Howler Monkey Foodways

Overview

The howlers are new-world monkeys, meaning they inhabit the jungles of Central and South America. Weighing about twenty pounds or so, they are diurnal so they feed during the day and sleep at night. They are technically folivores, eating about forty to eighty percent leaves--the only folivorous, new world monkeys (thus explaining why new world monkeys are smarter than old world monkeys). So that leaves are their primary food; but as we have seen, they do not just eat any leaves but like other folivores are selective, preferring leaves that are young and tender and presumably less toxic; in other words, they are selective folivores. Although mostly folivores, though, they actually prefer fruit but within the given constraints of their ecosystem and evolutionary design, fruit is not as available to them as other monkeys. When fruit is easily available it is preferred, but when fruit becomes harder to find, they tend to stick with leaves but, due to the scarcity of and competition for fruit in their ecosystem. Also, howler species that live in rainforests with low variation in rainfall eat the highest amount of fruit. In contrast, howler monkeys living in rainforests with high variation in rainfall eat the smallest amount of fruit. Also. too, the larger their terrain, the more fruit they consume--showing again that relationship between larger territory and more fruit--even amongst this folivore. They also eat buds, eggs, insects, honey, termites several times per week. So overall they are omnivores that specialize on leaves.

DIET

Flowers, buds, eggs and termites several times per week If do (Dias and Rangel-Negrin 2015) Howler monkeys are technically folivores. They are the only folivores of the New World monkeys. They do occasionally eat eggs from birds' nests or chicken coops, as well as honey, insects, etc. Also, howler species that live in rainforests with low variation in rainfall eat the highest amount of fruit. In contrast, howler monkeys living in rainforests with high variation in rainfall eat the smallest amount of fruit. The same goes for leaves. They also prefer young leaves to mature leaves. Rainfall plays a significant role in the dietary variability of howlers. Additionally, forest size matters, with howlers living in larger forests eating more fruit. (Dias and Rangel-Negrin)

As we have seen most animals need supplemental forms of, at least sodium and possibly chloride and calcium as well, and accordingly, the howlers are known to use natural mineral licks just like ruminants (Blake 2010). They also practice geophagy--that is, they eat clay or mud likely for the purpose of attaining minerals or deactivating plant toxins (Dias and Rangel-Negrin 2015, Blake 2010). Naturally, we have not discussed geophagy, but as we will see, it's regularly practiced by animals, especially primates, including humans and this human in particular (Blake 2010, Krishnamani 2000).

Overall, howlers were found to use at least 1,165 plant species, belonging to 479 genera and 111 families as food sources. Similarity in the use of plant taxa as food sources (assessed with

the Jaccard index) is higher within than between howler species, although variation in similarity is higher within species.

Rainfall patterns, group size, and forest size affect several dimensions of the dietary habits of howlers, such that, for instance, the degree of frugivory increases with increased rainfall and habitat size, but decreases with increasing group size in groups that live in more productive habitats. Moreover, the range of variation in dietary habits correlates positively with variation in rainfall, suggesting that some howler species are habitat generalists and have more variable diets, whereas others are habitat specialists and tend to concentrate their diets on certain plant parts. Our results highlight the high degree of dietary flexibility demonstrated by the genus Alouatta.

Source: Kinzey, Warren G. The Evolution of human behavior: primate models. Albany: State University of New York Press, 1987. Print.

