THE BEHAVIOR OF LOWLAND TAPIR (TAPIRUS TERRESTRIS) AT A NATURAL MINERAL LICK IN THE PERUVIAN AMAZON

By

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To the memory of my father

and to my mother, brothers and sisters

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Abstract of Thesis Presented to the Graduate School
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This study investigated the behavior of lowland tapir (*Tapirus terrestris*) at a natural mineral lick in the Peruvian Amazon. The objectives of the research were to determine the structure of a lowland tapir population that regularly visits a system of clay licks, to study the social and individual behavior of tapirs during their visits, and to characterize the chemical composition of the clay consumed by tapirs, as well as, to explore the significance of clay licks in the tapir ecology. The study was conducted at the Manu Wildlife Center located in northeastern Peruvian Amazon. Lowland tapirs were observed when visiting a large clay lick during the dry season of 1997. Observations were done from an elevated platform located to one side of the lick. Sex and age of tapirs, as well as diel pattern of visitation to the clay lick, duration of visits and all tapir behaviors, were recorded. Chemical composition of clay at the lick was determined from samples taken from the most used places and compared to samples from outside the clay lick. The studied tapir population had a higher proportion of adult than immature (young and juvenile) animals. Among adults, sex ratio was biased toward females and the opposite was observed among juveniles. Diel pattern of clay lick use is mainly nocturnal, with maximum visitation rates around midnight. Tapir visits to the clay licks lasted for around half an hour in average, without differences among sex/age classes. Tapirs spent most of their time at the lick in clay and water ingestion. Adults had higher rates of urination than juveniles. It is suggested that urination at the clay lick has a chemical communicative purpose. Direct vocal communication occurred in mother and young interactions, but it was not observed in other social encounters. Individual flight was the most common anti-predator behavior and was displayed at the arrival of other animals, including other tapirs. Clay from the lick had higher concentrations of Na, Ma, Ca and K than control samples. It is suggested that potential mineral deficiencies or imbalances in the tapir diet could be the factors that attract tapirs to clay licks. Also, it is suggested that another possible attraction of tapirs to soil consumption is the clay's buffering action to the toxicity of secondary compounds in the tapir diet. Finally, it is concluded that clay licks are very important components of lowland tapir habitat. Management and conservation plans should have the abundance and distribution of clay licks as important indicators of habitat quality. Further research in pattern of movements and spatial distribution of clay licks, as well as direct assessment of lowland nutrition and geophagy, is suggested.

CHAPTER 1

INTRODUCTION

Lowland tapir (*Tapirus terrestris*) are the largest native terrestrial mammals in the Amazon region. They belong to one of four surviving species of a taxon which was very successful in the past (Eisenberg *et al.* 1987, Eisenberg 1997). Tapirs are associated to tropical forests and are very important in the structuring and dynamics of their habitats (Fragoso 1997). However, tapirs are threatened to extinction in many places of their range due to over-hunting (Bodmer *et al.* 1993, 1997) and habitat loss (Bodmer and Brooks 1997). There has been many advances on the knowledge of lowland tapir ecology during the last decades, particularly on their diet, habitat use and their role as seed dispersers (Bodmer 1990a, 1991; Rodrigues *et al.* 1993; Salas and Fuller 1996; Salas 1996, Fragoso 1994, 1997). Similar advances exist for the Central American tapir (Terwilliger 1978, Fragoso 1987, Naranjo 1995a,b, Naranjo and Cruz 1998), the mountain tapir (Downer 1996, Acosta *et al.* 1996) and the Malayan tapir (Williams and Petrides 1980).

In contrast, less is known about tapir behavior. Behavior of lowland tapir has been studied only in captivity (Richter 1966, Hunsaker and Hahn 1965, Mahler 1984, Barongi 1993). In the wild, tapirs are very difficult to observe because of their shy nature

Feeding ecology and habitat use: Like Baird's tapir (Fragoso 1991, Naranjo 1995b), lowland tapir browse preferentially in gaps, especially at lower elevations (Salas, 1996). Lowland tapir browse selectively on as many as 88 species including trees, shrubs and lianas, and at least 33 species of fruits (Salas and Fuller 1996). Fruits account for an average of 33% of lowland tapir diet, which is relatively high for a large non-ruminant ungulate (Bodmer 1990b). These animals search actively in monotypic clumps of fruiting *Mauritia flexuosa* palms (Bodmer, 1990a). Frugivory in lowland tapirs is very interesting because, as large non-ruminant herbivores, they are expected to consume large quantities of low quality foods in order to maintain their nutritional requirements (Bodmer 1989). Lowland tapir are the only ungulate in the Amazon that frequently disperse intact seeds through the digestive tract (Bodmer 1991). Aside from *Mauritia flexuosa*, which is dispersed by seed spitting, lowland tapir also disperses seeds of other palms such as *Euterpe edulis* (Rodrigues *at al.* 1993) and *Maximiliana maripa*, swallowing entire fruits and defecating thousands of viable seeds at latrines located up to 2 km from the nearest palm clump (Fragoso 1994, 1997). Lowland tapir seed dispersal also allows secondary dispersion by rodents who remove seeds defecated by tapirs in latrines (Fragoso 1994, 1997). Secondary dispersion by water can also occur because tapirs frequently submerge parts of the body in rivers or pools when they defecate.

Lowland tapir and natural clay licks: Tapirs have a craving for salt and can travel long distances to find a salt lick (Eisenberg *et al.* 1987). Clay licks or salt licks are places in the landscape characterized by high mineral contents (Jones and Hanson 1985). In the Amazon forest, clay licks may occur on some river banks or ancient stream beds (Emmons and Stark 1979; Lips and Duivenvoorden 1991). Of the four species of tapirs, only *Tapirus bairdii* has not been reported using mineral licks. This could be due to the sea coastal effect, at least in Barro Colorado Island (Eisenberg, pers. com.), or limestone dominated landscapes of Central America (Fragoso, pers. com.).

Conservation Status of Lowland Tapir

Due to their large size, lowland tapir are one of the most important game species in the Amazon. Populations of lowland tapir in the Peruvian Amazon are being rapidly reduced due to over-hunting. Estimates of tapir harvests in the State of Loreto range from 15,447 to 17,886 individuals per year (Bodmer 1995). Lowland tapir are more vulnerable to over-hunting than other ungulates in the Amazon because of their low reproductive rate, long generation time and longevity (Bodmer *et al.* 1997). Aside from hunting, tapirs are threatened by severe habitat loss and fragmentation in most of their range. In spite of its wide distribution, compared to the other three species of the genus, lowland tapir could become locally extinct in many parts of its range if conservation actions are not implemented (Bodmer and Brooks 1997). In fact, local extinctions already occurred in several patches of the Atlantic forest in Brazil (Cullen 1997).

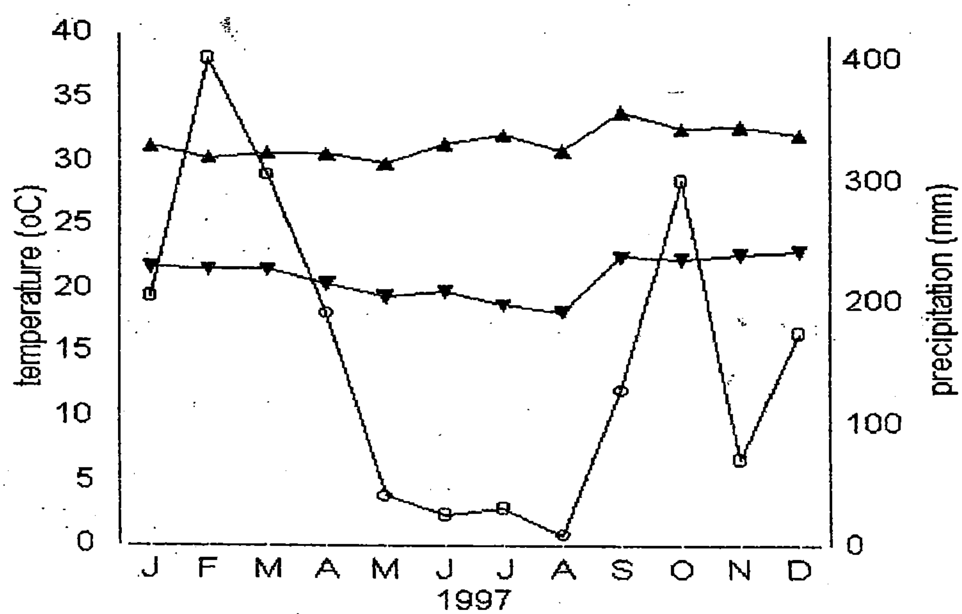

Fig. 2. Monthly mean maximum (▲) and minimum (▼) temperatures, and precipitation (○) during 1997 in the Madre de Dios river. Data from the Puerto Maldonado weather station (*Senamhi, Oficina general de estadistica e informatica*), Peru.

from the south (Terborgh 1983). This phenomenon is locally known as *friaje*, and happens as far north as the Colombian and Brazilian Amazon.

Vegetation comprises a dense lowland tropical forest with areas of seasonal flooding during the most humid months, and areas of non-flooded forest or *terra firme*. In some areas poorly drained soils and superficial draining lead to the formation of swamp vegetation, which is dominated by palms of *Mauritia flexuosa*.

Clay Licks

At least three clay licks have been found in this area since 1996. The largest one, to which I will refer as the tapir clay lick, is located about 2.5 km north of the lodge. The other two, which I will refer to as spider monkey clay lick and small clay lick respectively, are located to the north of the tapir clay lick, and are less than 1 km apart. Animal trails are common in this area and appear to connect the clay licks.

The tapir clay lick is an open area 16 m long by 12 m wide, and land is excavated up to 1.5 m deep. Four small islands remain from what was a continuous land. The largest island is 2 m in diameter and 0.75 m high, and the other three are narrower. Some small bushes and a few small palms are the only vegetation on these islands. Except for the islands, the soil of this clay lick is an exposed light brown clay devoid of vegetation and marked with numerous foot prints. Some of the tracks are from deer and peccary, but most are from tapir. Tracks are ubiquitous in the clay lick, but they seem to be more concentrated around the bordering cliffs and the well-defined entrance trails. Some of the trees on the cliff have their roots bare of soil, and the basal area of the islands and the cliff itself show marks of continuous excavation by animals. A platform 3 m high built on the south border of the lick allows observation of the animals by researchers and visitors.

The spider monkey clay lick is an area of 11.7 m long by 8 m wide, and is located on one side of a small narrow stream. Cliffs in this clay lick are lower and there are no islands. The only vegetation inside the gap is a dead tree partially fallen over the clay lick, which is occasionally used by black spider monkeys to reach the clay. A small hide built on the opposite side of the stream permits observation of the lick.

The small clay lick is located about 200 m form the spider monkey clay lick. It is 8 m long and 4.5 m wide, and is mainly formed by trails 1.5 m deep and 2.5 m wide. Large islands are present and covered by vegetation. Tapir and deer tracks are abundant in the deep trails, and cliffs show teeth marks everywhere. No infrastructure for observation exists at this lick.

Data Collection

The tapir clay lick was monitored during the dry season of 1997, from May to July. Observations were done from the platform for periods of 3 to 5 consecutive nights, alternating with diurnal observations for one to two days. Most observations were done from 17:00 to 8:00 with occasional variations, averaging 15 hours/night. Diurnal observations were done from 8:00 to 16:00. The spider monkey clay lick was monitored for a complete night and several times during the day. A total of 676 hours were spent at the clay licks; 598 of them (88.46%) at night and the remaining 78 hours (11.54%) during day time.

