young leaves, not hard palm nuts. They are also much bigger than capuchin monkeys, and if the supply of softer fruits is limited, they can chase capuchin monkeys out of fruiting trees and monopolize the fruit crop for themselves.

DIGESTION

Given their more refined diet, spiders have smaller, digestive systems as compared, say, to howlers, relative to the overall size of their body. More specifically, they have a more compact stomach because their food is not as bulky, longer small intestines to absorb more macronutrients, and much smaller colons for reduced fermentation. Following the usual pattern, they pass their food faster; howlers need twenty hours, spiders four hours--even as spiders also absorb less nutrients from their food, especially in the form of the short chain fatty acids from the ferment. But they compensate for this by eating food at a faster rate: in other words, they eat more refined foods that pass faster through their system, allowing them to extract more macronutrients, while expelling the waste faster.

Given the nature of their diet--that is, more refined-- their small intestines are longer to allow for more absorption of sugars, fatty acids and amino acids, while their colons are still functioning but smaller, to compensate for less dependence upon the ferments (maybe: "due to the fact they're less dependent upon fermentation for energy"; saying "to compensate" implies making up for a loss, which isn't really the case here. Also, maybe write "fermentation end products" or "fermentation", it's odd to just write "the ferments", particularly since there isn't simply one product that comes from fermentation. Also, because the spiders do not need to hold their food in their digestive tract as long to ferment, they can pass their food faster than the howlers, allowing for quicker movement of nutrients.

Since the fruit likely has lower fiber content, this means it's more easily digestible and absorbable, so they don't need to ferment as much fiber to extract nutrients. I'm also not sure that it's necessarily accurate to say that faster movement of food through the digestive tract is equivalent to 'quicker movement of nutrients', particularly since the nutrients are largely absorbed in the small intestines, and the spider monkeys have longer small intestines. I haven't read much about transit time in the digestive tract and nutrient absorption overall, or differences between species. Perhaps you have? I just think we need to make sure that whatever is written in this regard is accurate.

Milton found that the transit time for spider monkeys is about 1/5th of that of howler monkeys. It took howler monkeys 20 hours to pass food and spider monkeys only 4 hours. As you mention, this is because the spider monkeys have shorter, narrower colons; however, the digestive efficiency is lower in spider monkeys, as their smaller colons means they're less efficient at extracting energy from fiber in their diet. However, they make up for this inability to extract energy from fermented fiber by passing a lot of food quickly through the intestinal tract, and their choice of food- fruit- is easy to digest and contains a lot of energy, which suits their digestive capabilities. Indeed, spider monkeys have to eat a lot of fruit because they can't obtain sufficient

energy via fermentation leaves. Similar to other issues of evolution, this is a bit of a chicken or egg scenario, though I would hypothesize that eating more fruit started the process of differentiating the digestive tract to adapt this- of course this is only a hypothesis.

Source: Milton, Katharine. "Diet and Primate Evolution." *Scientific American Sp*, vol. 16, no. 2, Springer Science and Business Media LLC, June 2006, pp. 22–29. Crossref, doi:10.1038/scientificamerican0606-22sp.

METABOLISM

Although we do not have any data on the metabolism, storage and synthesis of nutrients of spiders, we can nonetheless hypothesize that they follow the same patterns as found in other primates and mammals in general. For brain catabolism, spiders consume mostly glucose and secondarily fructose from fruit. For muscle catabolism, they probably use some sugars from fruit as well as short chain fatty acids from colonic fermentation: they may also gather reasonable amounts of longer chain fatty acids from their diet. If you gather enough sugar, there will be lipogenesis for muscles.

For anabolism, they gather amino acids from both fruits and leaves. As we have seen already, wild fruits are more abundant in amino acids and then, combined with leaves, may provide descent ratios of amino acids for complete proteins or collagenous proteins.