Over fifty percent eat leaves, 30 percent fruits, eat over one hundred plants figs most preferred, focus on one or two food sources in the day, then supplement with others, dependent on availability: one time span ripe fruit, another tender leaves

wet seasons more active, dry less

"Abstract: The feeding behavior and general activity patterns of a howler monkey troop living in a 3.6 ha forest fragment were studied at Los Tuxtlas, Mexico, for an annual cycle. Monthly samples of their feeding behavior indicated that they used 52 species of 24 plant families as sources of food. Of these, 67% were trees, which accounted for 96% of total feeding time recorded. Ten species of Moraceae, Cecropiaceae, Anacrdiaceae. and Sapotaceae contributed to 70% of the trees used and to almost 90% of feeding time. The number of plant species used per monthly record varied from 7 to 31 with an average of 19.9 species. Young leaves and ripe fruit were the principal items in the monthly diet of howlers and average percent of time spent consuming these plant parts was 46.7% and 34.8%, respectively. The use of tree species was found to be associated to their importance value and to their pattern of spatial dispersal in the study site. Availability of young leaves was fairly constant from month to month, but it presented a seasonal pattern, and there was a significantly lower number of tree species bearing ripe fruit through the year with brief pulses of production. The monthly activity pattern was found to be related to variations in the availability of young leaves and ripe fruit as well as to the values of the intermonthly overlap in plant species used. Resting and feeding presented a bimodal pattern of occurrence throughout the day that seemed to be related to variations in maximum ambient temperatures. Results are discussed in light of the small size and shape of the forest fragment inhabited by the howler troop.

Howlers respond to the increase in population densities by increasing the (1) diversity of food species in the diet; (2) consumption of non-tree growth forms; and (3) consumption of new plant items. Home range size is also predicted by population density, but fragment size is a better predictor, probably owing to the fact that howler groups can overlap their home ranges. Our

results emphasize the importance of conserving the larger fragments and increasing the size of small and medium-sized ones."

-live 15 to 20 years, sleep fifteen hours per day

Source: Estrada, A et al. "Feeding and general activity patterns of a howler monkey (Alouatta palliata) troop living in a forest fragment at Los Tuxtlas, Mexico." American journal of primatology vol. 48,3 (1999): 167-83.

doi:10.1002/(SICI)1098-2345(1999)48:3<167::AID-AJP1>3.0.CO;2-6

SENSING

Overall, howlers follow the same patterns in sensing as found in other primates: less powerful sense of smell and hearing, and more powerful sight and taste. They have never been observed smelling their food--and thus we might conclude that they do not use their smell to find or identify their food but rather to smell and identify members of their group: they can discern differences in smells between males and females and differing states of reproduction. Howlers likely hear about as well as other primates, including humans; since they eat almost exclusively plants, they do not use their hearing to find their food, but rather to communicate with members of their same group.

All howlers possess trichromatic vision. Oddly enough, other New World monkeys are mostly dischromatics with only some females in some species being trichromats--this despite the fact that these monkeys are frugivores--and thus, you might conclude that they need to see a greater range of colors to identify their fruit. Meanwhile, howlers are trichromats--even though they eat leaves. In other words, new world monkeys broke the pattern in vision for reasons that are not really known. Side Notes: Howlers are thought to have evolved trichromatic vision independently of catarrhines (Old World monkeys and apes). Thus, the genetic changes leading to trichromatic vision occurred at least twice during primate evolution -- at the base of the catarrhines, before species in this primate subdivision diverged, and again, later on in an ancient ancestor of the howler. Among the other platyrrhines (New World monkeys), all males and ~33% of females have dichromatic vision, and only 66% of females have trichromatic vision. There is debate as to whether dichromatic vision has certain advantages that have prevented it from being entirely displaced by trichromacy in the evolution of primates. Dichromacy may be better for seeing movement, shapes and forms, and for spotting camouflaged predators and prey since there is less color to distract. (Matsushita 2014).

