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Sloth biology: an update on their physiological ecology, behavior and role as vectors of arthropods and arboviruses

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Abstract

This is a review of the research undertaken since 1971 on the behavior and physiological ecology of sloths. The animals exhibit numerous fascinating features. Sloth hair is extremely specialized for a wet tropical environment and contains symbiotic algae. Activity shows circadian and seasonal variation. Nutrients derived from the food, particularly in *Bradypus*, only barely match the requirements for energy expenditure. Sloths are hosts to a fascinating array of commensal and parasitic arthropods and are carriers of various arthropod-borne viruses. Sloths are known reservoirs of the flagellate protozoan which causes leishmaniasis in humans, and may also carry trypanosomes and the protozoan *Pneumocystis carinii*.

Key words
- Sloths
- Ecology
- Behavior
- Parasites
- *Bradypus*
- *Choloepus*

Introduction

We have recently reviewed the literature in terms of the physiological studies carried out on two- and three-toed sloths (1) since Goffart (2) published *Function and Form in the Sloth* 30 years ago. This paper is intended to update research undertaken since that time on other aspects of sloth biology. Topics covered include the general ecology, behavior, nutrition and digestion as well as the large range of arthropods associated with sloths and the number of viruses they transmit.

Of the two living species of *Megalonychidae*, *Choloepus hoffmanni* is found from the lowland forest to the higher altitudes of mountain forests south of Nicaragua through Central America and in Colombia, Venezuela, French Guiana, Ecuador, Peru, Brazil and Bolivia. The species is still common, but its numbers are fewer in areas where it coexists with the three-toed sloth. Its weight averages 5.72 ± 0.69 kg (3). The hair of this species is lighter than in *Choloepus didactylus*. The ears are rounded and thickened and almost always covered with hair. It has been reported (4) that the eyes can be partially retracted when the lids are tightly closed. This may make the sloth appear pop-eyed during periods of stress or prior to the onset of aggressive behavior when the lids appear to rise from their orbits. *Choloepus didactylus* is found from the delta of the Orinoco River west to the upper drainage of this river in Colombia, east through French Guiana and in Brazil to the State of Maranhão. Its weight is 6.07 ± 1.09 kg (3). It is less welladapted to the drier areas than is *Bradypus*. In 1992 its presence was recorded in the Yungas region of Bolivia, considerably further south than previously reported (5).

The distribution of the present day sloths was illustrated in the earlier review (1). *Bradypus torquatus* (the maned sloth) is regarded as an endangered species, its numbers having fallen catastrophically with the destruction of the Atlantic coast forest (Mata Atlântica) in southeastern Brazil. According to Wetzel (3), *Bradypus torquatus* is possibly the South American mammalian species closest to extinction. Remnant populations are thought to survive in the remaining fragments of the Mata Atlântica from Rio Grande do Norte to Bahia, Espírito Santo, and Rio de Janeiro.

Wetzel (3) reported that *Bradypus torquatus* appears to be smaller than *Choloepus*, with adults weighing about 4 kg, but Pinder (6) found the maned sloth to range from 4.05 to 6.20 kg in weight and from 520 to 672 mm in length. Infants were characterized by the absence of a mane. The widely distributed *Bradypus variegatus* has an average weight of 4.34 ± 0.85 kg, whereas the pale-throated three-toed sloth, *Bradypus tridactylus*, averages 4.01 ± 0.28 kg (3).

It is obvious that human activity is the major threat to the continued existence of sloths in particular localities. One of the few natural predators of the animals is the Harpy eagle (*Harpia harpyja*). Izor (7) gathered the skeletal remains of about 83 prey items from a Harpy eagle nest site in southwestern French Guiana and found that sloths (predominantly *Choloepus*) and cebid monkeys each constituted about one third of all the food prey. Beebe (8) found remnants of *Bradypus tridactylus* in the stomach of a large anaconda and in a margay cat. Izor discussed the reasons why sloths might constitute such a high proportion of the Harpy eagle's diet. The usual hunting time for this bird is around sunrise when ambient temperature is at its minimum. At this time too the activity of both two- and three-toed sloths is minimal and the animals, slowed by thermal stress, are high in the trees seeking early sunshine to warm themselves (9). The sloths are thus susceptible to aerial attack by the Harpy eagles which have enormously developed feet and talons. The formidable weapons enable the birds to strike and dislodge sloths from the canopy without losing flight speed.

General ecology and behavior

Neither *Bradypus* nor *Choloepus* are able to tolerate cool temperature latitudes. Nevertheless, both *Bradypus griseus* = *variegatus* and *Choloepus hoffmanni* have been recorded living at altitudes higher than 2400 m in the Braulio Carrillo National Park (Costa Rica) and a single specimen of *Choloepus hoffmanni* was collected in Costa Rica from the Turrialba Volcano at 3328 m where the annual rainfall is 2284 mm and the maximum annual temperature only 16.3^{o}C (10). At higher altitudes the coat of *Choloepus* is appreciably thicker than in individuals living at lower altitudes (11). *Bradypus* has a lower thermal conductance than *Choloepus* because only the former has a dense woolly undercoat below the coarse guard hairs, and *Bradypus* also has a lower limit of thermoneutrality (24^{o}C) than does *Choloepus* (18^{o}C). According to McNab (11), the cold temperature tolerance of some extinct ground sloths probably stemmed from their great size, larger muscle mass than their arboreal counterparts, thick fur and a constant food supply. This enabled them to extend their range into temperate regions of the Americas.

The hair of sloths is of special interest because of the presence of symbiotic algae in it at certain times. Sloths have two distinct coats, one made up of long coarse, but silky, hair which provides the distinctive color of the animal and the other made up of short fine and soft fur lying underneath. A detailed description of the pelage of both *Choloepus* and *Bradypus* was provided by Beebe (8) and updated by Goffart (2). The color pattern is especially variable in *Bradypus*, with some adult males possessing a "saddle mark" of black and white, yellow and black or bright orange. It has been reported (4) that in *Choloepus hoffmanni* the general coloration of the body hair may be almost blonde, buff, tan or light brown in adults. Shading of the hair from light to dark over the head and back is sometimes observed. The facial hair is characteristically lighter than that of the body and *Choloepus hoffmanni* lacks the dark shoulder and forearm markings seen in *Choloepus didactylus*. Interestingly, the abdominal hair is parted in the middle, flowing outwards. This allows for the efficient run-off of water from the abdomen of the animal which spends much of its life hanging upside down.