GEOPHAGY

Krishnamani found that several different species of spider monkeys do engage in geophagy, but Link et al. suggests there are only two species of spider monkeys that visit mineral licks. As mentioned previously, there are several hypotheses regarding geophagy, four related to alleviating GI distress: 1) Soil absorbs toxins and metabolites of toxins; 2) soil acts as an antacid; 3) soil acts as an antidiarrheal; and 4) soil counteracts effects of endoparasites. Two other hypotheses are that soil supplements nutrient poor diets and that it provides extra iron at high altitudes. All of these reasons are likely relevant in primates (Krishnamani 2000).

Link et al. specifically studied geophagy and use of mineral licks in brown spider monkeys and found that they only visit mineral licks on days with no or very little rain and that they visit them frequently throughout the year (~14% of days). They suggested that they visit on days with good weather because of the high risk of predation at mineral lick sites. This likely also explains why they come to mineral licks sites in groups. They still weren't sure why they use them- for minerals or to aid in detoxification (Link et al. 2011 (two different articles)).

ENCEPHALIZATION

Though about the same size, spider monkeys have brains twice as large as howlers--the same pattern that is echoed between most folivores and frugivores and overall are one of the most encephalized primates out there. Accordingly, they also display higher observed intelligence

with some scientists identifying them as the most intelligent, new world monkey--although I am partial to the capuchin.

Note: Milton points out specifically that spider monkeys' brains weigh twice that of howlers despite them being of similar size, and apparently similar-sized animals generally have like-sized brains. Milton hypothesizes that a larger brain likely helped the spider monkeys succeed in maintaining their very specific diet focused on ripe fruit, helping them to learn and remember where fruit-bearing trees existed in the forest and when they would be ready to eat. Since howler monkeys don't need such cognition to succeed with their diet, their brains were not as well-developed. She found support for her hypothesis that other primates who also consume diets based on ripe fruits had larger brains than leaf-eating primates, even when of the same body size. She then links this to human-evolution, arguing that our brains increased in size to accommodate the dietary challenges of a changing climate in which foods became more seasonal and humans had to search more often and more effectively for food. She also specifically notes that consumption of high quality foods, aided by changes in cognition and behavior, allowed humans' brains to expand. (Milton 2006). This is generally the book's argument, I just like how Milton explains it in her article, so thought I'd add it in here for reference:

"Recent meta-analyses on primate cognition studies indicated spider monkeys are the most intelligent New World monkeys.^[4] They can produce a wide range of sounds and will "bark" when threatened; other vocalisations include a whinny similar to a horse and prolonged screams. Spiders live in groups that are between fifteen to forty members. Like most primates, they raise their young for three years, suckling them for three years which also prevents them from producing more eggs--and thus slowing down the growth of the population. Once reaching adolescents, the females leave their group of origin while the males stay behind, making them patrilocal. In this scenario, the males are usually the alphas because they are more bonded than the females--as they are all related--which is the case with chimps and other primates. However, with spiders, that is not the case. While most primates are more sexually dimorphic, male and female spiders are about the same size. And somehow from all of this, the spiders ultimately have alpha females that run the group.

Perhaps females are the alphas because they possess the better vision--which then helps the whole group better find their fruit. Additionally females choose their mates, not the males. While the whole group sleeps together at night, they break like many primates into smaller groups led by females during the day. However, if the group is not successful in finding food, they then divide into even smaller groups, sometimes just pairs. They either tend to stay in smaller or larger groups, based on competition for food within the group, as well as tensions, and the threat of predation. Thus, they are a fission-fusion social group, similar to chimps and humans. They generally feed from dawn until mid-day and then spend the rest of their time playing with their children. But they always return to their larger group, likely for protection from predators. Generally, spider monkeys are not aggressive with one another and, if they are, it's due to limited food resources. Also, they don't tend to cause serious injury when they're aggressive with one another.

A large brain would certainly have helped spider monkeys to learn and, most important, to remember where certain patchily distributed fruit-bearing trees were located and when the fruit would be ready to eat. Also, spider monkeys comb the forest for fruit by dividing into small, changeable groups. Expanded mental capacity would have helped them to recognize members of their particular social unit and to learn the meaning of the different food-related calls through which troop members convey over large distances news of palatable items. Howler monkeys, in contrast, would not need such an extensive memory, nor would they need so complex a recognition and communication system. They generally forage for food as a cohesive social unit, following well-known arboreal pathways over a much smaller home range. Also, howlers tend to use only one or perhaps two large fruiting trees a day, whereas spider monkeys often visit five, 10 or more.”