To confuse matters more, some howlers, even though trichromats, also possess the equivalency of color blindness--so they do not see all the range of colors that we see. Also, as compared to other new world monkeys, howlers see with greater acuity, the result of having twice as many "cones" in their eyes. Overall, primatologists have speculated that howlers see better than their peers because of their need to target specific young and tender leaves, amidst an abundance of green leaves in general--also to reduce locomotion, so energetic trade off....young leaves are different texturally and chromatically than other leaves

HEARING

Based on their ear anatomy, howlers are expected to have hearing capabilities that are typical of a New World primate. This text claims that the hearing sensitivities of New World primates are broadly similar to those of Old World primates, and that the howls of howlers could be heard as well by a human as they could be by a howler. (Hernandez Salazar 2014)

We do not have complete research on their senses overall; but we do know that like most primates they have trichromatic vision (see note below), with the ability to see greater colors which, in turn, helps them identify specific fruits, as well as specific sorts of leaves, in their ecosystem (Hernandez Salazar 2014). However, it does appear that compared to other primates, they may have maintained more of their sense of smell--which is usually lost when primates start to see better--if only to help them better identify the pheremones of other howlers.

Source: Webb, D. M. (2004). Genetic Evidence for the Coexistence of Pheromone Perception and Full Trichromatic Vision in Howler Monkeys. Molecular Biology and Evolution, 21(4), 697–704. https://doi.org/10.1093/molbev/msh068

<u>VISION</u>

They have particularly high visual acuity in comparison to other primates. It is suggested that "a diet dependent on "young leaves, which differ texturally and chromatically from mature leaves, was the primary factor favoring the independent evolution of high-acuity routine trichromatic vision in primates" (Hernandez Salazar 2014). They are different from other New World monkeys with regard to trichromacy. Apparently, in other species of New World monkeys, some females are trichromats and some dichromats, while males are dichromats. Howlers are the only new world monkeys that are almost always trichromatic, which is due to having the presence of particular opsin genes (L and M) on the same X chromosome. In other New World monkeys, this isn't the case, which is why males are dichromats, because they only have one X chromosome, and hence only inherit one of the opsin genes. Females are di- or trichromats depending on whether they inherit two of the same opsin genes (dichromats) or two different opsin genes (trichromats) from their mother and father (Matsushita et al. 2014).

Howlers are commonly noted as being the exception among New World monkeys in having trichromatic vision as is found in the Old World monkeys, apes and humans. They are thought to use their trichromatic vision to detect young leaves tinged with red pigments. However, a recent study published in 2014 that analyzed the opsin genes (that code for the light sensitive protein pigments in the eyes) of wild howler monkeys revealed that some howlers have hybrids of the opsin genes, resulting in what is known as "anomalous trichromatic vision". In humans, this is considered to be a form of color blindness (i.e. color vision deficiency), suggesting that

some howler monkeys may not be able to see the full spectrum of colors as a normal trichromat. Still, howlers are thought to have better color vision than dichromats, and some have normal trichromatic vision. Note that among nonhuman Old World monkeys, not even mildly "anomalous trichromats" have been found, suggesting that there may be greater selective pressure against color vision deficiency among the Old World monkeys as compared to howlers. (Hernandez Salazar 2014 and Matsushita 2014).

Howlers are also unique in having a remarkably high density of cone photoreceptors in the fovea of the retina, giving them especially high visual acuity for seeing fine detail. The average value of cone densities reported among the howlers was more than twice the peak cone density observed in any other New or Old World monkey, again suggesting that among primates, howlers may be exceptionally good at seeing fine detail. (Hernandez Salazar 2014)

Side Notes: Howlers are thought to have evolved trichromatic vision independently of catarrhines (Old World monkeys and apes). Thus, the genetic changes leading to trichromatic vision occurred at least twice during primate evolution -- at the base of the catarrhines, before species in this primate subdivision diverged, and again, later on in an ancient ancestor of the howler. Among the other platyrrhines (New World monkeys), all males and ~33% of females have dichromatic vision, and only 66% of females have trichromatic vision. There is debate as to whether dichromatic vision has certain advantages that have prevented it from being entirely displaced by trichromacy in the evolution of primates. Dichromacy may be better for seeing movement, shapes and forms, and for spotting camouflaged predators and prey since there is less color to distract. (Matsushita 2014).