Most nocturnal observations (81%) were done using an ITT night vision scope. However, on some occasions when visitors were at the platform a tourch ligth was used to allow observation of the animals. All data were recorded by hand.

Population Structure

Tapirs' sex was determined by observation of external genitalia. Females with obvious developed and hanging udders were identified as nursing females. Since accurate age is difficult to establish in free ranging tapirs, relative ages were estimated in categories of young, juvenile, and adult. Young animals are clearly small and were always together with adult females. One tapir under 6 months old (with yellow and white spots and stripes covering the body) was recorded the week before field work began[1]. Juveniles were solitary, relatively small animals, sometimes with remaining vestiges of spotting in the face, throat, chest, belly and/or legs. Although lowland tapirs have very little and short hair, young and juveniles exhibit slightly longer hair. Adults are large animals, with no remanent spotting or stripes, and very short or absent hair on the rump.

Although individual tapirs are difficult to identify because they differ little in appearance (Barongi 1993), scars on the rump, cuts and patterns of the white border and spots on the ears (Fragoso 1987, Heráň 1989), and general overall appearance, allowed many individual identifications. Also, within periods of observation, patterns of clay spotting on the body helped in the identification of reentering tapirs.

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[1]Sophie Creet, personal communication.

Behavioral Sampling Methods

Time of arrival to and departure from the clay lick was registered for every tapir. All activities performed by the animals and their location inside the lick were recorded by instantaneous scan sampling every three minutes (Lenher 1996). The clay lick was divided into four approximately equal size areas for scoring, numbered 1 to 4. The relatively rectangular shape of the clay lick allowed this division. Location of numbered areas are clockwise and relative to the observation platform.

Behavioral categories used in this study were divided in states (on going behavior) and events (changes of states, or instantaneous occurrences) (Lenher 1996). These behavioral categories are listed and described as follows:

States	Description
Eating clay	Gathering clay from the ground, a cliff wall or a hole in a cliff. Mouth of the tapir is touching the surface of the clay source.
Chewing	Chewing clay with the head raised and mouth not touching any surface. Usually this behavior is noisy.
Drinking	Gathering water or water with urine from puddles.
Smelling	The animal not moving, sniffing either the ground or the air.
Exploring	Walking with the head down sniffing and testing water or with the head and proboscis up sniffing the air, stopping constantly and/or changing directions.
Walking	Walking directly from an initial location to another one without stopping.
Listening	Standing with the head up, moving ears in different directions.
Standing	Standing partially hidden from view.

Events	Description
Urinating	Urinating in standing position.
Vocalizing	Emitting vocalizations (nasal snorts, and whistles) .
Running	Running for some meters or completely out of the clay lick due to a sudden fright.

Physical Characterization of the Clay Licks

Ten soil samples were collected from the three clay licks in the area, and control samples from outside, in the surrounding forest (table 2.1). In the tapir clay lick, samples were taken from heavily used, occasionally used and non-used places (n=6). Samples from the other two clay licks (n=2) were taken from spots evidently craved by tapirs. Samples outside clay licks (n=2) were taken at random in the surrounding forest at 10 to 20 cm deep.

Table 2.1. Places sampled for chemical analyses of clays.

Sample	Location	Place[1]	Frequency of use
A	Tapir clay lick	1	Heavily used
B	Tapir clay lick	1	Heavily used
C	Tapir clay lick	1	Occasionally used
D	Tapir clay lick	2	Non-used
E	Tapir clay lick	3	Occasionally used
F	Tapir clay lick	4	Heavily used
G	S. monkey clay lick	-	Heavily used
H	Small clay lick	-	Heavily used
I	Outside forest	-	Non-used
J	Outside forest	-	Non-used

[1] Numbered places inside the tapir clay lick. See text for explanation.

Samples were analyzed for Na, Mg, Ca, Mn, Zn, Cu, Fe, Pb, As, Bi, Sb, Ba, Mo and Cd by the ICP method (digestion with chlorhydric, nitric, percloric and fluorhydric acids). pH was measured in a 1:25 soil-water suspension. All chemical analyses were done by the company SGS del Peru S.A. in Lima.

CHAPTER 3

POPULATION STRUCTURE

Introduction

Lowland tapir population structure has been studied in the northern Peruvian Amazon (Bodmer *et al.* 1993). In hunted areas, age structure of tapir populations is biased toward young animals, because many individuals are killed before they reach older ages (Bodmer *et al.* 1993). Except for these estimates, no other data about population structure in lowland tapirs have been reported. In non-hunted areas, age structure of the population is expected to show larger numbers of older animals, because of their natural longevity. However, population structure is not a species-specific characteristic, but changes depend on whether the population is stable or expanding (Owen-Smith 1988).

Estimations of sex and age composition based on counts at mineral licks have been accurate with some species, such as Dall sheep (Heimer 1973). However, differences in mineral lick use among sex/age classes may exist, making estimations more difficult. Individual identification of animals helps for more accurate estimations.

This chapter describes the sex and age composition of the tapir population that visited the clay licks studied at the Manu Wildlife Center.

Specific Methods

Total sightings include all observations in the clay licks. Estimation of sex and age composition of tapirs is based on 185 visits recorded during complete night observations at the tapir clay lick. Identification of sex/age categories was done as described in chapter 2. Frequency of visits by females and males was compared using a chi-square test. Minimum population size was estimated from individually identified tapirs.

Results

Tapir Sightings

A total of one hundred ninety-five visits of tapirs to clay licks were recorded from May to July, 1997. On 86% of the observation nights animals were seen at the clay lick. There was a mean number of 6 sightings per night with a range of 0 to 15 (Fig. 3.1.). A mean of 3 different tapirs per night were identified (range 1 to 6). Individual tapirs visited the clay lick on average two times per night, with a range of 1 to 6 visits per animal (Fig. 3.1.).

Sex and Age Composition

The cumulative number of nightly identifications totaled 85 by the end of the study period. There were twice as many nightly identifications of individual females (n=47) than males (n=24), and a cumulative of 14 identifications where the sex of the animal could not be determined (Fig. 3.2.). Also, females were seen at the clay lick 74% of the observation nights, whereas males were seen at only 46% of those.

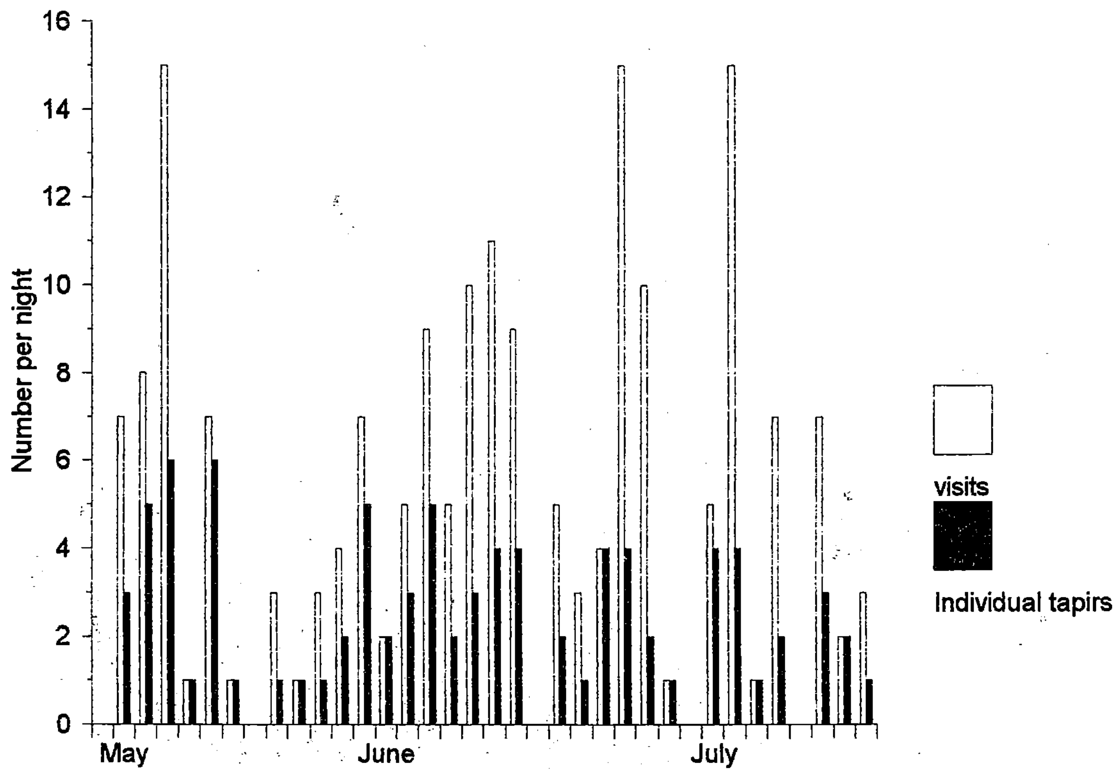

Fig. 3.1. Number of tapir visits compared to number of individual tapirs identified per night.

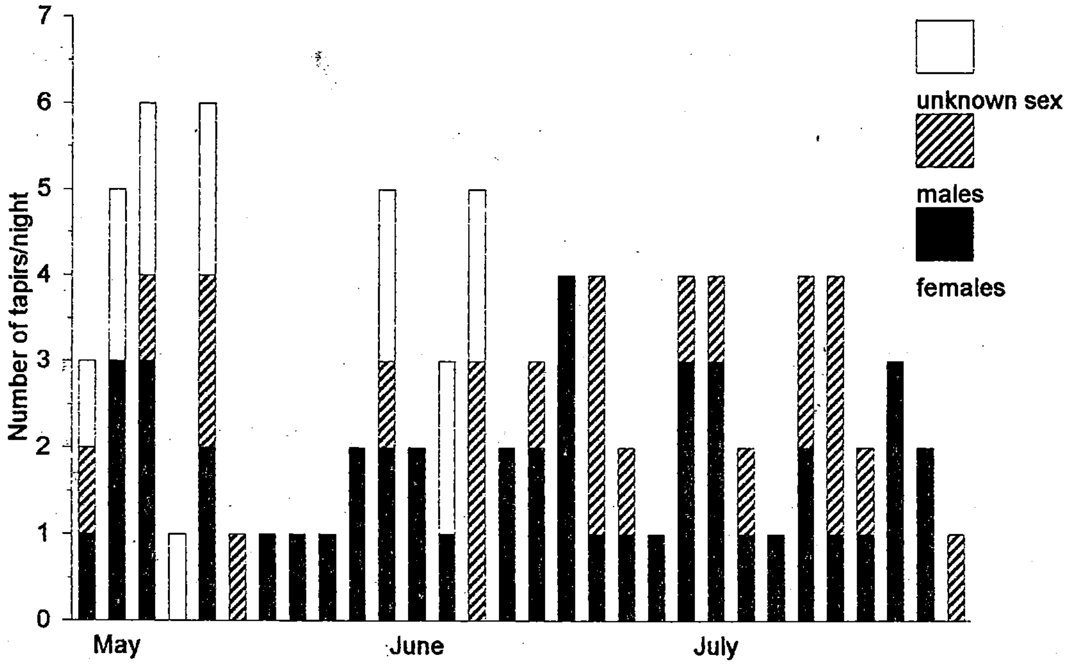

Fig. 3.2. Number of nightly identifications of visiting tapirs. Each bar represents number of individuals for each sex category.