In *Bradypus* the long hairs are oval-shaped with broad and narrow sides and a width of 0.4 mm. The soft underfur is round and never more than 0.05 mm in diameter, being colorless, translucent and usually wavy. In the two-toed sloth the long hairs are quite different, having a maximum width of 0.16 mm and being nearly all fluted with a series of longitudinal ridges and furrows (3-9) running the length of each hair and attenuating near the tip. This longitudinal fluting appears to be unique amongst mammals. Wujek and Cocuzza (12), who examined the hair of sloths using scanning electron microscopy, found that the intricate cuticular scales in the two-toed sloth's hair are interrupted by grooves. Freeze-fractured sections indicated that the cuticle is not continuous around the shaft. In *Bradypus* the hairs are more complex and beneath the cuticle there are scattered fusi (shallow air pockets) which do not, however, extend entirely unbroken along the shaft. Wujek and Cocuzza believe that the morphological differences in the hair lend further support to the assignment of the two genera of living sloths to separate families.

During the dry season the hair of the sloths usually has a dirty brown coloration, but during long periods of rain it may show a very appreciable greenish tinge brought about by the increased presence of symbiotic algae. According to Britton (13), the algae may already be present in the hair of animals only a few weeks old and it has been suggested that they provide camouflage for the sloths, while obtaining shelter for themselves (see 14). The algae have distinct distribution patterns in *Choloepus* and *Bradypus*, lying longitudinally along the grooves in the former and in short lateral tongues or lines in the latter. Algae representing four phyla have been cultured (15) from *Bradypus*, these being Chlorophyta, Chrysophyta, Cyanophyta and Rhodophyta. It has also been confirmed that the algae found on the coat of *Bradypus tridactylus* lie between the cuticle scales (14) and that the hair changes with age in apparently all species of *Bradypus*. Young hairs are white, gray, brownish or black and do not possess the deep cracks seen in older hairs. The first traces of algae appear on these young hairs as tiny dots or extremely narrow transverse lines. Older hairs have larger, wider algal colonies and obvious deep transverse cracks. When wet these cracks close considerably, but when dry give the effects of beads on a string. The oldest hairs are badly deteriorated with the spongy cuticle worn off on one side exposing the full length of the cortex. In the older hairs living algae are absent. It was suggested (14) that either the algae colonize the very narrow cracks in young hairs or the algae themselves initiate the cracks. The hair of all three *Bradypus* species readily absorb water, but those of *Choloepus* do not. Aiello (14) was unsure as to whether in *Choloepus* the algae rested upon the surface of the spongy cuticle in the grooves or were embedded in it. They were, however, confined to the grooves. Aiello discussed the different possibilities as to why sloth hair has evolved in such a way to encourage algal colonization. She does not believe that camouflage or thermal insulation are the only or necessarily the more important reasons and suggested that the algae may provide nutrition or a particular trace element. Lack of healthy algal colonies could thus provide an explanation why *Bradypus* does not survive long in captivity.

Meritt (4) points out that mutual grooming of the hair in captive sloths is rare, and only seen between infant and mother. Self-grooming takes place in response to food left on the face, nose, or wedged on the roof of the mouth. In the latter instance food may be dislodged with a foreclaw, while that on the face and nose is removed with a claw or brushed off with a forelimb footpad. Animals were frequently seen to scratch the sides of the abdomen, lower neck and neck region adjacent to the chest. This type of grooming, lasting 1 to 6 min, usually took place at night in sloths that had been inactive for an extended period of time. When the sloth was in a resting position, its back supported the upper neck near the junction of the jaws and the external genitalia was the area most frequently scratched.

A large number of workers have extensively studied the flora and fauna on Barro Colorado Island in the Canal Zone of Panama where it appears that the three- and, to a lesser extent, the two-toed sloths are major items (23%) of the mammalian biomass of the tropical rainforest (16). It has also been estimated that on Barro Colorado Island the two-toed sloth has a larger home range than the three-toed animal and exists at roughly only 25% of its density (16). In 1973 Sunquist and Montgomery (17) examined the movement and activity patterns of 6 adult *Choloepus hoffmanni* and 15 adult *Bradypus variegatus* on Barro Colorado Island. The two-toed sloths were observed to be nocturnal and their activity patterns were similar to those reported for other terrestrial nocturnal herbivores. No crepuscular activity was recorded, but activity started from an hour after sunset. Activity levels then decreased as the night progressed to a nadir just after midnight. This was followed by a resurgence in activity about 2 h before dawn. Most activity had ceased by sunrise, but some animals were occasionally active until mid-morning. Howarth and Toole (18) also investigated the circadian rhythm of activity over nine days in a two-toed sloth (*Choloepus hoffmanni*) using a movement-sensitive cage. Although the animal was in captivity, it was housed under natural illumination. It was observed that the sloth began to move at about 19:30 h (shortly after sunset) with peak activity continuing for 2 to 3 h thereafter. Movement only ceased at approximately 5:30 h (sunrise). This nocturnal nature of activity in *Choloepus hoffmanni* was also reported by Meritt (4). In contrast, Sunquist and Montgomery (17) found that three-toed sloths (*Bradypus infuscatus* = *variegatus*) were active during both day and night. With the exception of a 7-h period centered approximately at dawn, average levels were about equal throughout the 24 h. Three-toed sloths averaged 10.1 total hours of activity/ day compared to 6-7 h in the two-toed species. Although many of the periods of activity were of short duration, the bulk of the time spent moving around was in bouts of continuous activity lasting two or more hours. It was also confirmed that three-toed sloths (*Bradypus variegatus*), at least when in captivity, were active throughout the afternoon, with the period of greatest activity between noon and 18:00 h, and the periods of deepest sleep between 6:00 h and noon (19). More recently, the movements of 6 adult male three-toed sloths (*Bradypus variegatus*) in captivity were recorded every 5 min over a 48-h period (20). The animals moved about significantly more when it was dark, particularly between 21:00 h and midnight, than at other times.