<u>SMELL</u>

Researchers never observed howlers sniffing food and say this suggested that their olfactory senses are likely more important for social communication, particularly with regard to reproduction. This makes sense considering the role of the vomeronasal organ in detecting pheromones, as you mention above. Additionally, there are no physiological studies on olfactory sensitivity in howlers; however, behavioral observations suggest they can discriminate between odors, between male and female odors, and between different reproductive states (Baltisberger 2003 and Hernandez Salazar 2014).

The howlers' olfactory anatomy is considered typical for a New World primate. They also have a well-developed vomeronasal organ that is typical among New World primates, and is usually used to sense pheromones, although no research has confirmed that howlers use this organ for this purpose.

So far, scientists have not observed the use of smell in food selection among howlers. Smell may play a more important role in social communication and reproduction among howlers than it does in food selection. (Baltisberger 2003)

No studies have been done to determine howler's olfactory sensitivity to stimuli nor their ability to detect and discriminate certain smells. Thus, nothing is really known yet about the howler's sense of smell. (Hernandez Salazar 2014)

LOCOMOTION

Howlers follow the usual pattern in locomotion and terrain as other primates. They are the largest primates in the new world, as well as folivorous--that is, being folivorous and heavier, they inhabit smaller terrains and then move hardly at all within those terrains. For about fifteen to twenty animals, they inhabit about 77 acres--which is tiny, way less than one square mile. And within those territories, they move only about one quarter mile per day--evidently preserving their energy due to their rougher diet.

Otherwise, they have five toes on their feet, as well as prehensile tails and move mostly by walking both of their fore and hind legs. When descending down trees, they use their tails to support their weight but otherwise avoid leaping, unlike smaller primates: because of their heavier weight, trees will not support them as much and the consequences of fall are much greater for larger primates as compared to smaller primates.

-stockier, preserve heat better, but lower metabolisms

Random fact: Red howlers communally defecate- typically a whole group simultaneously defecates from the same tree or group of trees- in the morning after waking up and at midday after resting (Braza 1981- wisc.edu).

Black howler monkeys in particular are the largest monkeys in Latin American rainforests. Important to note- They have a prehensile tail. It has no hair on the bottom side, so they can use the tail to grasp during locomotion. They also have five-toed feet for grasping. Also, they have such a large Adam's apple that it restricts their arm movement, so they rely heavily on their tail for locomotion. According to the Smithsonian, their total home size is about 77 acres for 15-20 animals. Interestingly, they only move about 1,300 feet per day-that's less than one-quarter of a mile-interesting factoid! (https://nationalzoo.si.edu/animals/black-howler-monkey). They also have one unique form of locomotion- their vertical descent- where they face the ground and walk quadrupedally down a support with their tail helping to control the descent (Youlatos & Gase 1994- http://pin.primate.wisc.edu/factsheets/entry/red_howler). Their most important form of locomotion is clambering, then quadrupedal walking and running. They rarely leap and, when they do cross gaps in the trees, they always maintain contact with support with at least one extremity or the tail (Youlatos 1993 & Youlatos & Gase 2001-wisc.edu).

CAPTURE

young and tender leaves, fewer toxins

To overcome plant def, the howlers eat many different types of leaves and fruits, following one of the usual patterns.

DIGESTION

Howlers follow the usual patterns in the anatomy and function and timing of their digestion--that is, as folivores, they have relatively larger digestive systems with enormous colons and accordingly pass their food slowly--in fact, slower than just about any other animal. While some few folivers, like the colobus and proboscis monkeys, have fermenting forestomachs, most do not, including the howler. Instead they have the usual configuration with the acidic stomach, the small intestine, and the colon (Milton 1998). with the size of these various chambers designed more specifically to their diet. Their digestive systems are larger compared to the rest of their bodies but they have relatively smaller stomachs and shorter long intestines but enormous colons for fermenting the fiber from so many leaves. (Milton 1998). Since their food contains lower amounts of sugars and fatty acids and even perhaps amino acids, they do not need that much surface area for absorption. But, because they eat so much fiber, they have relatively enormous colons and because their microflora needs longer to ferment the fiber, to create the nutrients therein, they typically pass their food from mouth to excretion in about twenty hours, longer than other primates (Crissey 1990). Overall, they get about thirty percent of their overall "total nutrition" from the fermentation of fiber, which creates the three organic acids for their metabolism Milton 1983). All in all, with the larger colon that holds considerable amounts of plant fiber and water for longer periods of time, they have thus heavier digestive systems as you would expect from rougher diets (Milton 1983 and 1998).