COMMUNICATION

They communicate quite loudly; interesting enough their calls can be heard from around one mile away, about the size of their territory, usually to stay in touch with their whole group or subgroups. They make friendly sounds, whinnies, sobs, tee tee, while feeding. When scared, they trill, twitter or squeek. : If a spider monkey is scared, they may shake their head, scratch their arm and chest, their hair will stand on end, they'll shake branches, and defecate. They also aren't very susceptible to predation due to their size, but there are some predators, including raptors, jaguars, pumas, and some large snakes. Apparently predation events are rare in spider monkeys (wisc.edu). When threatened, they will bark at the source of danger, drop sticks and even shit and piss on them--thus showing some evidence of tool use.

However, they do not use tools, other than to drop sticks and shit and piss on their predators--even as, because they are larger, they do not have many predators.

Their communication is quite loud, apparently, the 'whoops' they make can be heard up to .62 miles away on the forest floor, and up to 1.24 miles if they're made above the canopy. They often make these noises to communicate with neighboring subgroups and larger social groups. They make other friendly sounds (whinnies, sobs, tee-tee) while feeding and during friendly interactions. When they're scared, they trill, twitter, or squeak (wisc.edu).

AGGRESSION

Spider monkeys are characterized by a low degree of manual dexterity and small teeth, which are useless for cracking hard-shelled palm nuts. But spider monkeys specialize in soft fruits and tender young leaves, not hard palm nuts. They are also much bigger than capuchin monkeys, and if the supply of softer fruits is limited, they can chase capuchin monkeys out of fruiting trees and monopolize the fruit crop for themselves.

SUMMARY

As compared to the howlers, the spiders start with more refined diets,

enhanced nutrition (more refined)

equals

sensing (no difference)

locomotion (enhanced)

capture (enhanced)

digestion (reduced)

metabolism (the same as howlers, based on size, possibly slightly higher to account for larger brain)

synthesis (reduced, assumably, gluconeogenesis)

encephalization (enhanced)

In other words, spiders start with enhanced or more refined diets and accordingly reduce their digestion as well as their synthesis while taking the available nutrition and enhancing mostly their locomotion and intelligence--which, in turn, helps them to find their more refined diets--all more or less, the reverse of howlers, even though both are close to each other on the evolutionary tree, inhabit the same environment and even weigh about the same. They both inhabit the same ecosystem but nonetheless inhabit different ecosystems within that nich, with some crossover, and take different evolutionary paths that help them survive and make them both magnificent in their own way.

SPIDER MONKEYS VS OTHER PRIMATES

Notes from Milton

It's curious to note that these same patterns also apply to two other primates, close to each other in evolution, the gorillas and chimps, with the gorillas being more like the howlers in their evolutionary development and the chimps more like the spiders.

If I was correct that the pressure to obtain relatively difficult-to-find, high-quality plant foods encourages the development of mental complexity (which is paid for by greater foraging efficiency), I would expect to find similar differences in brain size in other primates. That is, monkeys and apes who concentrated on ripe fruits would have larger brains than those of their leaf-eating counterparts of equal body size. To pursue this idea, I turned to estimates of comparative brain sizes published by Harry J. Jerison of the University of California, Los Angeles. To my excitement, I found that those primate species that eat higher-quality, more widely dispersed foods generally have a larger brain than do their similar-sized counterparts that feed on lower-quality, more uniformly distributed resources.

I gained my first insights into the evolutionary consequences of selective feeding in primates in the mid-1970s, when I noticed that howler monkeys and black-handed spider monkeys (*Ateles geoffroyi*)--two New World primate species--favored markedly different diets. Howler and spider monkeys, which diverged from a common ancestor, are alike in that they are about the same size, have a simple, sacculated stomach, are totally arboreal and eat an almost exclusively

plant-based diet, consisting for the most part of fruits and leaves. But my fieldwork showed that the foundation of the howler diet in the Barro Colorado forest was immature leaves, whereas the foundation of the spider monkey diet was ripe fruits.