Working at the same location on Barro Colorado Island, Montgomery and Sunquist (9) studied habitat selection and its use by *Choloepus hoffmanni* and *Bradypus variegatus*. They found that home ranges were usually less than two hectares, and that three-toed sloths were less particular about the tree species which they used, being located on 40 of 91 trees that grew in two study areas. Individual three-toed sloths were found in the same tree on successive days 38% of the time, whereas in contrast two-toed sloths were seldom located on the same tree on successive days. Two-toed sloths were found in about 20% of the trees used by *Bradypus*. The latter, however, tended to choose trees more for the extent to which the crown was exposed to sunlight while *Choloepus* was most likely to be found in trees with masses of lianas in their crowns. It was discovered (9) that the tendency of three-toed sloths to use trees with open crowns was related in part to the vertical movements the animals made in the forest canopy into and out of direct sunlight according to their thermoregulatory needs.

In a recent paper, Chiarello (21) has reported some interesting information about patterns of activity in the maned sloth *Bradypus torquatus*. Three animals were studied using radiotelemetry over a 14-month period in the Santa Lucia Ecology Preserve (7 km from Santa Teresa) in the State of Espírito Santo. This area lies between 550 and 1000 m above sea level and the vegetation consists of subtropical moist lower mountain forest. Individual home ranges varied from 0.6 to 6 hectares and sloths were recorded to travel an average of only 24 m during any 24-h period. Most of this movement occurred during daylight indicating a predominantly diurnal rhythm of activity. The sloths started to move about and feed between 7:00 and 8:00 h, and rested or slept for only an average of 74% of the time during the day. The time spent active is about double that observed in other studies. Self-grooming also took place for short periods of time. Daytime activity was maximum around 10:00-11:00 h, although feeding remained relatively constant between 9:00 and 14:00 h. Chiarello suggested that the prevalent diurnal activity behavior of these maned sloths, and the comparatively long period spent moving about, were probably related to the lower ambient temperatures found in the Atlantic forest compared to other more equatorial regions where the animals have been studied. During the dry season (April to September) the sloths spent significantly less time resting and more time feeding than in the wet season (October to March), when day range lengths were reduced. Pinder (22) had previously observed that in the Poço das Antas Biological Reserve in Rio de Janeiro the activity of *Bradypus torquatus* was essentially nocturnal, with the sloths starting to move about after sunset and little action taking place during daylight hours. However, it is estimated that the temperature is around 10^{o}C warmer in the Rio de Janeiro location, which may account for this difference between the two populations.

Beebe (8) never observed more than one adult three-toed sloth in the same tree as another and Montgomery and Sunquist (23) reported it to be very rare for sloths of the same species to be on one tree together. However, an agonistic encounter between two three-toed sloths (*Bradypus variegatus*) was observed at La Selva Biological Station in Costa Rica (24). An adult male sloth was high in a *Cecropia* tree eating leaves, when another male ascended and struck the first from below with a forefoot. The animals then began to pummel each other with their forelegs while vocalizing frequently before disengaging, after which the intruder descended and left the vicinity. The whole incident lasted no longer than 3 min.

Nutrition and digestion

Goffart (2) described in detail the anatomy of the sloth digestive tract, summarizing studies carried out by earlier workers including Beebe (8) and Britton (13). More recently esophageal pressure profiles in *Bradypus variegatus* were investigated by Duarte et al.

(25). Three functionally distinct regions were found: a cranial one located at 7.3 ± 1.4 cm, a caudal one located at 27.0 ± 2.6 cm, and another between these two. The resting pressures of the cranial and caudal esophageal sphincters were 20.5 ± 6.8 and 12.8 ± 4.9 mmHg, respectively. The maximal pressure and its duration (mean ± SD) were 40.4 ± 12.4 mmHg and 2.8 ± 0.75 s (cranial) and 35.7 ± 11.5 mmHg and 4.3 ± 1.2 s (caudal), respectively. These findings for the three distinct regions were correlated with the results of a histological study (26).

Luis da Mota et al. (27) carried out a morphological and histochemical investigation of the intestinal tract in the three-toed sloth (*Bradypus tridactylus* = *variegatus*). The animals studied were two male and two female specimens captured in the forests outside Recife. It was found that the intestine averaged 198.5 cm in length and that it was almost totally uniform in diameter, although very dilated in the rectal region. The wall of the intestine was seen to consist of mucosa, submucosa, tunica muscularis and serosa. The mucosa itself could be subdivided into epithelium, a lamina propria (consisting of loose connective tissue containing collagenous and elastic fibers amongst which were fibroblasts, small lymphocytes, eosinophils and macrophages) and a thin layer of smooth muscle (the muscularis mucosae). The submucosa was also made up of loose connective tissue and the tunica muscularis of an inner circular and outer longitudinal layer of smooth muscle between which ganglion cells of Auerbach's plexus were present. The serosa was seen to consist of mesothelial cells resting on delicate fibrous connective tissue. The duodenum was recorded as averaging 9.5 cm in length with a thicker wall than the remainder of the intestine. On the luminal surface of its proximal third were five or six distinct longitudinal folds and in the medial third packed circular folds running in a sinuous fashion. The folds in the distal third were small and irregular. From the submucosa of these folds numerous leaf-shaped villi containing lamina propria, small blood vessels and smooth muscle cells projected into the intestinal lumen. The epithelium of these villi contained tall columnar cells with a striated border and also some goblet cells. In the duodenum the crypts of Lieberkühn were shallow and Brunner's glands were confined exclusively to the lamina propria and were more abundant in the proximal region. The muscularis mucosae was poorly developed and the submucosa was straight and consisted of relatively dense connective tissue containing large blood vessels.

The same authors (27) also reported that the jejunum possessed circular folds on its luminal surface and that these resembled those seen in the duodenum except that the villi were longer and narrower. The villi were lined with a simple columnar epithelium with a well-developed striated border; goblet cells were scattered throughout the epithelium. As in the duodenum the crypts of Lieberkühn were shallow, but sometimes branched. In the ileum there were alternate smooth areas, occasional branched folds and small sinuous rugae. The mucosa was lined with a simple columnar epithelium containing goblet cells. The villi in this region became shorter distally near the large intestine. The crypts of Lieberkühn contained more goblet cells at their base than in the jejunum.