When considering effects of fiber on digestibility, they only absorb about 77% of protein from fruit and 89% from leaves. Additionally, it's suggested that the fermentation end products are likely particularly important to the howlers for survival when foods rich in readily available energy are in short supply (Milton 1980). Milton specifically says that 'finding an efficient solution to the high percentage of indigestible material present in most plant parts- fruits as well as leaves-appears to be the single greatest dietary problem in terms of food composition that anthropoids have had to resolve in their evolutionary history" (Milton 1998, p. 518).

METABOLISM

Although we do not have specific studies on the metabolism of howlers, we can hypothesize that they have the same or similar metabolism as other folivorous primates, as well as any mammal that eats rougher diet. For heart and muscle catabolism, they use the short chain fatty acids from colonic fermentation of leaves and other plants, accounting for about thirty percent or way more of their overall "calories." Additionally, they use any fatty acids directly in their food--but these amounts would be low to negligible, meaning most of those fatty acids were probably anabolized for cell membranes. (accounts for limited movements.) Overall, they in other words do not create much fuel for muscle anabolism--thus describing their small territories and even shorter range of movement over the course of one day.

For brain, nervous, kidney and skin catabolism, they use any glucose/fructose found in the fruits they consume or other plants. But more than anything, they use one of the short chain fatty acids from colonic fermentation, propionic acid--and then convert that into glucose in their liver. Again, since they receive limited glucose in their diet, they have as we shall see small brains--twice as small as our next monkey, the spider.

For protein anabolism, they use amino acids in leaves: though leaves are low in amino acids, howlers nonetheless eat enough of them to cover their needs. As mentioned before, preliminary studies suggest that leaves contain amino acid profiles similar to "complete proteins," thus providing amino acids for muscles and many of the organs. However, howlers, too, using their taste may target other amino acids in plants similar to those in collagenous proteins to promote the growth of connective tissues, including skin, tendons, ligaments, guts, veins, valves and the like. If that is not the case, then they must synthesize an enormous amount of amino acids from one form into another--essentially converting complete proteins into collagenous proteins.

Additionally, they receive additional amino acids from termites and other insects--which would likely provide a mixture of amino acids that conform to both complete and collagenous proteins; in fact, they may not eat termites for the additional and total protein but rather specifically for collagenous proteins.

For fatty anabolism mostly for their cell membranes, they use the fatty acids found in the cell membranes of leaves. In this case, they synthesize shorter chain polyunsaturated into longer chain polyunsaturated, specifically for their brain cell membranes. At the same time, they eat insects, muscles, hearts, stomachs, brains, eyes and all--which in turn provides them with a greater range of fatty acids--thus limiting the amount of synthesis.

Through eating leaves and fruits, they receive more than enough of all electrolytes in this order: potassium, magnesium, calcium, phosphorus, sodium and chloride. From eating insects, they receive higher amounts of phosphorus and perhaps, too, sodium and chloride from the blood. Like other primates, they also target plants, rocks, clays, dirt or waters rich in sodium to compensate for the dearth of sodium found in plants.