Visitation rates were higher in females than in males ($\chi^2 = 7.45$, df=1, $p<0.05$). Age composition of all tapirs visiting the clay lick was as follows: adults 66 % (n=56), juveniles 14.5% (n=12) , and 3.5% young (n=1) (Fig. 3.3).

At least 12 individual tapirs were recognized during the study period. Sex and age composition of these known animals were 5 adult females, 1 juvenile female, 1 young female, 3 juvenile males and 2 adult males. Thus, the minimum population size of tapirs visiting the clay lick is 12 animals, with a sex ratio of 5♂ : 7♀. Overall sex ratio was not different from the expected 1:1 ($\chi^2 = 0.285$, df=1, $p>0.05$). However, adult sex ratio was 1:2.5 (n=7) in favor or females, whereas juvenile sex ratio was 1:3 (n=4) in favor or males.

Letters from A to L were assigned to these 12 tapirs as their names. These tapirs did not visit the clay lick at the same time. Some individuals entered on different days of the study period, whereas others entered several times during a night (Fig.3.4). Tapir A seems to be a resident adult female that regularly visited the clay lick during the study period (Fig. 3.4). An adult female and her young (tapirs B and C) and a juvenile male (tapir E) visited the lick on at least two different months, and could be overlapping part of their range with tapir A. Males J and K seem to be occasional visitors to the area, entering the lick several times in a single night, but not in subsequent nights. It is possible that those males have large home ranges and spend a little time at this clay lick. Other males, such as H and I may stay several nights around the lick, entering one or two times per night. Adult female F also seems to be an occasional visitor, entering the lick on three consecutive nights, but not on subsequent dates.

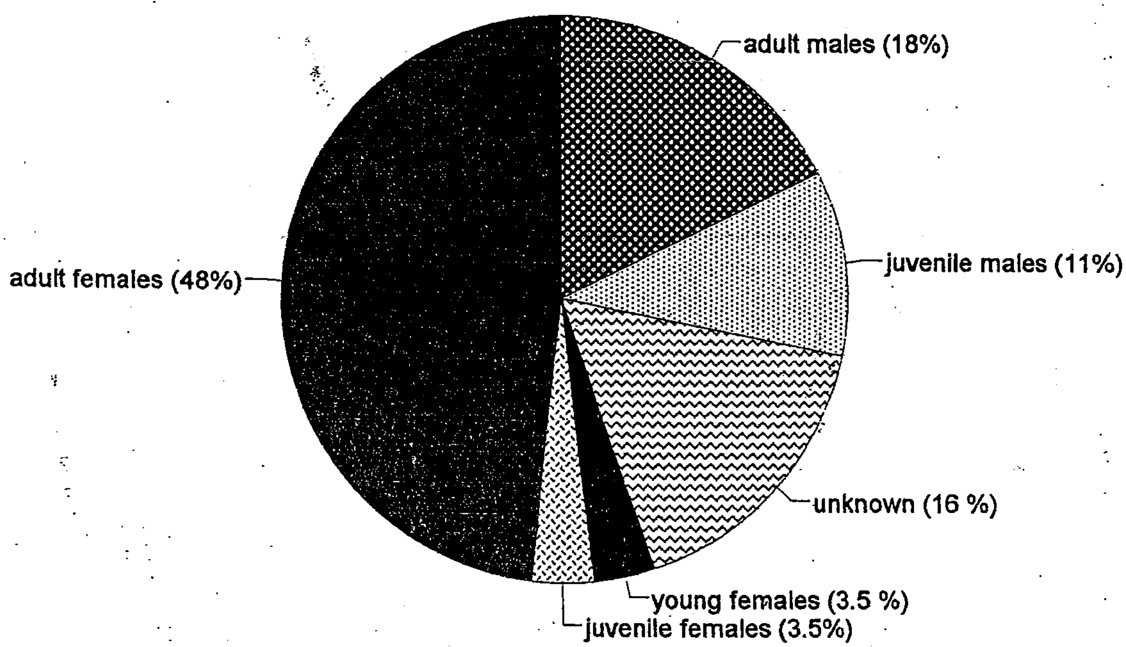

Fig. 3.3. Overall age and sex composition of visiting tapirs.

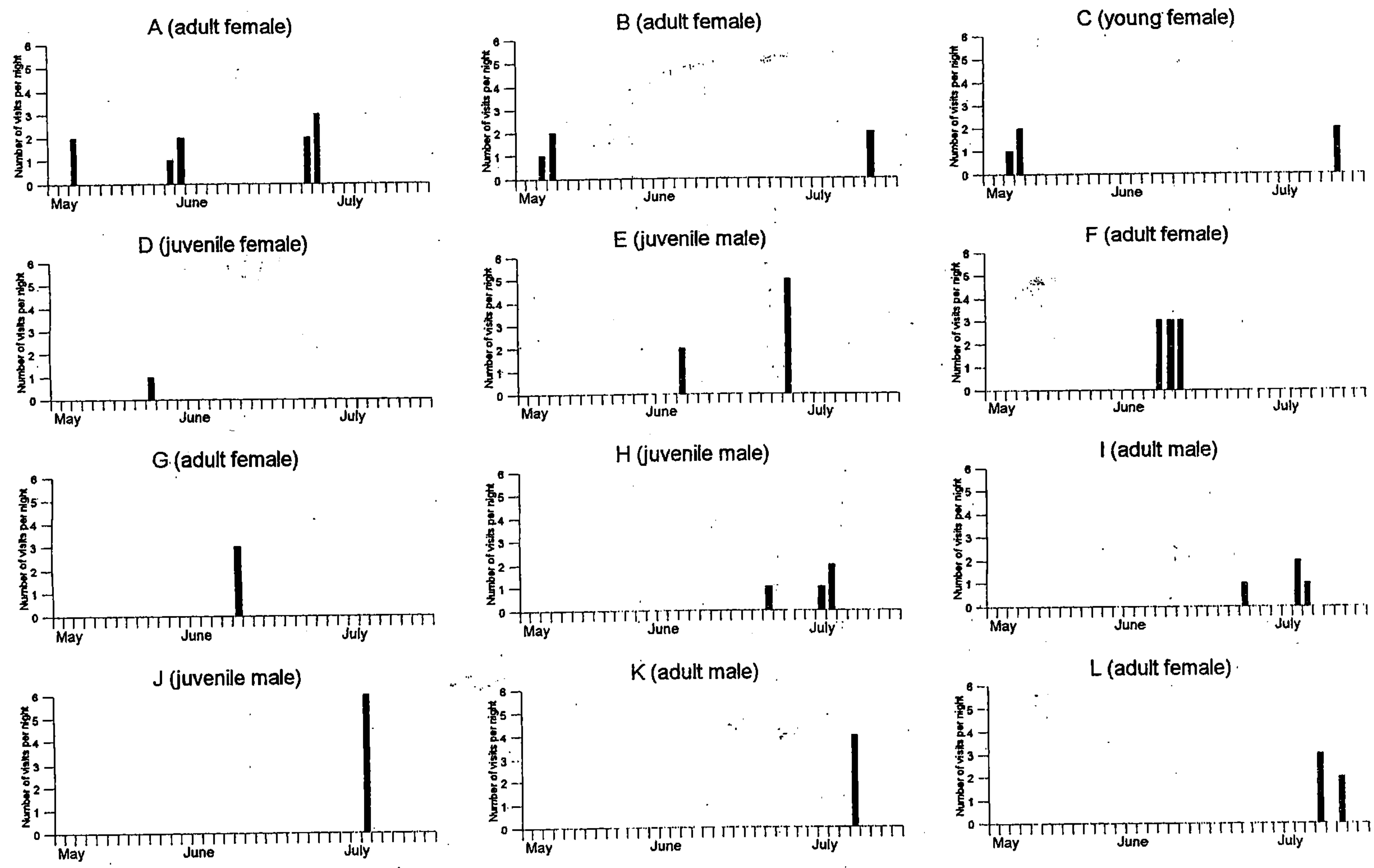

Fig. 3.4. Number of entrances and dates of visits by the 12 known tapirs. Letters from A to L were assigned as names.

Discussion

Tapir population density in the southern Peruvian Amazon is estimated at 0.5 animals per km^2 (Jason and Emmons 1990). Since the minimum population size of tapirs was 12 individuals, the clay lick is probably attracting animals from a rather large area.

Although overall sex ratio of the 12 known animals did not show biases toward either sex, among adults there were more females than males, and the opposite occurred among juveniles. If counts at the clay lick really reflects the actual sex ratio of the tapir population, a shift in sex ratio seems to occur from juvenile to adult ages. For some ungulates, it has been suggested that male-biased sex ratio of offspring is promoted when daughters remain in the maternal home range, to reduce competition among females and their daughters (Clutton-Brock and Albon 1982). In adults, however, sex ratio maybe biased toward females because males disperse and then suffer higher mortality than females (Owen-Smith 1988).

If counts at the clay lick do not reflect the actual tapir population sex ratio, an alternative explanation is possible. Adult females and juvenile males could be visiting the clay lick more often than other sex/age groups because they could have higher nutritional needs. As it will be shown in chapter 5, clay may provide source of some minerals that could be deficient in the diet. Adult females could have high nutritional needs during lactation and juvenile males during dispersion. If that is the case, the observed sex ratio may reflect this situation. However, it is not known what percentage of the whole population are the 12 identified tapirs and if they really reflect the actual sex ratio in the whole population.

It is not know how large is the area tapirs are using. It is possible that several animals that visited the clay lick overlap their home ranges. Some males seem to have large home ranges and they probably visit clay licks in other areas. Other tapirs, in contrast, show more fidelity to the studied clay lick, and they are probably residents of this area.

Aside from the other two clay licks in the area, no other licks have been found close to the study site. Thus, it is possible that some animals travel long distances to reach these clay licks. Reports of tapir home ranges indicate that they may use a large area. For example, home range of an adult female lowland tapir in the Brazilian Atlantic forest was estimated at 151.65 ha during four months.[1] It is possible that distribution and abundance of clay licks is an element of habitat quality that influences to some extent the size of tapir home ranges.

Age composition of this population of tapirs shows a larger proportion of adult than juvenile and young animals. This contrasts with the age composition of tapir populations estimated in hunted populations in northern Peru (Bodmer *et al.* 1993), where age structure is biased toward younger animals. Unfortunately, statistical comparison with Bodmer *et al.* (1993) data are not possible because they used tooth wear to establish age classes, whereas age estimation in this study was based on external characters. However, it seems that in the non-hunted area where this study was conducted, population structure is not biased toward young animals. A population of Central American tapirs in a protected area in Costa Rica also showed higher proportion of adults (80%) than

[1]Patricia Medici, personal communication, 1997.

juveniles (12%) and young (8%).[2] Determination of age classes of those tapirs was based on the same external characters used in this study.

Direct counts of mineral lick visitors has provided accurate estimations of age/sex ratios of some ungulates (Heimer 1973). However, in many cases, a given sex or age class seems to visit the licks more often (see table 5.2, Chapter 5). Also, a species may exhibit different pattern of visitation by sex/age classes in different habitats. For example, subadult male moose visit mineral springs more often than the other sex/age classes in Alaska (Tankersley and Gasaway 1983), whereas adult females were the most frequent visitors in Northern New Hampshire (Miller and Litvaitis 1992) and adult and calves of both sexes were equally frequent at mineral licks in the Gaspé Peninsula of Quebec (Couturier and Barrete 1987). Both females and males of white-tailed deer visited mineral licks in North America (Fraser and Hristienko 1981, Weeks and Kirkpatrick 1976), except in South Dakota, where adult females were the most frequent lick users (Kennedy *et al.* 1995).