In the sloth the large intestine has been seen to consist of a short colon and a dilated rectal pouch; no cecum exists. On the inner surface of the colon alternate smooth areas and longitudinal folds are present (27). No villi are apparent and the surface epithelium is again composed of columnar cells with a striated border, but these are less prominent than in the small intestine. More goblet cells are present than in the jejunum and ileum. The luminal diameter of the rectal pouch is very large in comparison to the rest of the intestine and the markedly thickened walls possess several well-developed folds of varying size running in a sinuous manner. The mucosa is similar to that seen in the colon, but the muscularis mucosae is very well developed. The tunica muscularis, containing many elastic fibers, is also thicker in the rectal pouch than in any other part of the intestine. Some further details regarding the histology of the rectum in *Bradypus variegatus* were supplied by Padovan et al. (28), who also emphasized that water absorption mainly occurs in this region of the digestive tract.

It has been observed (27) that the longitudinal and circular folds seen in the intestine of the three-toed sloth have the same histological structure as those seen in most other mammals. Argyrophilic and argentaffin cells are found throughout the entire length of the sloth intestine, but Paneth cells are absent. It was suggested (27) that the absence of a cecum is probably compensated for by the enzyme activity that takes place in the large sacculated stomach and that the slow absorption of nutrients may be assisted by the numerous villi present in the small intestine.

Concentrations (ng/g wet weight of tissue) of 4 neuropeptides have been measured (29) in the colon of *Choloepus didactylus* and found to be as follows: VIP, 275 ± 26; PHI, 225 ± 18; substance P, 97 ± 17, and met-enkephalin, 128 ± 32. Mechanical and intracellular electrical activity has also been recorded (29) in the smooth muscle of the colon. Spontaneous mechanical activity was found to consist of 5 to 6 individual phasic contractions during each 4-min period. The resting membrane potential averaged 58 ± 4 mV and the amplitude of the inhibitory junction potential ranged from 1-3 mV with no accompanying circular muscle relaxation. It was suggested (29) that the absence of a prominent inhibitory innervation may be associated with low concentrations of VIP and PHI and might account for the sloth's *in vivo* pattern of colonic motility.

As pointed out by Goffart (2), the different species of *Bradypus* live principally on the leaves, flowers, shoots and fruit of the ymbahuba (embauba) tree (*Cecropia* sp). It was once believed that these were the primary if not only source of food for these animals, but Montgomery and Sunquist (23), who studied *Bradypus variegatus*, found that the animals ate the leaves of not less than 28 different trees and 3 vines. It was observed that the choice of leaves eaten by an individual sloth was influenced by those eaten by its mother during the 6-month period when it was carried by her. Leaves eaten from other trees included those from the various species of *Ficus*, the wild plum (*Spondus lutea*), *Protium panamense*, *Poulsenia armata*, *Eriobotyra japonica*, *Luhea* and *Bombax longiflorum*. In the Santa Lucia Ecology Preserve (Espírito Santo) Chiarello (30) reported that 99% of the diet of *Bradypus torquatus* was composed of leaves. These were predominantly young ones and especially so during the wet season when they were more abundant. Chiarello listed all the plants consumed and also reported the percentage of time spent feeding on each. The most important species making up the diet were *Prunus* sp, *Ficus* sp, *Micropholus venulosa*, and the vine *Mandevilla* sp. Flowers and fruit of *Mandevilla* sp and *Cecropia hololeuca* were consumed. The diet of these maned sloths, as in other species, was highly selective as less than 4% of the 476 trees recorded as present were utilized as food. Moreover, the species mostly chosen were not those present at highest density.

In captivity, citrus fruits, lettuce and bananas are accepted by three-toed sloths, although it is very difficult to maintain the animals alive for long periods of time. It has been argued (23) that three-toed sloths may starve to death on a full stomach if the wrong selection of food is made, due to the slow digestion of leaves. The same workers also estimated that sloths on Barro Colorado Island cropped only 0.63% of the total annual leaf production of the forest, much less than the 7% attributed to insects. Manganese is an element naturally occurring in the leaves eaten by three-toed sloths, but is not assimilated. Nagy and Montgomery (31), by measuring the increase in concentration of manganese between the food ingested and the feces produced, estimated that three-toed sloths (*Bradypus variegatus*) on Barro Colorado Island in the Panama Canal Zone consumed 15 g dry food (kg/day) during the dry season. This is higher than the earlier estimate of 6.9 g kg^{-1} day^{-1} (32) calculated from measurements of oxygen consumption and the time budgets of free-living animals. It is also appreciably more than that of 5.1 g kg^{-1} day^{-1} calculated (23) from measurements of feces production rates in the field with an assumed assimilation efficiency of 50%.

Choloepus is much easier to maintain in captivity outside its normal habitat than *Bradypus*, and survives indefinitely on *Cecropia*, bananas, oranges, figs and even meat and fish. Colonies of *Choloepus hoffmanni* and *Choloepus didactylus* were kept healthy in Chicago on a wide variety of food including diced apples, oranges, bananas, lettuce, spinach, bread, sweet potatoes, green beans, peas, canned salmon, freshly ground smelt and ground meat sprinkled with a powder containing vitamins and minerals (4,33). Meritt (4) observed that daily food consumption by individual adult two-toed sloths (*Choloepus hoffmanni*) averaged 350 g/day, i.e., 85 g/kg body weight. This was during a period of acclimation after capture. In fully acclimated sloths food intake averaged 250 g/day, dropping off a little just before the periodic defecation, when 30% of the body weight could be lost. This is not surprising, as it has also been recently found (34) that the proportion of body mass contained in the gut ranges from 17 to 37%, values similar to those reported in earlier studies. It was noted (33) that in captivity the period between evacuations varied from 3 to 8 days and that the feces were always deposited in the same spot. In confined two-toed sloths, the longest period between eliminations was observed to be 6 days (4). In free-living *Bradypus variegatus*, about 56 g (dry weight) of feces was seen to be deposited every 8 days in a shallow depression punched out by the sloth with its tail on the forest floor within 3 m of a tree used by the animal (9). It was also reported (23) that two-toed sloths, which lack a proper tail, usually left their feces on the soil or litter surface. In the two-toed sloth the feces were found to be firm and were passed as single pellets or as a large compacted mass of compressed individual pellets (33). It was also observed (9) in three-toed sloths fitted with gastric fistulae that young leaves were digested more rapidly and that the oldest leaves which were digested fastest were those from trees that were ranked highest in use by some sloths. The rates at which leaves were digested were much slower than those reported for other herbivorous mammals and the rate of passage of food was the slowest recorded for any mammal. Around two and a half days were required for the passage of 5% of glass beads 3 mm in diameter fed to the animals, and 50 days before 95% of them were passed. Foley et al. (34) believe that these results are questionable, because the beads probably accumulate and are retained in the pre-pyloric region of the stomach. Foley et al. (34) examined digestion near Cayenne, French Guiana, in 6 captive specimens of *Bradypus tridactylus* fed exclusively on *Cecropia palmata*. Digestive passage was measured by use of various markers dosed in liquid form. The particulate digestive phase was marked with three rare earth elements administered in solution and the solute digestive phase with three complexes of ethylenediaminetetraacetic acid. After the animals were killed at pre-determined intervals following feeding, ranging from 6 to 288 h, samples were collected from 10 regions of the gut. By analysis of the marker content in the different parts of the digestive tract it was possible to construct cumulative excretion curves. These indicated that the mean retention time of the particulate and solid digestive markers was around 150 h. Seventy-three per cent of this retention was in the stomach and 17% (because of storage of feces) in the rectum. From these observations it was argued (34) that there is now little support remaining for the earlier view (13) that a diverticulum acts to prolong the retention of food. Foley et al. (34) observed that the proportion of short-chain fatty acids present in the stomach was broadly similar to that present in other foregut fermenters eating fibrous diets, but the rate of fermentation measured *in vitro* was very slow in comparison to the latter animals. It was therefore postulated (34) that the slow fermentation rate is most likely due to the lignified nature of the *Cecropia* foliage the animals were fed, but perhaps also to the low body temperature of sloths. The same investigators further argued that although digestion in sloths is characterized by both slow rates of passage and fermentation of a large volume of digesta in the forestomach yielding energy only gradually, this is feasible because of the sloths' low energy expenditure.

