Observations on the ecology and behavior of the giant river otter Pteronura brasiliensis in Suriname

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OBSERVATIONS ON THE ECOLOGY AND BEHAVIOR OF THE GIANT RIVER OTTER *PTERONURA BRASILIENSIS* IN SURINAME

by Nicole DUPLAIX *

CONTENTS

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I. — *INTRODUCTION*

A. The Problem

While the giant Brazilian otter *Pteronura brasiliensis* Gmelin 1788, the largest river otter, is listed as rare and endangered in the IUCN Mammal Red Data Book (1972), virtually nothing is known of its ecology or biological requirements in the wild. Early authors

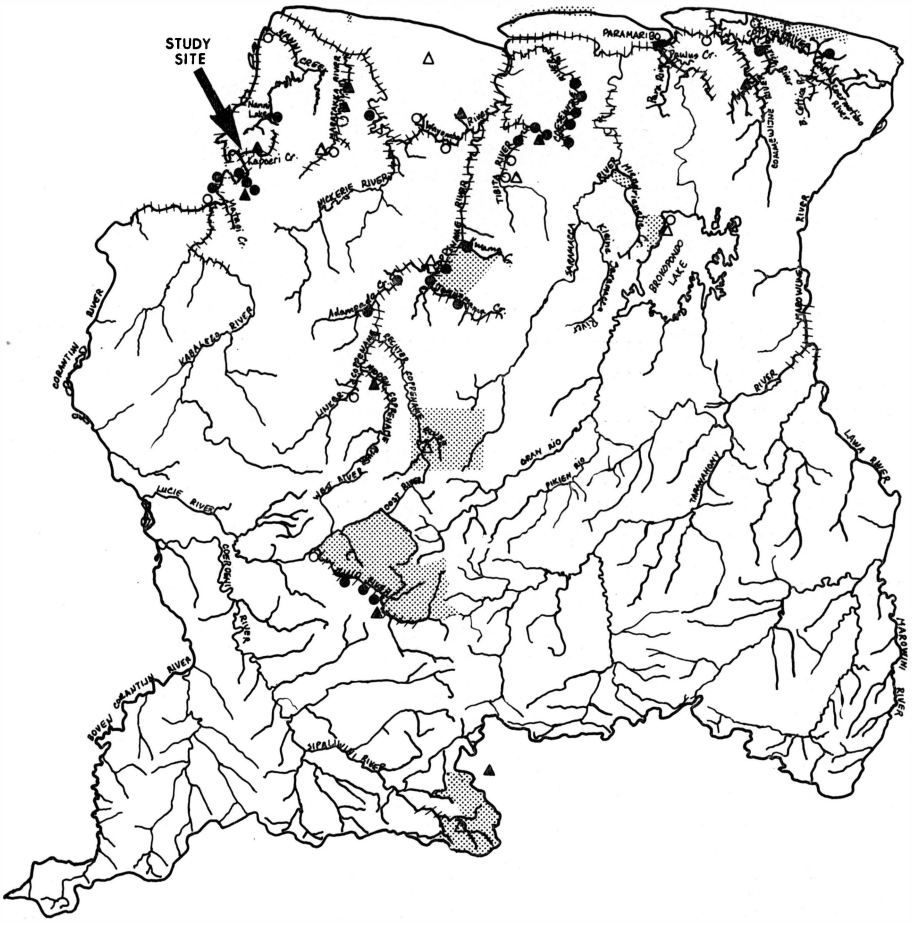


Fig. 1. — Map of Suriname, showing the rivers visited during the giant otter survey 1976-1978.

(Desmarest, 1820 ; Harlan, 1825) reported on its social habits and apparent fearlessness towards man ; noisy groups surrounded the canoes of the Amazon Basin explorers. Such a large, gregarious and diurnal species makes an easy target for pelt hunters and it is the demands of the fur industry which are responsible for *Pteronura's* endangered status today.

A study of *Pteronura* in the wild became an urgent priority of the IUCN Otter Specialist Group. Practical survey methods had to be devised which could be applied in other countries throughout its South American range. Population density estimates, food habits and habitat requirements were lacking, making long-term conservation strategies impossible. Hitherto the paucity of information on this otter's natural history could be attributed in part to the inaccessibility of the rivers where it might still occur in reasonable numbers. The field reports that had been received were usually speculative and fragmentary in nature but all expressed concern that *Pteronura* might become extinct before any scientific data had been collected.

The northeastern portion of its range was investigated in an effort to find a suitable study area where giants otters were not subject to constant hunting pressure. A preliminary survey in Suriname in November 1975 determined that it was still possible to make direct observations of the otters. Suriname has implemented an effective conservation program with nine Nature Reserves (Schulz *et al.*, 1977) and the giant otter is still considered common along most of the rivers of the interior. Centermost of the three Guyanas, Suriname is underpopulated by Latin American standards (383,000 people live in 10 % of the 160,000 km²) and the giant otter is not hunted for food or profit. Consequently this country seemed an ideal choice and a 20-month field study was initiated in July 1976, ending in April 1978.

B. The Suriname Habitat

1. Topography

The low-lying and flat northern coastal region contrasts with the rolling forested mountain ranges of the southern interior ; the highest Wilhemina mountain peak is only 1280 m. Plateaus (e.g. Brownsberg 514 m) and isolated granite outcrops (e.g., Volksberg 240 m) are widely scattered.