Most of the year howlers divided their daily feeding time about equally between new leaves and fruits. But during seasonal low points in overall fruit availability, they ate virtually nothing but leaves. In contrast, spider monkeys consumed ripe fruits most of the year, eating only small amounts of leaves. When fruits became scarce, spider monkeys did not simply fill up on leaves as the howlers did. Their leaf intake did increase, but they nonetheless managed to include considerable quantities of fruit in the diet. They succeeded by carefully seeking out all fruit sources in the forest; they even resorted to consuming palm nuts that had not yet ripened. These observations raised a number of questions. I wanted to know how howlers obtained enough energy during months when they lived exclusively on leaves. As already discussed, much of the energy in leaves is bound up in fiber that is inaccessible to the digestive enzymes of primates. Further, why did howlers eat considerable foliage even when they had abundant access to ripe fruits? By the same token, why did spider monkeys go out of their way to find fruit during periods of scarcity; what stopped them from simply switching to leaves, as howlers did? And how did spider monkeys meet daily protein needs with their fruit-rich diet? (Recall that fruits are a poor source of protein.)

Because howler and spider monkeys are much alike externally, I speculated that some internal feature of the two species--perhaps the structure of the gut or the efficiency of digestion--might be influencing these behaviors. And, indeed, studies in which I fed fruits and leaves to temporarily caged subjects revealed that howler monkeys digested food more slowly than did spider monkeys. Howlers began eliminating colored plastic markers embedded in foods an average of 20 hours after eating. In contrast, spider monkeys began eliminating these harmless markers after only four hours. Examining the size of the digestive tract in the two species then revealed how these different passage rates were attained. In howler monkeys the colon was considerably wider and longer than in spider monkeys, which meant food had a longer distance to travel and that significantly more bulk could be retained.

Collectively, these results implied that howlers could survive on leaves because they were more adept at fermenting fiber in the cecum and colon. They processed food slowly, which gave bacteria in the capacious hindgut a chance to produce volatile fatty acids in quantity. Experiments I later carried out with Richard H. McBee, then at Montana State University, confirmed that howlers may obtain as much as 31 percent of their required daily energy from volatile fatty acids produced during fermentation.

In contrast, spider monkeys, by passing food more quickly through their shorter, narrower colons, were less efficient at extracting energy from the fiber in their diet. This speed, however, enabled them to move masses of food through the gastrointestinal tract each day. By choosing fruits, which are highly digestible and rich in energy, they attained all the calories they needed and some of the protein. They then supplemented their basic fruit-pulp diet with a few very

select young leaves that supplied the rest of the protein they required, without an excess of fiber.

Hence, howler monkeys never devote themselves exclusively to fruit, in part because their slow passage rates would probably prevent them from processing all the fruit they would need to meet their daily energy requirement. And the amount of fruit they could consume certainly would not provide enough protein. Conversely, spider monkeys must eat fruit because their digestive tract is ill equipped to provide great amounts of energy from fermenting leaves; efficient fermentation requires that plant matter be held in the gut for some time.

SPIDER MONKEYS VS HUMANS

We have concentrated on these evolutionary dynamics because they also apply to ourselves; in our own path, we obviously selected along the lines of the Spider--not the Howlers. We will also see that the Chimps selected the same as the Spiders; and the Gorillas more towards the Howlers.

But then we, specifically, took the concept to the extreme. As we evolved from our common ancestor, we started to slowly consume even more refined foods than our ancestors that eventually, and over the course of millions of years, resulted in smaller guts, about the same senses as other primates, enhanced and different locomotion, enhanced capture, reduced digestion, reduced synthesis, enhanced basal metabolism, and greatly enhanced encephalization--which in turn allows us to acquire and process our more refined diet.

In the end we have the most refined diet on earth: it's generally not only free of toxins and easy to digest; it also contains, when optimized, the greatest balance of total nutrition for both catabolism and anabolism. We also have the greatest encephalization, the largest territories of any species on earth.