McNab (35) examined the energetics of a large variety of arboreal leaf eaters and confirmed that the xenarthrans have low basal rates varying from 40 to 60% of the expected values. Earlier the same author (35) had found that the basal metabolic rate for *Choloepus* was only 45% and that of *Bradypus* only 42% of the values expected from their respective body weights. He suggested the following explanations as to why these low basal metabolic rates may exist: a) In arboreal mammals muscle mass makes up only a relatively small proportion of the body which therefore has a larger proportion of tissue with low metabolic rate. b) Leaves have only a low available caloric density. Since the maximal daily bulk that can be processed is limited, the energy available from this diet is low. c) A number of toxic substances including alkaloids, phenols and terpenes are present in leaves. As mentioned earlier, the low basal metabolic rate in leaf-eating mammals may reduce the absorption of these substances.

The mean energy expenditure for *Bradypus* has been estimated to be 95.5 kcal/day (32). This does not agree with another study (23) reporting that the daily intake of food provided energy of only about 54.4 kcal. McNab (32) suggested that the difference between these estimates of energy expenditure and the energy provided by the food eaten may reflect higher rates of decay in the feces than assumed by other workers (9).

Arthropods associated with sloths

Sloths act as hosts to a wide variety of arthropods, which include biting and blood-sucking flies such as mosquitoes and sand-flies, triatomine bugs, lice, ticks and mites. However, there is a noticeable absence of fleas and anoplurans associated with the animals, although the flea *Polygenis atopus*, which feeds primarily on rodents and marsupials, has been recorded from *Bradypus infuscatus* = *variegatus* in Venezuela (36). Sloths also carry a highly specific community of commensal beetles, mites and moths. Waage and Best (37) investigated in detail a number of the different arthropods associated with *Bradypus tridactylus*, *Bradypus variegatus* and *Choloepus didactylus* in the vicinity of Manaus, while Wolda (38) carried out a comprehensive study of the seasonal distribution of sloth moths in Panama.

Up to 6 species of ticks of the genus *Ambylomma* have been recorded from both two- and three-toed sloths in Central and South America, but the opinion is (37) that only *Ambylomma geayi* and *Ambylomma varium* are truly specialized for living on sloths as these ticks are rarely found on other hosts. The other four ambylommid ticks apparently only occur on sloths accidentally. It was also observed (37) that adult males of *Ambylomma geayi* may remain on their hosts for more than three weeks, but the females leave after engorging to oviposit. Infestation with ticks can be extremely high. At the Instituto Nacional de Pesquisas da Amazonia in Manaus, Waage and Best (37) recorded that 99% of three-toed and 86.7% of two-toed sloths carried *Amblyomma* spp. There was no apparent correlation between the numbers of ticks at any life stage per sloth and the seasonal difference in rainfall in Manaus and nothing is known about the host-finding behavior of either *Ambylomma geayi* or *Ambylomma varium*. Pinder (6) recorded many ticks (*Ambylomma varium*) underneath the thighs of maned sloths (*Bradypus torquatus*) examined in the Poço das Antas Biological Reserve in the State of Rio de Janeiro; one specimen of *Boophilus* sp was also found. Interestingly, Pinder reported that 83% of the ticks were males and on 60% of the sloths only male ticks were present.

A number of commensal beetles, mites and moths are found in association with sloths and their dung. Adults of several scarab beetle species are frequently found in the fur of three-toed sloths, but have not been reported to be associated with *Choloepus*. Waage and Best (37) discovered more than 980 such beetles (*Trichilium adisi*) in the fur of a single sloth (*Bradypus variegatus*) collected on Curari Island in the Central Amazon region, and stated that beetles of the genus *Uroxys* have been recorded from sloths in Bolivia, Brazil, Colombia and Panama. The scarab beetles occur near the elbow or on the flanks behind the knees buried deep inside the fur. Waage and Best observed that although the numbers of scarab beetles fluctuated during the year, seasonal factors affecting the populations were unknown. Beetle larvae feed on sloth dung and the adults may utilize this as food too. The presence of *Trichilium* sp has been reported in the underfur of the lower back and thighs of *Bradypus torquatus* (6). Wolda and Estribi (39) identified and counted sloth beetles (*Uroxys gorgon*) captured in light traps at five locations in Panama, although in three of these very few beetles were caught. On Barro Colorado Island in Gatun Lake, higher numbers of beetles were captured during the rainy season. In Fortuna (a dam site on the Chiriqui River and a relatively non-seasonal region) there was a tendency towards a bimodal distribution in the numbers captured which, however, were comparatively low as the species was also rare in the area. Wolda and Estribi suggested that the beetles have dispersal flights at the beginning and end of the rainy season and that part of the population might enter reproductive diapause and disperse from the sloths to sites with some moisture and then resume reproduction at the end of the dry season and return to the sloths. In Fortuna, where the rain falls either as drizzle or in tropical storms, flight activity (and therefore capture) of the beetles could be affected. On the other hand, beetles caught in Fortuna may have been merely dispersing from elsewhere.