Estimates of population structure from direct counts at mineral licks may give a preliminary idea of the actual ratios, but it has to be complemented with other alternative methods to have accurate estimations. The estimations of size and structure of the tapir population that visit the clay licks around the Manu Wildlife Center should be taken as preliminary, until other complementary estimations are conducted.

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[2] Eduardo Naranjo, personal communication, 1998.

CHAPTER 4

LOWLAND TAPIR BEHAVIOR AT THE CLAY LICK

Introduction

The use of clay licks have been studied in several species of mammals, mainly in ungulates (Jones and Hanson 1985). In North America, the species that have been studied in some detail are moose (*Alces alces*) (Tankersley and Gasaway 1983; Couturier and Barrete 1987; Fraser and Hristienko1981; Miller and Litvaitis 1992), white-tailed deer (*Odocoileus virginianus*) (Fraser and Hristienko1981, Wiles and Weeks 1986; Weeks 1976, 1978; Schultz and Johnson 1992), mountain goat (*Oreamnos americanus*) (Hebert and Cowan 1971, Singer 1978), and mountain sheep (*Ovis canadensis nelsoni*) (Holl and Bleich 1987). In tropical areas, the use of mineral licks by wild species has been addressed to a lesser extent (Henshaw and Ayeni 1971; Moe 1992). The use of mineral licks by tapirs has been reported in few studies (Seidensticker and McNeely 1975; Acosta *et al.* 1996; Ayres and Ayres 1979; Peña *et al.* 1996). In most cases, the use of clay licks by tapirs has been noted through the examination of tracks inside the licks, or by information from local hunters who look for tapirs at clay licks. Direct observation of the animals inside licks is not well documented, and the data have usually been gathered *at libitum*. In consequence, the pattern of visitation to mineral licks by tapirs and their behavior during their visits are poorly known. This aspect is of great interest because mineral licks, besides being a source of minerals (see chapter 5), may play an important role in the communication of these solitary animals. Indeed, some researchers have called mineral licks "social gathering places" (Couturier and Barrete 1987: 522). The purpose of this chapter is to describe the behavior of lowland tapir at the clay lick and to discuss some aspects of their social interactions.

Specific Methods

Diel Pattern of Clay Lick Use

Patterns of visitation were analyzed by recording the time when each tapir entered the clay licks. The time of day when other species visited the lick were also recorded and classed as diurnal or nocturnal.

Duration of Visits

The length of a visit was defined as the lapse of time between the entrance to and departure from the clay lick. Repeated visits by the same tapir were counted separately if the animal left the lick for more than five minutes. Duration of visits were compared among sex and age classes when possible. Although samples may not be completely independent because repeated entrances of the same animals were not always identified, it was thought that some statistical comparisons might be useful, due to the relatively large sample size of visitations. Descriptive statistics (means ± standard deviations) were calculated for overall time spent at the clay lick using all observations. These observations exclude tapirs that were seen at the lick's edge without entering and those that were already inside the lick when the observation periods began. A chi-square test of independence was used to evaluate if the use of light interfered with the total time a tapir spent at the clay lick. The following 4 categories of time intervals were used for this test:

Category	Duration of visits
5	Between 1 to 15 minutes
15	Between 16 to 30 minutes
25	Between 31 to 45 minutes
35	More than 46 minutes

Since the use of light affected the time tapirs spent at the clay lick (χ^2=12.155, df=3, p=0.007), only visits scored using the night scope were used for subsequent analyses (n=140). Mean length of visits and standard deviations were calculated for sex/age classes (n=109), excluding observations of animals of unknown sex and/or age. Likewise, a chi-square test was used to compare length of visits among the sex/age groups with large enough sample sizes. This test was conducted using the same categories of time intervals mentioned above.

<u>Arrival and Departure Directions and Most Used Places</u>

The tapir clay lick was divided into four approximately equal size areas, as stated in chapter 2. The frequencies of entrances and departures in each area were tabulated and percentages were calculated. Also, the places most used inside the lick were determined by calculating the percentage of each behavior in a given location.

<u>Overall Behavior of Tapirs at the Clay Lick</u>

Behavioral categories used in this study are describe in chapter 2. States (on going behavior) were analyzed for all visits and also for sex/age groups, when possible. As previously stated, instantaneous scan sampling was scored every three minutes. Each score represents a sample. Percentages of each behavioral category were calculated as the number of samples in each category over the total number of samples in each group. Events (instantaneous occurrences) were scored any time they occurred. Urination and vocalization rates were calculated by dividing the number of occurrences by the number of visits in each sex/age class that exhibited those behaviors.

Results

Diel Pattern

Although some tapirs began activities at the lick before sunset, the highest frequency of visits occurred from 18:00 to 04:00, with a maximum around midnight (Fig. 4.1). No tapirs were seen visiting the licks before 16:00 or after 8:00 (except for one tapir observed at 10:00 at the spider monkey clay lick). Although diurnal hours of observation were only 11.54% of the total (78 hours out of 676), this diel pattern of visits was confirmed by examination of the clay lick for new tracks at the beginning of every observation period. These observations suggest that even though tapirs may be active during the day, their pattern of visitation to the tapir clay lick is markedly nocturnal. No differences were evident among sex or age in the diel pattern of visitation.

Other animals that visit the clay lick include ungulates, primates, and birds (Table 4.1). Pattern of visitation by those species may be diurnal (peccaries, primates and birds), or both diurnal and nocturnal (red brocket deer).

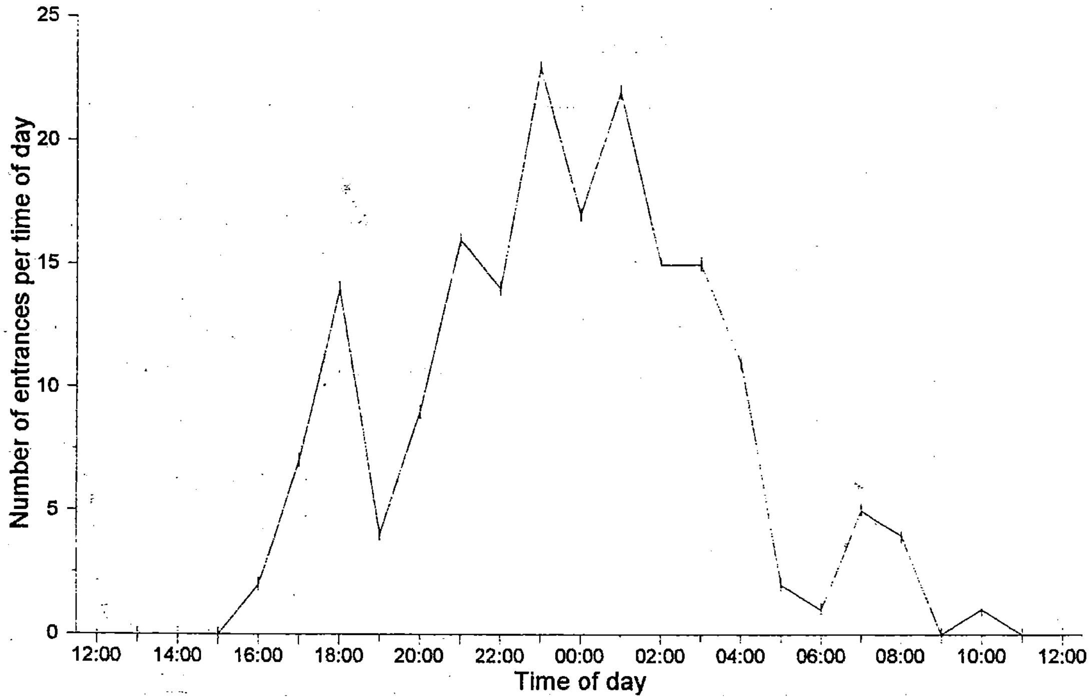

Fig. 4.1. Diel pattern of visitations to the clay lick.

Table 4.1. Species visiting the mineral clay licks and their time of visits

Species	Clay lick		Time of visits	
	Tapir	Spider monkey	Day	Night
MAMMALS				
Tapir (*Tapirus terrestris*)	x	x	x	x
Red brocket deer (*Mazama americana*)	x	x	x	x
White-lip peccary (*Tayassu pecari*)	x		x	
Collared peccary (*Tayassu tajacu*)	x	x	x	
Red howler monkey (*Alouatta seniculus*)	x		x	
Black spider monkey (*Ateles paniscus*)		x	x	
BIRDS				
Common pigeon (*Columba subvinacea*)	x		x	
Painted parakeet (*Pyrrhura picta*)	x		x	
Green and blue parakeet (indeterminate)	x		x	
Spix's guan (*Penelope jacquacu*)	x		x	
Common Piping-guan (*Aburria pipile*)	x		x	

Duration of Visits

Tapirs visited the clay lick on average for about 23 minutes, with a range from 1 minute to 1 hour 13 minutes. Most visits lasted for less than 40 minutes, and very few reached one hour or more (Fig. 4.2). Short visits were more common during the nights when several tapirs visited the lick. Very long visits were uncommon, but were observed for both females and males. Some animals returned a few minutes after departure, but others did not return until several hours had passed, or not at all during that night.

Length of visits were not different among adult females, adult males and juvenile males (χ^2= 5.301, df=3, p=0.151), (Table 4.2). Juvenile and young females were not

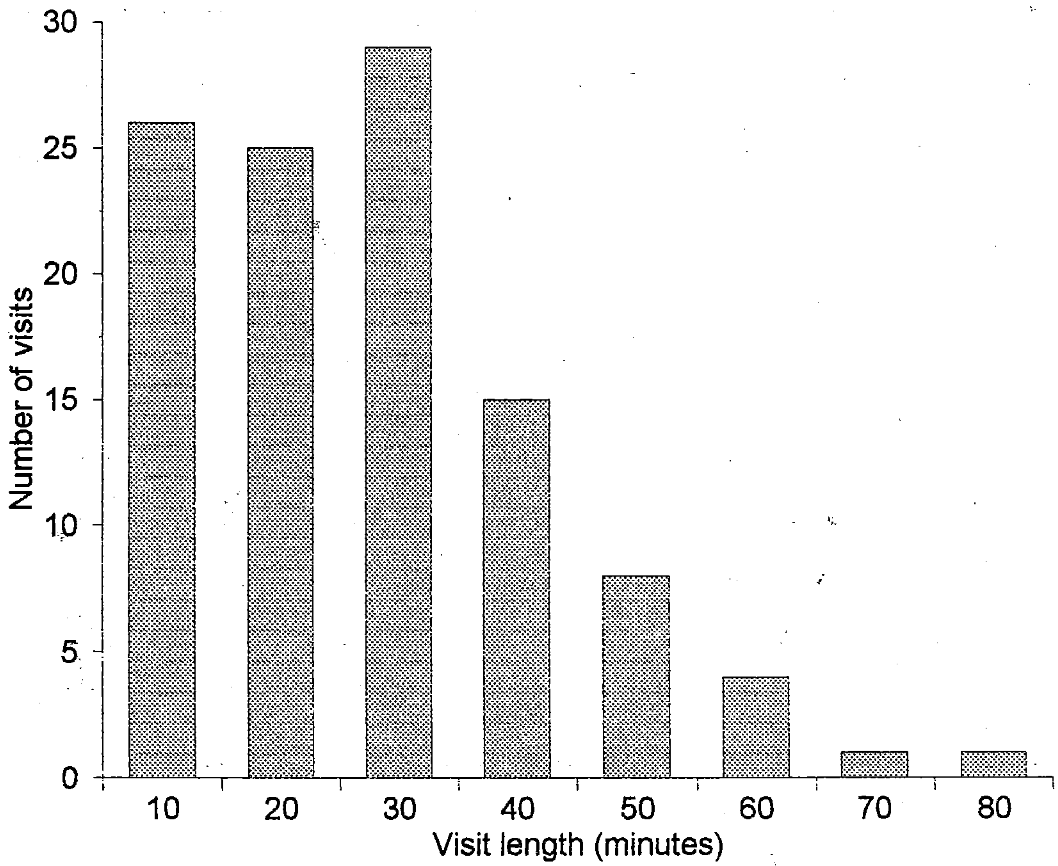

Fig. 4.2. Length of visits to the clay lick and their frequency distribution.

included in the test because of their small sample size. Data for young females correspond to a single calf that joined the mother on three different occasions. This calf spent less time than the mother inside the lick, but remained in the area, keeping constant communication with the mother during the time she was inside the lick (see the overall behavior section below).