As noted before, howlers like other primates, including humans, practice geophagy--that is, they eat various forms of earth, including dirt, clays and muddy waters. They do this primarily to help neutralize the enormous amount of toxins found in tree leaves: the negative charge of the clay binds to the positive charges of these toxins, preventing them from being absorbed and otherwise rendering them harmless. Accordingly, when eating more leaves during the dry season, they eat more clay; when eating more fruit, they eat less clay since fruit contains fewer toxins. They also eat "earth" for other reasons, as an "antacid" to adjust the ph of their gut: the negative charge of the clay raises the ph of their gut; also as an antimicrobial as the charge of the clay will damage bacteria as well as worms.

PUFA:SFA ratio is around 0.85, in comparison to human recommendation of 0.6-1.1. (Reiner 2014), and fat intake only accounts for about 17% of daily calories in the howler monkey (Milton 2000, p. 481). Overall, an 8-kg wild howler monkey consumes about 300 g of dry weight of plant foods/day. (Milton 2000).

Note: Other reasons for geophagy include: 1) As an antacid to adjust gut pH; 2) As an antidiarrheal; 3) To counteract the effect of parasites in the gut; and 4) At high altitudes-To provide extra iron. (Krishnamani 2000). In Howler monkeys, geophagy is primarily practiced to detoxify compounds and they practice geophagy more often during the dry season. Also, when they have high leaf consumption, they are likely to have high geophagy as well. Species, like howlers, that eat a lot of plant material are more likely to practice geophagy (Blake 2010). (The review by Dias and Rangel-Negrin is an entire chapter on howler monkey diets) It's also suggested that the insects that infest the fruits they eat also contribute substantially to mineral intake. (Dias and Rangel-Negrin 2015)

FOOD SYNTHESIS AND STORAGE

As folivores who receive only some of the macronutrients in their diet, they theoretically practice lots of synthesis--that is, converting one nutrient into another. As already mentioned, they practice gluconeogenesis, especially whenever fruit is scarce, converting propionic acid into glucose and perhaps amino acids as well; they practice lipogenesis, converting shorter chain polyunsaturated into longer chain ones for cell membranes; and they likely convert more of the amino acids found in complete proteins into the ones found in collagenous proteins. And assumable convert beta carotene into vitamin a. Usual forms of storage of glucose, amino acids and body fat.

ENCEPHALIZATION

As compared to other primates, spiders are not encephalized: in fact the spiders, which are about their same size, are twice as encephalized than them and exhibit more observed intelligence. However, they use their intelligence to know their terrains (which are smaller) and know the identities and behaviours of their foods in their environment--even as they also eat fewer types of rougher foods that are easy to find. Despite their sociability, however, howlers are not all that encephalized; they have brains half the size of the spiders, even though they both weigh about the same (Milton-2006-Diet and primate evolution). At the same time they are not described by primatologists as comparatively smart (Milton-2006 p.89-90).

CULTURE

Howlers bond together to care for their young. Howlers are indeed social animals. Like most other primates, they care for their young for longer periods of time. Also, to protect against predators, to find food, call and communicate (not much information on this). Seems limited

There are quite a few kinds of sounds produced by the howlers. This includes loud grunts, roars, barks and of course, howls. The monkeys are most vocal at dawn and dusk. A troop's cries give information about their size and location. No food sharing, except between mother and child

COMMUNICATION

As you might imagine, they use their howl to define their territory, communicate with each other, and establish dominance.

Our findings suggest that loud calls in black howler monkeys are multifunctional, but most frequently occur in the defense of major feeding sites. These calls also may function in the defense of infants and mates during encounters with extragroup males.

Source: Van Belle, Sarie et al. "The function of loud calls in black howler monkeys (Alouatta pigra): food, mate, or infant defense?." American journal of primatology vol. 76,12 (2014): 1196-206. doi:10.1002/ajp.22304

SOCIAL STRUCTURE

They form into groups of about ten to twenty members who are not direct kin. Each group contains about three to four females per male.