Waage and Best (37) identified three species of macrochelid ascarine mites (*Macrocheles impae*, *Macrocheles uroxys* and *Macrocheles lukoschusi*) in the anus and inside the rectum of three-toed sloths from Curari Island and Manaus. They also reported earlier findings of blood-sucking mites (*Liponissus inheringi*, *Lobalges trouessarti* and *Edentalges bradypus*) on three-toed sloths collected in southern Brazil. Fain (40) recorded the mite *Edentalges choloepi* on *Choloepus didactylus*. An interesting relationship apparently exists between the mites *Macrocheles impae* and *Macrocheles uroxys* and the sloth beetles *Uroxys besti* and *Trichilium adisi* on which they occur. Only adult female mites have been observed and only occasionally on *Trichilium adisi*. Waage and Best (37) postulated that the role of the beetles may be to transport the adult female mites from a diminishing dung pile to another sloth. The third macrochelid mite (*Macrocheles lukoschusi*) was not found in association with the scarab beetles.

Moths of the subfamily Chrysauginae

spend their lives as adults in the fur of sloths, particularly the three-toed species. It was found (6) that the most common ectoparasite on maned sloths (*Bradypus torquatus*) was *Cryptoses* sp which were found hiding in the fur. It has been suggested (38) that there the sloth moths may receive some protection from avian predators and possibly find nutrients in secretions of the sloths' skin and/or the algae present on the fur. Waage and Best (37) reported that some three-toed sloths may carry in excess of 120 moths; lower numbers may occasionally be seen on two-toed sloths. They also pointed out that there is considerable sympatry amongst moth species found on sloths and that several different species may coexist on the same animal. Waage and Best (37) concluded that the most striking characteristic of the various arthropods associated with sloths is the large number of coprophagous species which appear to depend on the animals for phoresis. They speculated that the great diversity of phoretic coprophages on sloths has evolved because of a strong selection for phoresis and the ideal conditions existing for transport on the sloths. Larval stages of the moths live in and feed on the sloths' dung, the adult females presumably leaving the sloths during defecation to deposit their eggs there. Waage and Best described how early larval stages of the pyralid sloth moth *Cryptoses choloepi* are covered by a light silken web; later this becomes a long silken tube within which the larva feeds and then pupates. Newly emerged moths migrate to the forest canopy to locate a sloth. Waage and Best also reported that the sex ratio of the moth *Cryptoses choloepi* is 1:1 at emergence, but on *Bradypus* the females are outnumbered 3:1 by males. This led Waage and Best to suggest that females are possibly lost from the sloth-bound population when they leave to oviposit. The life histories of sloth moths other than *Cryptoses choloepi* are less well known, but several are believed to be broadly similar to this species. However, *Bradypodicola hahnelli* is found deep inside the sloth's fur where it is able to move very rapidly; most adults have truncated wings (presumably broken by abrasion) and are thus incapable of flying. Waage and Best (37) also pointed out that the population sizes and dynamics of the sloth moths are dependent on the availability of sloth dung and thus on the density of these mammals; seasonal factors such as rainfall may have secondary effects.

Wolda (38) investigated the seasonal distribution of *Cryptoses choloepi* at three locations in Panama where it is associated with both *Bradypus infuscatus* and *Choloepus hoffmanni*. He used light traps to collect moths on Barro Colorado Island, in Las Cumbras (a residential area near Panama city) and at Fortuna. Wolda observed that although there were some notable differences between the years in the seasonal patterns of abundance of sloth moths on Barro Colorado Island, numbers were generally very low during the early part of the dry season (January to mid-March). They then increased to peak around mid-May before declining again towards the end of the rainy season. During the dry season most moths were captured close to the ground, but during the rainy season more were caught in the canopy. At the end of the year approximately equal numbers were collected from both situations. At Las Cumbras a broad abundance of moths was again seen during the early part of the rainy season, but numbers then continued to increase to peak in January. Numbers fell only during the very end of the rainy season or in the first half of the dry season. At Fortuna, during the early part of the year when the light trap was in the canopy, more moths were captured than later in the year when it was transferred close to the ground. Wolda believes that although seasonal changes in rainfall may have little direct effect on moth numbers, indirectly this might be very important. Wolda (38) also speculated that a rise in sloth mortality during periods of increased cloudiness (due to interference with the animals' thermoregulatory mechanisms) might result in more moths becoming air-borne in search of new hosts. Furthermore, after a peak in sloth reproduction (around September) there would be consequently more sloths defecating on the forest floor making it easier for the moths to find hosts.

Arboviruses and other diseases associated with sloths

Seymour (41) has reviewed the role of sloths as the possible hosts to a whole variety of arthropod-borne viruses (arboviruses), citing work carried out in Belém (Brazil), and in Panama. However, whether or not sloths are essential or only incidental to the natural cycle of an arbovirus, their long experimental viremias are remarkable and Seymour suggests that these may be due to the animals' low metabolic rate.

Antibodies to the mosquito-borne Venezuela encephalitis virus, which can prove fatal in horses, have been found in *Bradypus variegatus* and *Choloepus hoffmanni* collected in Panama. Seymour (41) concluded that *Bradypus* in particular is a potential source of infection for this virus as it develops higher concentrations of it in blood, detectable for longer periods of time than for most other forest species tested. In contrast, two-toed sloths had low concentrations of the Venezuelan encephalitis virus in blood; the duration was unreported. Another infection carried by mosquitoes (the Mayaro virus) causes sporadic outbreaks of human febrile illness in forested areas of South America and Trinidad. Although sloths can be infected in the laboratory, this, according to Seymour, only occasionally takes place in the wild. Similarly, sloths would appear to play no important role in the transmission of the yellow fever virus. Although the animals can be inoculated with it, the infection patterns are erratic and there are no apparent signs of illness.