Table 4.2. Duration of tapir visits to the clay lick for sex/age categories

Category	Number of visits	Duration of visits in minutes (mean ± standard deviation)
Adult females	64	25.71 ± 15.67
Adult males	16	22.06 ± 15.87
Juvenile males	24	17.41 ± 11.24
Juvenile and young females	5	13.80 ± 9.83
All groups	109	22.80 ± 14.96

Arrival and Departure Directions

Many trails were clearly visible in the forest surrounding the clay lick, forming a web of alternative trails that converged at the lick. However, tapirs entered the lick more often by two of the four areas of the lick. Tapirs entered the clay lick by areas 1 and 4 eighty-two percent of the time (n=159). They left the lick in the direction from which they had come 66% of the time (n=98). Only occasionally, tapirs entered by areas 2 and 3 (11.5% and 6.5% of times, respectively).

Most Used Places Inside the Lick

Tapirs ingested clay or water form several spots. Ninety-nine percent of the time they gathered the clay from specific spots located in areas 1 (52.8%, n=209) and 4 (46.2%, n= 183). In area 1, four places were heavily used by tapirs. Those places were located separately at the base of a cliff, where holes were slowly being carved by the animals. In area 4, only the wall of a cliff just at the entrance of the lick was used. At the end of this study a hole was carved by tapirs and deer at the base of this wall, forming a pond after heavy rains. Three times tapirs ate clay from area 2 and only once from area 3. Area 3 appears to have been heavily used in the past, because of old marks on the remnant small island located in that area.

Tapirs drank from small puddles and a small pond in area 1 most of the time, when this behavior was recorded (92.6%, n=189). Those puddles were formed by the deep tracks tapirs gouged on the muddy surface. The small pond seemed to be formed by continuous carving by tapir clay eating and gouging by their feet. After heavy rains, the pond fills with water and tapirs may go inside to reach the cliff wall, immersing most of their body underwater. When the pond dries out, the water is deep enough to only submerge their legs.

Tapirs urinated several times inside the clay lick. Urination occurred mainly in area 1 (65.4%, n=17). Some of the puddles from which tapirs drank contained water mixed with urine. In area 4, urination was less frequent, accounting for 15.4% of occurrences (n=4). Tapirs urinated at area 2 and 3 few times (11.5%, n=3 and 7.7%, n=2, respectively).

Exploring and walking were also more frequent at area 1 (55.2%, n=16 and 64.4%, n=112), fairly frequent at area 4 (37.9%, n=11, and 16.7%, n=29) and very uncommon at areas 2 (6.9%, n=2; 12.6%, n=22) and 3 (0% and 6.3%, n=11).

Overall Behavior of Tapirs at the Clay Lick

Tapirs spent most of their time at the clay lick in ingestive activities (eating clay, chewing and drinking) (Fig. 4.3). Animals avidly gathered clay from the cliff wall or the ground. Tapirs spent more time chewing when they had taken clay from the cliff wall. Adult females and males spent around 50% of their time at the lick, either gathering clay or drinking, whereas juvenile males spent around 70% of their visit time in such activities (fig. 4.3). Animals often took clay from more than one spot during their visits, changing their location several times. This is reflected in the proportion of time spent walking inside the lick (Fig. 4.3). Data for the young females are illustrated as a reference, since only one individual was observed in this sex/age category. This young female, spent a high proportion of her visits walking close to her mother, although she also ate clay.

Both females and males spent part of their time at the lick in an alert position, listening. They usually stopped eating and kept the head up, moving the ears constantly. The young female spent little time in this behavior.

Animals also stopped eating to raise the proboscis, smelling in different directions. On some occasions they raised the upper lip showing their teeth, or opened the mouth towards the air, holding this position for several minutes. This behavior was scored as "smelling" but it corresponded to the posture and grimace adopted when sampling urine

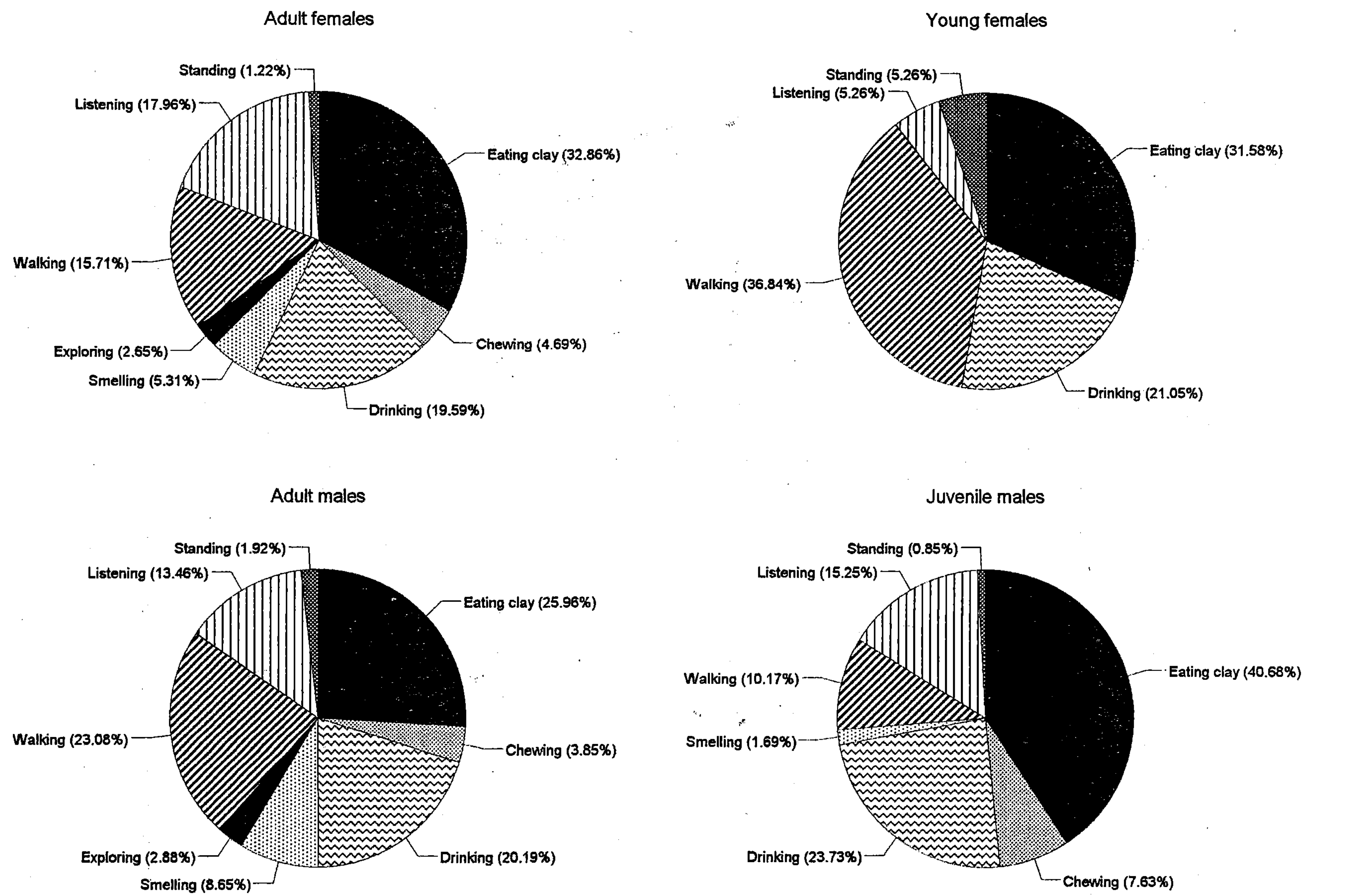

Fig. 4.3. Proportion of each behavioral category during the visits to the clay lick.

usually termed *flehmen* (Estes 1991). Juvenile males spent little time in this behavior, and it was not observed in the young female.

Some adult females and males explored inside the lick, usually at their arrival, mainly if they entered by area 1. They walked in different directions and very often tested the water held in the small puddles formed by deep tracks. Some of them urinated in that area, mixing the water with urine. That mix was usually tested when exploring, and many times it was actually drunk. It was not clear if the same animals that had urinated, drank from those puddles in subsequent visits.

Tapirs urinated either at their arrival to the lick, in the middle of their visits or before leaving. Overall rate of urination was 0.25 occurrences /visit for adult females and 0.18/visit for adult and juvenile males combined. However, analyzing juvenile and adult males separately, urination rates were 0.008 occurrences/visit and 0.31 occurrences/visit respectively (Fig.4.4).