Once reaching a certain age, both males and females leave their group of origin to join other, neighboring groups. In other words, howlers are neither patri or matrilocal--which means that neighboring groups share family members which may account for the reduced aggression between groups with conflicts and territory being defined merely by howling not conflicts. But once their young reach certain ages, both sexes actually leave their group of origin and join other groups, which is unusual, but may explain in part why howlers tend to be less territorial as their neighboring groups are full of their parents and children. Also, due to this, neither the males or females form particularly strong relationships based on kin with each other that allow them to dominate the group: one the one hand, howler females are more strongly bonded and stay in one group while males travel more between groups; but on the other hand, males are anywhere from forty to ten percent larger than the females, allowing for their dominance; and accordingly, the group is led by one, alpha male. The alpha also has more access to the females--and therefore propagates more of his genes into the future while at the same time having to fight more with other males to maintain his position.

Competition between Males

Breeding males will not leave a group voluntarily, they have to be forced out by challengers. Also, females are rarely able to integrate into established troops, so they have to form new troops, but males can join existing troops by challenging other males in the troop- They do this 2-on-1, with 2 non-troop males challenging 1 troop male- bullies!

(The males exhibit a high rate of infanticide, which raises infant mortality rates in the howlers. This is supposedly due sexual selection and the desire, by males, to shorten the interbirth interval of a given female. 44% of infant mortality in howlers likely due to infanticide)

TOOLS

They do not regularly use tools but one researcher has observed one Howler repeatedly beating one sloth over the head with a stick (Richard-Hansen 1998-wisc.edu) --but since this did not seem to serve any functional purpose, I am fairly certain that it was all just slapstick. At night, they all sleep in the same tree and during the day break into smaller groups to pursue their food.

All of the above, except when otherwise noted, from: "Primate Info Net." *WNPRC*, primate.wisc.edu/primate-info-net/.

SUMMARY

With Howlers, we can see our evolutionary pattern in action, so to speak. With their rougher diets, they have larger guts and especially colons needed to ferment enormous amounts of leaves. With their rougher diets, too, they have smaller territories since leaves are more condensed in space. With their smaller territories and larger guts, they have less efficient locomotion and cannot even cover larger distances if needed. (Note-It's not just their guts that affect locomotion. Their large Adam's apple also forces greater reliance on their prehensile tail.). With their rougher diet, which renders inferior nutrients, and larger guts, they have smaller brains as they are about half as encephalized as the spider monkeys. Perhaps they evolved their howl in part to compensate for this lack of locomotion and intelligence; as the howl, while probably not requiring much metabolism, nonetheless can project outward to help define territory and keep the group together and thwart predation, in rather crude ways, sort of like bullies with loud voices but little to show underneath. Additionally, perhaps since their diet creates such little energy, they tend to sleep more than other primates, both night and day. They typically eat more in bouts, one bout in the morning, when they prefer fruits, and another later in the afternoon, when they show preference for leaves. Relative to other primates, Howlers tend to spend more time at rest, so over fifty percent of their day is spent either sleeping at night or napping, which may be attributed to needing more time at rest to digest their rather rough, fibrous diet (and save energy).

Perhaps their most unique adaptation is: to compensate for reduced locomotion and encephalization, they developed superior eyesight, allowing them to see more of their food without moving or thinking; and they also developed the howl: instead of travelling to protect their territories or engaging in fights, they just scare the hell out of everyone. Assumably, both the howl (hyoid bones) and eyesight (limited neurons) require smaller amounts of metabolism to maintain, whereas active metabolism requires enormous amounts of energy.

To compensate for that lower nutrition, they reduced the metabolism of some tissues: basal metabolism, active metabolism...

In other words, they took another evolutionary path different from ourselves that ultimately leads towards reduced intelligence, sociability and locomotion--even though they are indeed perfectly adapted to their environment.

Sources: Gron KJ. 2007 November 26. Primate Factsheets: Red howler (Alouatta seniculus) Taxonomy, Morphology, & Ecology .

http://pin.primate.wisc.edu/factsheets/entry/red_howler/taxon.