Other investigations (42) in Panama have indicated that there is a high prevalence of the St. Louis encephalitis virus in sloths, particularly *Choloepus*. This virus, which can cause human encephalitis, occurs throughout the Americas from Canada to Argentina but in the tropics is presumed to be enzootic and probably only causes sporadic human illness (42). Seymour (41) suggested that although sloths may be important hosts for the St. Louis encephalitis virus, they are presumably only infrequently infected and gradually build up antibodies over a lengthy period of time; infected animals show no overt signs of disease. It has been found (42) that captive two- and three-toed sloths responded to inoculation with the St. Louis encephalitis virus with remarkably long-lasting viremias of high titer. The duration of detectable viremia ranged from 7 to 27 days (median 11) in *Choloepus hoffmanni* and from 13 to 24 days (median 18) in *Bradypus variegatus*. Interestingly, the onset of experimentally induced St. Louis encephalitis viremias was delayed and the maximum titer levels were depressed in two sloths concurrently infected with the Bradypus-4 virus and an agent related to the Changuinola virus. When mosquitoes (*Culex pipiens quinquefasciatus*) were allowed to feed on infected sloths 80% were able to transmit St. Louis encephalitis to chicks or mice after 14-27 days intrinsic incubation. Whether, however, sloths play an important role in the transmission of the St. Louis encephalitis virus to humans is as yet uncertain. Somewhat surprisingly, a young three-toed sloth housed with its experimentally infected non-lactating mother became infected with the St. Louis encephalitis virus, indicating that contact transmission is possible. Another virus antigenically related to the St. Louis encephalitis virus and to yellow fever is the Ilheus virus which occasionally causes human febrile illness and encephalitis. However, Seymour (41) has reported that as antibodies to the virus were found in only one of 167 three-toed and just one of 99 two-toed sloths tested in Panama, this is a good indication that these animals are not important vectors of the disease.

Seymour (41) has reported that the Oropouche virus (apparently transmitted by *Culicoides* midges) has been isolated from a small number of sloths (*Bradypus tridactylus*) in Brazil. The virus is known to cause periodic epidemic febrile illness amongst humans in the State of Pará. Sloths are also possible reservoirs for the Utinga virus also carried by *Culicoides* midges and by *Anopheles* mosquitoes. Seymour stated that the virus has been isolated from *Bradypus tridactylus* and that *Bradypus variegatus* and *Choloepus hoffmanni* from Panama have been found to be positive for the virus too. However, the antibody results concerning wild sloths are confused by possible cross-reactions with the Utive and Pintupo viruses; all three, which are members of the Simbu serogroup, are sloth-specific. Antibodies to the Utive virus have been found in two- and three-toed sloths collected in Panama.

According to Seymour (41), different phleboviruses (carried by phlebotomine sandflies) have on occasion been identified in sloths. Strains of the Changuinola virus have been isolated from both two- and three-toed sloths in Panama and this complex of viruses appears to be sloth-specific. Seymour et al. (43) also reported the isolation of the previously unidentified infectious agent (the Bradypus-4 virus) from a male sloth (*Bradypus variegatus*) captured in Panama. Seymour et al. (43) believe this to be an RNA virus with a lipid-containing envelope; it was negative when tested against 216 world-wide arboviruses.

Seymour (41) finally concluded that the wide variety of arboviruses isolated from sloths can be characterized according to antibody and virus isolation data as being sloth-specific (Utinge, Utive and Changuinola viruses), incidental in sloths (such as the Venezuelan encephalitis viruses), or others (including the St. Louis encephalitis and Oropouche viruses) for which the role sloths play in the natural cycles is as yet uncertain. Simultaneous productive infections appear to be possible in these animals.

It has been reported (44) that the phlebotomine sandfly is also a known vector of the flagellate protozoan *Leishmania* which causes cutaneous leishmaniasis in humans. All species belonging to the genus *Leishmania* are morphologically similar, except for minor differences in their size. It was also pointed out (45) that sloths are proven or suspected reservoirs of at least five *Leishmania* species belonging to the *Leishmania braziliensis* complex of the subgenus *Viannia,* i.e., *Leishmania b. colombiensis*, *Leishmania b. equatoriensis*, *Leishmania b. guyanensis*, *Leishmania b. panamensis* and *Leishmania b. shawi*, responsible for human cutaneous and/or mucosal leishmaniasis.

Shaw et al. (46) noted that in the eastern region of the State of Pará in Brazil, south of the Amazon River, *Leishmania b. shawi* frequently infected humans, whereas north of the river *Leishmania b. guyanensis* was the most common cause of human leishmaniasis. *Leishmania b. colombiensis* has also been isolated from humans, sandflies and a two-toed sloth (*Choloepus hoffmanni*) captured in Panama (47). Herrer and Christensen (48) found that in Panama *Choloepus hoffmanni* showed the highest infection rate with *Leishmania b. guyanensis* amongst all forest mammals in which natural *Leishmania* infections were demonstrated. Of *Leishmania b. guyanensis* infections in 95 sloths, 33.7% were seen in the skin only, 42.1% in the viscera (including blood and bone marrow) only, and 24.2% in both regions. Infection rates were proportional to the age of the animals, rates being higher in young sloths than in juveniles and adults. Herrer and Christensen (48) suggested that sloths probably become infected during the first few months of life and remain infected for a long time, although since the parasites disappear from some animals the disease might be self-limiting. Herrer and Christensen (48) concluded that *Choloepus hoffmanni* is the principal reservoir for *Leishmania b. guyanensis* in Panama and that because the animals survive infections without evidence of pathology this indicates a long association which appears to have evolved into a commensal relationship. Ecological and epidemiological investigations (48) also revealed a close relationship between geographical distribution of human cutaneous leishmaniasis and the presence of leishmanial infection in two-toed sloths. Furthermore, it was found (49) that *Choloepus didactylus* was a reservoir for *Leishmania b. guyanensis* in French Guiana in areas where dermal leishmaniasis is frequent among humans.