Most of the vocalizations inside the lick occurred during the visits by mother and young. The rate of vocalizations was 2 occurrences/visit for the adult and 6.25 occurrences/visit for the young. Those vocalizations were nasal snorts. The same type of vocalization was heard from other animals immediately preceding their entrance, while walking inside or outside the lick. On one occasion, after several vocalizations outside the lick, the young entered the lick to join its mother. Fifteen minutes afterwards, a third tapir entered, causing panic among both the mother and her young. The mother initiated flight, running outside the lick. The third tapir also ran away from the lick in an opposite direction to the female, whereas the calf uttered shrill squeals, while in panic tried to

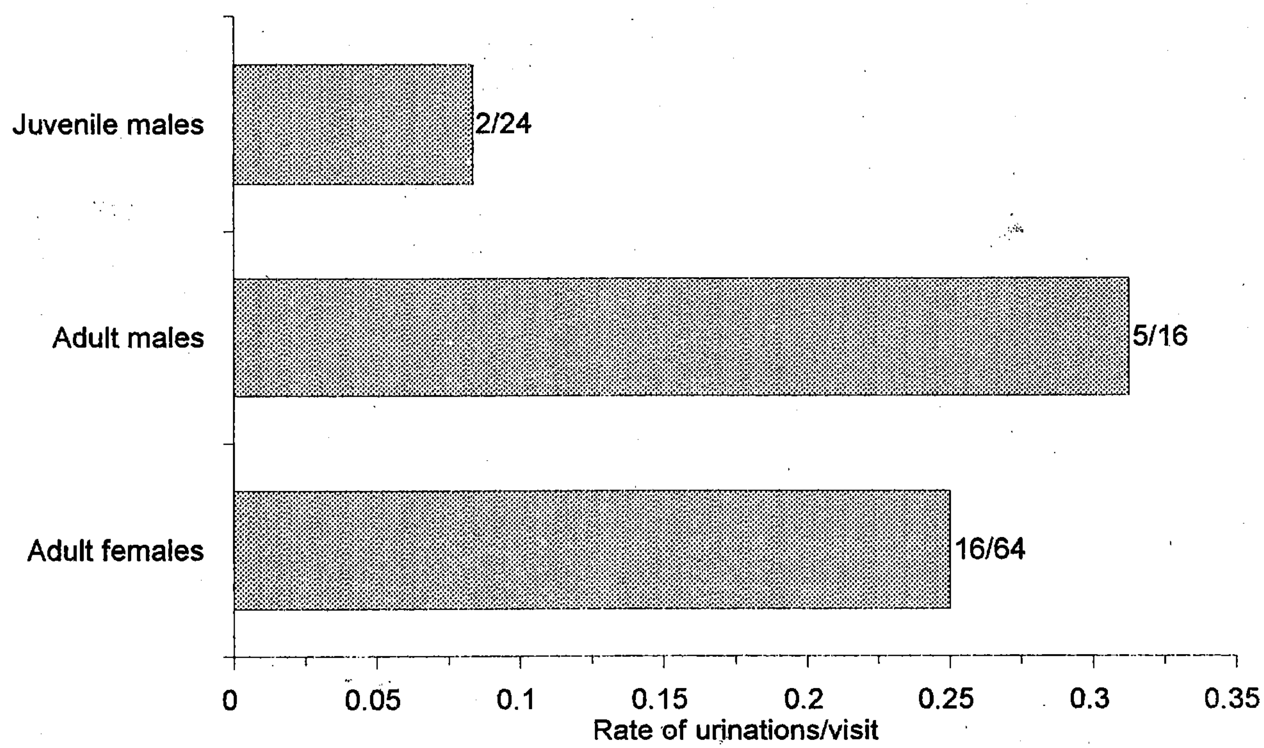

Fig. 4.4. Rate of urinations per visit by sex/age category. Numbers in front of each bar indicate the number of urinations/number of visits.

Duration of Visits

The average time tapirs spent at the lick (around half hour) is similar to that reported for other ungulates (Kreulen and Jager 1984). Length of visits were not different among sex/age classes. This contrasts with other species in which nursing females seem to extend their visits longer than other animals, as was noted in elk (Carbyn 1975). Young moose tend to spend longer than adults at mineral licks (Fraser and Hristienko 1981).

Differences in nutritional needs among sex and age classes are usually suggested as an explanation for longer visits by a given sex/age class. If those differences exist in tapirs, they are not reflected in the total time an animal may spend at the lick.

Arrival and Departure Directions and Most Used Places Inside the Lick

It was clear that tapirs constantly used the same trails, and entered the lick at two main spots. Those places, that were arbitrarily numbered (as described in chapter 2), were two borders of the cliff that tapirs used most in geophagy and drinking. Two factors may explain this spatial pattern of lick use. The first is the relatively greater availability of exposed clay at areas 1 and 4. The second is that in areas 2 and 3 the cliff wall is drier and the soil looks compacted. Clay seems to be softer in areas 1 and 4. In general, area 1 was the most heavily used because there were several spots for gathering clay and a higher availability of water.

Overall Behavior of Tapirs at the Clay Lick

The overall behavior of lowland tapir at the clay lick may be grouped in the following four types: behaviors associated with ingestion (eating clay, chewing and drinking), communication (vocalizations and urination), predator defense (listening-alarm positions, running) and investigation (smelling and exploring).

Evidently, tapirs visited the lick primarily to consume clay and water. The possible reasons why tapirs consume soil material are related to their nutritional balance, and are discussed in chapter 5. The following discussion focuses on the other behaviors observed at the lick, including some aspects of mother-young relationships.

Communication.

Walther (1984) stated that in comparatively primitive ungulates acoustical and olfactory signals play the major roles in their communication, whereas visual signals are of minor importance. That seems to be true for tapirs.

Tapirs uttered three types of vocalizations at the clay lick or surrounding areas. Those vocalizations correspond to the shrill fluctuating squeal, sliding squeal and nasal snort described by Hunsaker and Hahn (1965). The clicking noise, used as species specific characteristic, was not heard probably because this noise can be heard just up to 9.15 m (30 feet) (Hunsaker and Hahn 1965).

Similar to Hunsaker and Hahn's (1965) observations, the shrill fluctuating squeal was associated with fear since that was the vocalization the calf uttered when panicked. The sliding squeal was heard outside the lick, but a tapir never uttered this call when it was inside. Hunsaker and Hahn (1965) suggest that this vocalization appears to keep animals in contact with one another, functioning also as an exploratory call, since it was uttered by all animals in absence of an apparent stimulus and when the animals were moving randomly around the area. Walther (1984) suggests that the sliding squeal in tapirs is related to advertising of presence, position, state and status. In fact, the majority of tapir calls uttered by dominant animals in a social hierarchy formed in captive conditions were sliding squeals (Hunsaker and Hahn 1965). Few sliding squeals were heard around the clay lick, and they seemed to be used to announce the presence of an animal before entering the lick. However, it is not clear why most animals did not use this vocalization at the lick.

It is frequently noted that tapirs respond to the sliding squeal and may even approach the source of the sound. Hunsaker and Hahn (1965) suggest that this call may function also to attract mates or induce investigatory behavior. It is possible that tapirs use this vocalization as suggested by Walther (1984) and Hunsaker and Hahn (1965), but tend to avoid it around the lick to do not call the attention of potential predators.

Most of the vocalizations at the lick were associated with short distance communication between mother and young and most of them were nasal snorts. The calf frequently produced those calls at higher rates than its mother, perhaps to keep permanent contact with her. Also, repeated snoring vocalizations were uttered by the adult female from outside the lick, when her calf was lost and in panic inside the lick. Those vocalizations did not cease until the calf left the lick in the direction of the calls. Thus, it seems that the nasal snort that tapirs uttered at the lick functions as an appeasement and orienting call. Hunsaker and Hahn (1965) described a nasal snort as a threat sound in aggressive encounters. It is difficult to state if it is the same type of vocalization heard between mother and young at the lick. Maybe the vocal repertory of tapirs is larger than previously thought and they can produce more than one type of nasal snort. This is suggested because vocalizations in mother-young interactions are expected to emit a completely different message than those used in aggressive encounters.

Urination at the clay lick is interpreted in this study as a behavior associated with communication. Although urination and defecation function as the normal deposition of physiological waste matter, the process of elimination is behaviorally emphasized (Walther 1984) or semiritualized (Eisenberg 1981) when they function as communicative signals. In captivity, male tapirs may urinate in a "normal"and "ritualized" fashion (von Richter 1966). In ritualized urination, tapirs spray urine in one or more marking sites.

Both males and females urinated at the clay lick. Females urinated in a squatted posture while males did it in a saw-horse posture, as described in most ungulate species (Walther 1984). Male tapirs urinated in the "normal" posture and "ritualized" urination was not observed. However, the function of urination as a communicative behavior at the clay lick can not be discarded, since tapirs frequently sniffed the sites were other tapirs had urinated.

Also, tapirs often showed the *flehmen* posture which is related to urine testing and seems to be associated with stimulation of the Jacobson's organ (Eisenberg and Kleiman 1972). The Jacobson's organ or vomero-nasal organ helps the animal in the perception of chemical molecules present in urine and feces (Wysocki and Meredith 1987), being very important in the chemical communication among animals.

The information transmitted in mammalian chemical signals include species identity, sexual identity, reproductive state, discrimination of individuals, age and mood (Eisenberg and Kleiman 1972). "Scent marks are a means of information exchange, orientation of animal movements and integration of social and reproductive behavior" (Eisenberg and Kleiman 1972:24).

The following two results in this study support the suggestion that tapir urination at the clay lick may be seen as a communicative behavior: a) the higher rate of urination by adult males, and b) the higher proportion of time adult males spent '"smelling" at the lick (8.65%) as compared to adult females (5.31%) and juvenile males (only 1.69%). Dominance hierarchies have been observed in captive tapirs (Hunsaker and Hahn 1965). In free ranging tapirs, the existence of such hierarchies had not been reported, but it is possible that juvenile males tend to be subordinate to adult males. A higher rate of urination by adult males may reinforce their dominant rank over juveniles. In addition, if adult males were testing urine for potential mates, that may explain why they spent comparatively more time in "smelling" behavior than juvenile males.

Urination at mineral licks has also been reported in moose (Couturier and Barrete 1987). In this species, however, both normal and ritualized urination (hock urination) were observed. In other localities, however, moose left the lick to urinate, returning afterwards (Fraser and Hristienko 1981), indicating that scent marking does not always occurs inside the licks.

Defecation may also function as a communicative behavior. Creation of dung piles is very common in territorial ungulates, although some non-territorial species may also form them (Walther 1984). Since tapirs may create large dung piles (Fragoso 1997, Naranjo and Cruz 1998), it is possible that some chemical signals are also deposited in those dungs. The role of the clay lick as a site for defecation is not likely, since tapirs never defecated inside it. This contrasts with the behavior of elephants at clay licks, where they usually defecate.[1]

Anti-Predator Behavior

Excluding humans, jaguar and puma are potential predators of tapirs. Although no predators were actually seen at the clay lick, tracks of jaguar were observed on the tapir trails. Tapirs often exhibited alert positions inside the clay lick and invariably ran away when other animals entered the lick. Distress squealing associated to this "flight" behavior was heard only from the young. Anti-predator behavior in tapirs is individualistic. In a situation of threat, the mother initiates the flight.

Although the mother calls the young when a percieved threat occurred, she did not actually defend the calf. This behavior seems to contrast with the anti-predator behavior of rhinoceroses, members of the same suborder as tapirs (Ceratomorpha). Like tapirs, rhinos do not form cohesive groups, except for the mother-calf couple. Adult rhinos, like other megahervibores, often respond with indifference or aggression to a predator attack (Owen-Smith 1988). Mothers defend their calves aggressively, in some cases killing the predator (Owen-Smith 1988).

This protective behavior was not observed at the clay lick, but it could occurr in areas outside the lick. In captivity a nursing female showed aggression toward another adult female (Maher 1984), but it is not clear if the aggression was elicited as protection of the young. In fact, in zoos adult males are often removed from the mother-young pair to avoid injuries (Barongi 1993) or even the death of the new-born (Kuehn 1986). There

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[1]Ricardo Holdo, personal communication

are also anecdotical accounts of female tapirs with young or solitary animals attacking and killing dogs.[2]

Although tapirs may be aggressive in some circumstances, in a clay lick they prefer to leave in the event of a possible threat. Other ungulates may show some aggression toward other animals at the lick to displace them. For example, some moose may displace aggressively other conspecifics to drink from mineral springs (Couturier and Barrete 1987). Congregation of moose in mineral licks is considered an "extreme social situation" (Couturier and Barrete 1987), since they are otherwise solitary. Like moose, tapirs are usually solitary animals, but they react in a different fashion in mineral licks. Rhinos usually form brief but amicable associations when they meet at water holes or mineral licks (Estes 1991).