Christensen et al. (50) carried out precipitin tests on blood taken from over 2500 engorged female sandflies collected in the forest alongside the Torquato Tapajós highway near Manaus. The most prevalent sandfly collected was *Lutzomyia umbratilis* and xenarthrans were found to be the most common hosts of this insect and also of *Lutzomyia anduzei*. Interestingly, the overwhelming majority of sandflies feeding on sloths were found on *Choloepus didactylus*. Christensen et al. (50) therefore decided that this would implicate two-toed sloths as the major reservoirs of *Leishmania braziliensis* in the northern Amazon region and also probably throughout these animals' total range (i.e., from Nicaragua to central Brazil). Shaw (51) also concluded that in this region the two-toed sloth is the major vertebrate host of *Leishmania b. panamensis*, although *Bradypus variegatus* is occasionally infected as well; here the sandfly *Lutzomyia trapidoi* is the vector for the disease. In Costa Rica *Leishmania herreri* has been isolated from both *Choloepus hoffmanni* and *Bradypus variegatus*. All the *Leishmania* of xenarthrans that have been studied in sandflies are peripylarians, a type of *Leishmania* found in New World mammals; it was suggested that they may have evolved in the group.

Many striking similarities exist between *Leishmania* and parasites of the genus *Endotrypanum* which have at least three distinct stages in their life cycle. In sloths they exist as intra-erythrocytic epimastigotes (*Endotrypanum schaudinni*) or trypomastigotes (*Endotrypanum monterogeii*) while the promastigote stage is seen in sandflies and in culture. Shaw (51) reported that *Endotrypanum schaudinni* has been recorded in *Choloepus didactylus* and *Choloepus hoffmanni* and in *Bradypus variegatus* and *Bradypus tridactylus* in Costa Rica, Panama, French Guiana and Brazil. In all instances, however, far more two- than three-toed sloths were infected with this parasite. *Endotrypanum monterogeii* has been isolated from two-toed sloths (*Choloepus hoffmanni*) in Costa Rica. Another previously undescribed erythrocytic parasite was identified in a two-toed sloth (*Choloepus didactylus*) captured in French Guiana (52). The organism, morphologically related to the Babesiidae family, was named *Babesia choloepi* and is the first *Babesia* species to be identified in a xenarthran.

Flagellates of the genus *Trypanosoma*, which occur as trypomastigotes in their vertebrate host, have been found in a variety of xenarthrans including sloths. Shaw (51) reported that *Trypanosoma mesnilbrimonti* and *Trypanosoma preguici* were isolated from *Choloepus didactylus* in northern Brazil and French Guiana. *Trypanosoma preguici* has been identified from *Choloepus hoffmanni* in both Costa Rica and Panama and from *Bradypus variegatus* in Costa Rica. *Trypanosoma leewenhoeki* occurred in both *Choloepus hoffmanni* and *Bradypus variegatus* in Costa Rica and Panama. Moreover, *Trypanosoma leewenhoeki* has been isolated from *Choloepus hoffmanni* inhabiting the Pacific coast of Colombia (53). Although *Trypanosoma cruzi* has been recorded from *Choloepus hoffmanni* and *Bradypus variegatus* in Panama, Shaw (51) believes they are accidental hosts and not reservoirs. Shaw (51) discussed in some detail the relationship of infections to host behavior and habitat, and pointed out that if a vector has a narrower habitat preference than its vertebrate host there will consequently be uninfected populations of the latter. Shaw pondered whether differences in behavior and the wider habitat range of *Choloepus* compared to *Bradypus* might at least partly explain some of the observed variations in hemoflagellate infection rates between two- and three-toed sloths. Herrer and Christensen (48) examined 498 sloths captured in the Panamanian forest over a 10-year period and, interestingly, found that 19.3% were infected with *Leishmania braziliensis*, 29.5% with *Endotrypanum schaudinni*, 19.0% with *Trypanosoma rangeli*, and just one animal with *Trypanosoma cruzi*.

Toxoplasmosis has also been identified by Shaw and Lainson (54) in a two-toed sloth (*Choloepus didactylus*), although in this instance it was uncertain as to whether the infection had been acquired in captivity or in the wild. Nevertheless, these authors did point out that the disease has been recorded in other xenarthrans (the nine-banded armadillo *Dasypus novemcinctus* and lesser anteater *Tamandua tetradactyla*). The sloth, collected from the Barcarena district of Pará, had been in the laboratory for 66 days when it was found to be infected with *Toxoplasma gondii*. Hamsters and mice inoculated with homogenates of liver and spleen from this animal died within 7 days. The largest number of parasites was present in the liver, lungs and spleen, but endozoites were also detected in stained smears of blood, heart, kidneys and peritoneal exudate.

The protozoan *Pneumocystis carinii*, which causes lung infections in a wide variety of mammals and is implicated as a cause of pneumonia in patients with AIDS, has been found in the lungs of sloths. The disease has been identified in a three-toed sloth (*Bradypus tridactylus*) in Pará, Brazil (55). The animal had been kept in captivity close to a group of coatimundis (*Nasua narica*) which carried the infection. Some time later an apparently healthy two-toed sloth (*Choloepus didactylus*) also captured in Pará was autopsied. Abundant division stages of *Pneumocystis* were found in the lungs. It was concluded (55), however, that human contact with infected wild animals in their natural environment is so slight that there would be little chance of direct transmission, although there is an obvious risk to those handling captive animals. This is borne out by the identification (56) of *Pneumocystis carinii* in the lungs of 23 zoo animals that died in the Netherlands over an 11-year period. One of these was a three-toed sloth (*Bradypus tridactylus*) that had been imported from Surinam three months earlier. *Pneumocystis* has also been isolated from a female three-toed sloth (*Bradypus variegatus*) collected from the Panamanian jungle (57).

Diniz and Oliveira (58), who carried out a 20-year retrospective study on 17 two-toed and 34 three-toed sloths in the São Paulo Zoo, noted that malnutrition accounted for 45.7% and respiratory disease for 13.8% of the clinical disorders recorded. Digestive dysfunction was responsible for 12.3% of the illnesses - just under half of these involving the presence of *Ascaris* spp. Bacteria including *Escherichia coli*, *Citrobacter freundii* and *Salmonella enteritidis* were isolated from the feces and/or organs of 13 sloths.

Interestingly, parasites have even been recorded in dung balls of the extinct Shasta ground sloth (*Nothrotheriops shastensis*) collected from Rampart Cave at the western end of the Grand Canyon in Arizona. These animals appear to have been completely herbivorous and Schmidt et al. (59) identified juveniles of two different nematode species, two morphotypes of coccidian oocysts and eggs of two species of helminths in their feces. The dung was dated to 10,000 ± 80 years and, like the sloths, these parasites are now also believed to be extinct.

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