Mother-Young Relationships

Although the main interaction among mother and young at the lick was limited to vocal communication, other observations are worth to discuss. The presence of young tapirs at the lick indicates that these animals begin using licks early in their lives. The young tapir observed in this study was approximately 6-8 months old (she had already lost most of the infantile striped and spotted coat). Since young are weaned at four months of age (Barongi 1993), the presence of this mother-young pair indicated that maternal care extends beyond weaning. In Barro Colorado Island, semipermanent associations between mother and young of Baird's tapir were also observed (Montgomery & Sunquist, unpublished data).

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[2]Jose Fragoso, personal communication.

Observation of these tapirs in Barro Colorado indicated that during the first days, the new born is hidden in a safe place, and does not accompany the mother on foraging trips. After ten to fourteen days the calf begins to follow the mother in grazing or foraging (Montgomery & Sunquist, unpublished data, Eisenberg 1981, Eisenberg *et al.* 1987, Padilla & Dowler, 1994).

Only once a very young tapir (still with the stripped and spotted coat) was observed at the clay lick. The young was standing at the border of the cliff while the mother was eating clay inside the lick. The young never entered the lick, but it was clear that he/she was following the mother.

Although most ungulates clearly fall into the “following” or “hiding” categories (Lent, 1974), depending on whether the young follow the mother or they hide in a safe place, tapirs seem to have both hiding and following phases during their infant development. Hiding occurs during the first two weeks of life and following behavior begins after two weeks of age, and the young maintains close proximity to the mother during foraging (Eisenberg 1981). Vocalizations are used by females to call the young, both during hiding and following phases (Padilla & Dowler 1994, Eisenberg *et al.* 1987). Color patterns of young are related to the hiding strategy (Eisenberg, unpublished data).

Summarizing, this chapter described the main aspects of lowland tapir behavior at a mineral lick. Activity of tapirs at the lick was mainly nocturnal and their visits lasted for about half hour. Adult tapirs spent most of their time at the lick in ingestive behaviors. Direct vocal communication was frequent in mother-young interactions. Also, tapirs seem to have an active chemical communication through urination. Anti-predator behavior inside the clay lick involved rapid flight as response to any potential threat. Aggressive behavior was not observed probably because of the potential vulnerability of tapirs in licks. Tapirs initiate lick use early in their lives.

CHAPTER 5

CHEMICAL COMPOSITION OF THE CLAY AT THE LICKS AND GEOPHAGY BY LOWLAND TAPIR

Introduction

Deliberate soil ingestion (geophagy) is common in many herbivores and omnivore mammals, as well as some birds and reptiles (Kreulen and Jager 1984). Geophagy is usually selective, occurring in specific locations commonly termed natural licks, mineral licks, and salt licks. As noted by the last two terms, it is thought that the main purpose of geophagy is mineral or salt intake. Indeed, eating soil has been suggested as a way to satisfy mineral deficiencies in the diet (Jones and Hanson 1985). Sodium is the most commonly reported mineral sought by animals at licks (Hebert and Cowan 1970; Stark 1986; Moe 1992; Jones and Hanson 1985; Jenks and Jones 1995; Tracy and McNaugthon 1995; Klein and Thing 1989). However, some mineral licks may have several elements whose concentrations are considerably higher than control samples (Hensahaw and Ayeni 1971, Lips and Duivenvoorden 1991, Emmons and Stark 1979) suggesting that more than one element might be sought by animals. Moreover, in some places mineral composition of licks and non-lick areas is so variable that it is not clear which elements are attracting wildlife (Seidensticker and McNeely 1975). Also, other properties of the soil such as buffering and adsorption capacities are also suggested as factors attracting animals to soil intake (Kreulen 1985).

The purpose of this chapter is to describe the chemical composition of the clay from the three licks visited by tapirs and other mammals, as well as to explore the significance of soil consumption by lowland tapir. The terms mineral licks, natural licks and clay licks will be used interchangeably.

Specific Methods

Eight samples of soil were taken from the three clay licks, and two from the surrounding forest. Samples were analyzed for total chemical composition by the laboratory GSC of Peru, as described in chapter 2. Contents of Mg, Ca, K, Mn and Fe were initially expressed as MgO, CaO, K_2O, MnO and Fe_2O_3. Total content of each mineral in those oxides was calculated using their atomic weights.

Results

Table 5.1 summarize the concentrations of the nine main elements found in the soil samples. Contents of the other elements analyzed were very small. Concentration of those elements were as follows: As <15 ppm, Bi, Sb, Mo < 5 ppm and Cd < 1 ppm. Contents of Ba ranged between 116 to 647 ppm.

Except for the spider monkey clay lick, contents of Na, Mg, Ca and K were consistently higher at the clay samples from the licks than the samples from the surrounding soils (Table 5.1). Overall elemental concentration of the spider monkey clay lick was dramatically lower than the other two licks and even the control samples.

Concentrations of Na, Mg, Ca and K at the lick samples (except those from the spider monkey lick) were up to one order of magnitude larger than those from the

Table 5.1. Mineral content (in ppm) of clay at the licks and control samples.

Sample	Location	Place	Frequency of use	Na	Mg	Ca	K	Mn	Zn	Cu	Fe	P	pH
A	Tapir clay lick	1	Heavily used	3519	4240	17796	11208	743	80	34	38679	197	8.00
B	Tapir clay lick	1	Heavily used	2165	4272	89337	9797	759	65	36	35112	243	7.45
C	Tapir clay lick	1	Heavily used	2114	3236	71827	8717	700	132	30	28117	223	7.32
D	Tapir clay lick	2	non-used	2220	2412	83619	6145	507	142	24	22942	189	7.59
E	Tapir clay lick	3	Occasionally used	3131	5386	43811	12786	1206	85	36	39518	305	7.66
F	Tapir clay lick	4	Heavily used	2529	3523	54388	10959	273	79	38	41826	200	7.82
G	S. monkey clay lick	-	Heavily used*	345	553	654	2238	70	15	13	7694	109	5.84
H	Small clay lick	-	Heavily used	2420	2667	18796	7726	324	53	27	29306	126	7.69
I	Outside forest	-	non-used	869	972	1221	4403	877	34	12	17836	347	5.37
J	Outside forest	-	non-used	572	891	1018	3708	395	78	12	10911	185	6.13

* sample from the edge were mainly collared peccaries were observed

surrounding forest. Calcium, in particular, was the element with the highest concentration. Amounts of Fe were also relatively high in all samples, especially those from the licks. Concentrations of Mn, Zn, Cu and P were variable among samples, without consistent differences among lick and non-lick samples. No consistent differences were found in elemental composition among the different places inside the tapir clay lick, although not all of them were used with the same frequency by animals (see chapter 4). Soil alkalinity (pH) was higher in the samples from the licks, except for the spider monkey lick.

Discussion

High concentration of one or several minerals is a frequent characteristic of natural licks (Kreulen and Jager 1984). That was the case of most of the samples from the licks, except for the very low concentration of all elements in the sample of the spider monkey clay lick. Since only one sample from the spider monkey clay lick was taken, in contrast to the six samples taken from different places inside the tapir clay lick, and this sample was collected from an edge of the lick not used by tapirs, it is difficult to determine if low mineral content occurs in the whole spider monkey lick. It is possible that properties of the soil, other than mineral contents at the spider monkey clay lick are attracking the animals. However, since the tapir clay lick was more representatively sampled, the possible role of mineral-rich clay intake from this site by tapirs will be discussed. Other possible reasons for geophagy will be also examined in the second section of this discussion.

Soil Ingestion and Dietary Mineral Deficiencies

Sodium, as well as calcium, phosphorus, potassium, magnesium, chlorine and sulphur are needed in relatively large quantities (milligrams per gram) in animal diets and are termed macroelements or major elements (Robbins 1983, McDonald *et al.* 1995). Trace elements, needed in relatively small amounts include iron, zinc, manganese, copper, molybdenum, iodine, selenium, cobalt, fluoride and chromium (Robbins 1983, McDonald *et al.* 1995).

Animals derive their mineral needs from their food. For herbivores, however, sources of some minerals may be limited, depending on the characteristics of the soil and vegetation. Poor mineral contents in vegetation may result in nutritional deficiencies if animals do not find alternative sources.

Also, concentration of essential minerals in the diet may occur in such proportions that one or more elements may affect the retention or availability of others (Kreulen 1985). For example, excess of phosphorus reduces calcium absorption by forming insoluble complexes (Robbins 1983).

Soil consumption at mineral-rich areas has been interpreted as a strategy to aleviate mineral deficiencies or unbalances in the diet. Evidence supporting the hypothesis that soil intake may help in reducing mineral deficiences were sumarized by Kreulen and Jager (1984) and include: 1) the ability of grazing livestock of free-choosing supplemented salts containing elements that are deficient in their diets, 2) *in vivo* and *in vitro* experiments showing increase of macro and micronutrient levels in digestive liquors by elements released from ingested soil and 3) increase in absortion and retention of several minerals by adding soil or clay to the diet of some domestic animals.

The minerals sought by animals at natural licks seem to vary among geographical regions (Table 5.2). Sodium was inferred to be the main mineral sought by a variety of ungulates in the temperate region. Jones and Hanson (1985) in their extensive study of mineral licks concluded that the main elements sought by ungulates are Na and Mg in eastern North America licks and Ca and Mg in western North America licks. In the tropical region, sodium, calcium and magnesium seem to be the main minerals sought by animals (Table 5.2).

Sodium sources represent a problem for a herbivore, especially because a few terrestrial plants require sodium and they usually do not accumulate it. Since sodium is easily leached, soils and vegetation of alpine and continental areas with high snow or rainfall are commonly sodium depleted in contrast to coastal and desert areas (Robbins, 1983).

Heber and Cowan (1971) found normal concentrations of Na in goat blood samples and increased Na loss in feces during the spring, in spite of that vegetation eaten by goats which was clearly deficient in this element. Spring was the season when goats used licks the most. In mammals, sodium requirements are not constant, but increase with behavioral stress, reproduction (since fetal growth and milk production require this element), and excessive potassium or water intake (since high concentration of potassium reduces sodium retention) (Robbins, 1983).

Table 5.2. Use of natural licks by wildlife in temperate and tropical regions and suggested elements sought by animals.

		Lick users				
Site	Ecosystem	Species	Sex/age	Season	Suggested elements sought by animals*	Reference
Temperate Region						
Black Hills, South Dakota, USA	Pine forest, Rocky Mountains	white-tailed deer (*Odocoileus virginuanus*)	mostly adult females.	spring and early summer	Soluble salts, Na, and NO_3N	Kennedy *et al.* 1995
Jameson Land, northeast Greenland	Tundra	muskox (*Ovibos moschatus*)		summer	Na	Klein and Thing 1989
Yukon Arctic Coastal Plane, Canada	Tundra	barren-ground caribou (*Rangifer tarandus granti*)	females and yearlings	spring	Na, Cl, SO_4 and NO_3	Calef and Lortie 1975
Rocky Mountain Trench, Brithish Columbia, Canada	??	Mountain goat (*Oreamnos americanus*)	males and females	spring (♂) and early summer (♀)	Na	Hebert and Cowan 1971
Denali National Park, Alaska	open white sprude forest, low and tall shrublands	moose (Alces alces)	both sexes but subadult ♂ more often	spring and early summer	Na	Tankersley and Gasaway 1983
Sibley Provintial Park, Ontario, Canada.	boreal forest	white-tailed deer (*Odocoileus viginuanus*) and moose (*Alces alces*)	females and males	late spring (♂) and middle summer (♀)	Na	Fraser and Hristienko 1981
Northern New Hampshire, USA	Ecotone between coniferus and deciduos forests	moose (*Alces alces*)	both sexes, but adult ♀ more often	Summer and autumn	Na	Miller and Litvaitis 1992
Matane Wildlife Reserve, Gaspé Peninsula of Quebec, Canada.	Mixed forest?	moose (*Alces alces*)	adults and calves of both sexes	summer (early July)	Na	Couturier and Barrete 1987
San Gabriel Mountains, California, USA	?	mountain sheep (*Ovis canadensis nelsoni*)	?	spring and summer	Ca and Mg	Holl and Bleich 1987
Martin County, souther Indiana, USA	old-fields and woodland	white-tailed deer (*Odocoileus virginianus*)	both sexes, all ages	Spring	Na	Weeks and Kirkpatrick 1976
Konza prairie, Kansas, USA	tallgrass prairie	ungulates	-	-	Al, B, K, Mg, Mo, Na	Tracy and McNaughton1995
Yellowstone National Park, Wyoming, USA	?	ungulates	-	-	B and Na	Tracy and McNaughton1995

Table 5.2. continued

Site	Ecosystem	Lick users: Species	Lick users: Sex/age	Season	Suggested elements sought by animals*	Reference
Tropical Region						
Serengeti National Park, Tanzania, East Africa	tropical savanna	ungulates	-	-	Al, Fe, K, Na and P	Tracy and McNaughton1995
Yankari Game Reserve, Nigeria	northern guinea savanna woodland	elephant (*Loxodonta africana*) , buffalo (*Syncerus caffer brachyceros*), roan (*Hippotragus equinus*), western hartebeest (*Alcelaphus buselaphus*), waterbuck (*Kubus defassa*), oribi (*Ourebia ourebi*), red-flanked duiker (*Cephalophus rufilatus*), warthog (*Phacochoerus aethiopicus*), baboon (*Papio anubis*)	both sexes, but ♂ buffalo more often than ♀	year around but more often during rainy season	Ca, Mg and Na	Hensahaw Ayeni 1971
Wankie National Park, Central Africa	aeolian Kalahari sand	elephant (*Loxodonta africana*)	-	dry season	Na	Weir 1972
Murchinson Falls National Park, Unganda	grassland and river banks	elephant (*Loxodonta africana*)	-	dry season	Na, Ca	Weir 1973
Manovo-Gounda St. Floris National Park, Central African Republic	gallery forests, riverine wooded savanna and open planes	elephant (*Loxodonta africana*) and 20 more species of large mammals	-	-	Na, K, Ca, Mg	Ruggiero and Fay 1994
Kanyawara, Kibale Forest Reserve, W. Uganda	moist evergreen forest	guereza monkeys (*Colobus guereza*)	-	-	Mg, Fe, Cu (in clay) and Na, Fe, Mn, and Zn (in water-plant samples)	Oates 1978
Bardia National Park, Nepal	tropical lowland forest (*Shorea robusta* forest)	Axis deer (*Axis axis*), common langur (*Presbytis entellus*) and 10 more mammalian species	-	dry season	Na	Moe 1993
Benoue National Park, Cameroon, West Africa	-	elephant (*Loxodonta africana*) and hippopotamus (*Hippopotamus amphibius*)	-	year around but more often during dry season	Na	Stark 1986
Huai Kha Khaeng Wildlife Sanctuary, Thailand	evergreen tropical forest	elephant (*Elephas maximus*), sambar (*Cervus unicolor*), and barking deer (*Muntiacus muntjac*). Occassionaly: swine (*Sus scrofa*), banteng (*Bos javanicus*), gaur (*Bos guarus*) and tapir (*tapirus indicus*)	-	after rainy season?-	Not clear. Element contents very variable among samples	Seidensticker and McNeely 1975

Table 5.2. continued

		Lick users				
Site	Ecosystem	Species	Sex/age	Season	Suggested elements sought by animals*	Reference
High Aripuaná River, south of Amazon region, Brazil	tropical rainforest	peccaries (*Tayassu tajacu* and *T. pecari*), lowland tapir (*tapirus terrestris*), red brocket deer (*Mazama* sp.) agouti (*Agouti paca*), spider monkey (*Ateles paniscus*), red howler monkey (*Alouatta seniculus*) and several species of birds.	-	Dry season	Ca ?, Mg?	Ayres and Ayres 1979
Middle Caqueta River region, Amazon, Colombia	tropical rainforest	lowland tapir (*Tapirus terrestris*) and monkeys	-	-	P, Ca, Mg, Na, K and Cl	Lips and Duivenvoorden 1991
Amacayacu National Park, Amazon, Colombia	tropical rainforest	mammals and birds	-	-	Ca, Mg and K and Na	Narvaez and Olmos 1990
Manu National Park, Peru	tropical rainforest	parrots and macaws	-	-	Ca, Mg, and Na	Emmons and Stark 1979
Manu Wildlife Center, Madre de Dios, Peru	tropical rainforest	lowland tapir (*Tapirus terrestris*), red brocket deer (*Mazama americana*), collared peccary (*Tayassu tajacu*), white-lip peccari (*T. pecari*), red howler monkey (*Alouatta seniculus*), black spider monkey (*Ateles paniscus*), parrakeets, pigeons and guans	both sexes, but ♀ more often (lowland tapir)	dry season	Ca, Mg, K, and Na	This study

* Elements which concentrations were substantially greater in the lick samples than in the associated controls and/or found to be deficient in the diet during the season when mineral licks were more often used.

amazonian fruits (Lopes *et al.* 1980). Thus, detailed information about the availability of minerals from plants eaten by tapirs and analyses of mineral fecal excretion would help to better understand of the relationship among mineral balance and geophagy in lowland tapir.

Soil Ingestion and Plant Toxicity

One mechanism plants use as a defense against hervibory is to build chemical deterrents, toxins or digestibility-reducing compounds in their tissues (Crawley 1983). Some of those chemical substances are called "secondary plant compounds" and include tannins, alkaloids and cyanogenic glycosides, among others. Tannins act as protein complexing agents, binding to proteins, inactivating digestive enzymes and forming indigestible marocromolecules (Robbins 1983). Alkaloids and cyanogenic glycosides act as toxins, poisoning specific metabolic process (Crawley 1983). Although some types of tannins (hydrolyzable tannins) may be degraded by enzymes present in the saliva of many ruminants and monogastrics (Van Soest 1982), condensed tannins are extremely resistant to enzymatic attack (Swain 1979). Oates (1978) suggested that Colobine monkeys may consume clay because its absorptive properties could help in detoxifying secondary compounds in their diet. It is believed that kaolin (a group of clay minerals) provides a protective coating in the digestive tract that prevents tanning of the gut wall, while absorbing toxins and promoting their excretion (Oates 1978). In fact, kaolin has been used in veterinarian practice to reduce digestive problems in some animals (Oates 1978).

Like tapirs, browsers and mixed feeders like giraffe, kudu and eland visit clay-providing licks probably for the anti-toxic action of the clay (Kreulen 1985).

The lower concentrations of chemical and mechanical defenses that occurs in pioneer species may explain why tapirs prefer browsing in gaps (Salas and Fuller 1996). However, part of the diet of lowland tapir possibly contains high levels of secondary compounds. For example, a species of *Cecropia* (*C. sciadophylla*) is common in lowland tapir's diet (Salas and Fuller 1996). *Cecropia* trees have very variable concentrations of tannins. Young trees of *Cecropia peltata* have high concentration of tannins compared to older trees (Coley 1984). Tannin levels are lower in *Cecropia* trees grown under shade, compared to those growing in open areas (Coley 1984).

It is possible that tapirs are gaining the additional benefit of toxin absorption from the clay they eat, which is probably rich in kaolinite. Kaolinite is the structurally simplest and abundant clay mineral in the Amazon region (Irion 1984).

Another benefit of soil ingestion may be its action as antiacid. In Colobine monkeys, the forestomach drops its pH during fermentation as fatty acids are produced, which may affect the stomach bacterial population. Clay may reduce acidity by supplementing the buffering action of stomach secretions (Oates 1978). In ruminants, the introduction of concentrates induces soil eating behavior that ceases when bentonite clay is added to the food (Kreulen 1985).

Whether tapirs eat clay to alleviate dietary mineral deficiencies, protect themselves from toxic plant secondary compounds or reduce acidity, is not clear. Although part of the diet of lowland tapir is known, the chemical composition (mineral nutrients and toxic

Only solitary tapirs or couples of mother and her young visited the clay lick. Visits occurred mainly around midnight, and only occasionally during the day. Some tapirs seem to be residents of the area, whereas others appear to be around the clay lick only for a few consecutive days. Tapirs stay at the lick in average for close to half an hour when not disturbed. Few animals stay longer time. Tapirs spend much of their time in ingestive activities which indicates a significant intake of clay. Young tapirs learn to consume clay early in their lives, when they join the mother at the mineral licks. Adults frequently urinate at the lick, by which they seem to maintain active chemical communication. Direct vocal communication was frequent among adult females and their young. Tapirs are vulnerable at mineral licks because they are exposed to an open area with little defense against predators. Their anti-predator behavior involves immediate and individualistic flight in front of a potential threat. Although tapirs may be aggressive in some circumstances, aggressive behaviors were not observed when more than one tapir entered the lick. Instead, immediate running and avoidance was the invariable response.

Chemical composition of clay at the mineral lick is characterized by higher concentrations of Na, Ma, Ca, and K compared to soil samples from the surrounding forest. Two possible reasons may explain the tapir use of clay licks. First, tapirs might alleviate potential mineral deficiencies or imbalances by consuming mineral-rich clay. Sodium is very often suggested as one of the main elements sought in mineral licks. This hypothesis needs to be tested for tapirs. An alternative, non-excluding explanation is that clay may help tapirs in detoxification from secondary compounds that may be present in their diet. Clay buffering properties have been also suggested as the attracting factor.

The results of this study imply that natural mineral licks are important sites for tapirs, not only because of the nutritional benefits they may get from clay consumption, but also because of the communication system they establish in those places. Chemical communication may be telling the animals about reproductive condition, sex and social status of other visitors. Tapirs, however seem to be very vulnerable at clay licks. Natural predators may find tapirs easily in the open mud, where they do not have any protection different from running away. Predation by humans is also favored at clay licks, and is a common practice in many places of tapir distribution. These two factors (importance of clay licks for tapirs and their vulnerability at those places) should be taken in consideration in management and conservations plans for tapirs. Abundance and distribution of clay licks should be considered as important elements of habitat quality for lowland tapir. Habitat restoration for tapirs should include reduction of hunting pressure by humans at mineral licks.

From the research point of view, observation of tapirs at mineral licks represent an inexpensive method to address some aspects of their behavior and population features. Tapirs are very difficult to observe in free ranging conditions. However, in this study a large number of tapir sightings were recorded, in a relatively short time. Further research is needed to: 1) understand how the pattern of movement of tapirs is related to the distribution of clay licks, 2) determine whether some sex/age classes have higher nutritional needs that induce them to use clay licks more often than other animals, 3) directly measure nutritional deficiencies in the diet and clarify which are the key elements sought by tapirs at licks, 4) directly measure the relation between mineral deficiencies in

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