Suriname is divided by six major river systems and their tributaries, most of them flowing from south to north (Fig. 1). The rivers are, from east to west, the Corantijn bordering Guyana, the Nickerie, the Coppename, the Saramacca, the Suriname, the Commewijne and the Marowijne bordering French Guiana. The northern portions of the rivers and those running parallel to the coast are wide and slow while the upper reaches below 5°N in the interior are crisscrossed by numerous rapids and waterfalls.

2. Climate

Due to its proximity to the equator, Suriname has a genuine tropical climate with high temperatures throughout the year (average 23°C). The mean monthly temperatures vary by 2° during the year, the highest occuring in September-October, the lowest in January-February (Fig. 2). Daily variations are greater ranging from 22-36° in open areas and 22-32° in the rain forest during the dry season. The highest temperatures are usually 5° lower in the wet season (Schulz, 1960).

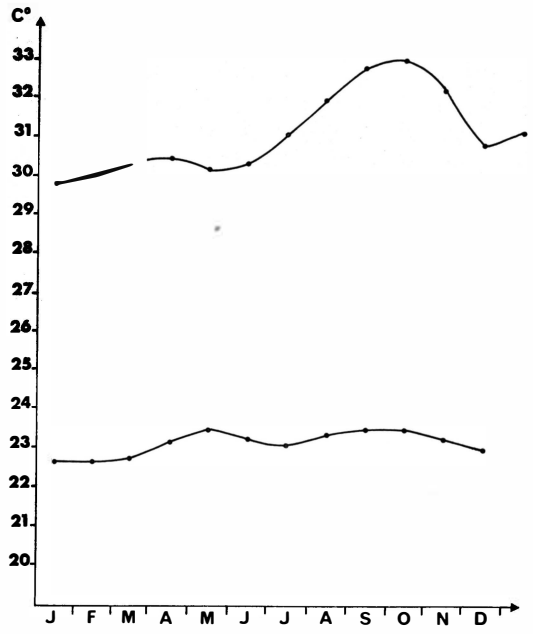


Fig. 2. — Annual temperature, minimum and maximum, averages recorded in Paramaribo.

Relative humidity is high (82 %-95 %) in the rain forest, reaching its maximal point at night. In open spaces and on rivers, the daily amplitude is more marked, reaching 40 % at midday (Hoogmoed, 1969).

A climatic factor which varies markedly from one year to the next is the amount of precipitation as well as the onset, duration and end of the rainy and dry seasons. The long rainy season (April-July) is followed by a long dry season (August-November) while the winter months are divided into short rainy season (April-July) and short dry season (February-March) (van Donselaar,

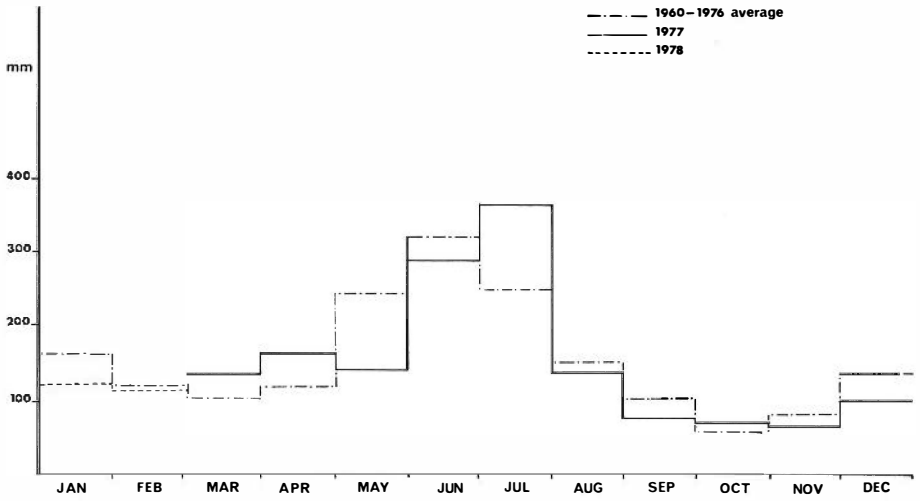


Fig. 3. — Average annual rainfall recorded at Apoera on Corantijn river (Nickerie district).

1965) (Fig. 3). Other authors, like Haverschmidt (1968) for instance, may lengthen or shorten these seasons by two weeks or more. Mean annual precipitation is between 2000 and 2400 mm (Lindemann & Moolenaar, 1959). May is usually the wettest month with precipitations of up to 400 mm locally ; and October the driest with as little as 20 mm (Hoogmoed, 1969). During the long rainy season, the water level in rivers and creeks may rise by more than 2.5 m (pers. obs.), flooding the banks and surrounding low-lying forest areas.

3. Vegetation

The vegetation of northern Suriname has been described in detail by Lindeman and Moolenaar (1959) and I will only give a synopsis of vegetation types occuring in otter habitats.

1) *Coastal region* : Mangrove forests are found only in the flat coastal region, estuaries, and in the lower portions of the creeks affected by sea water or brackish tides. Three types of mangrove exist depending on the solidity of the silty substrate : *Avicennia nitida* preferring harder ground than *Rhizophora* and *Laguncularia*. All three types of mangrove coexist in some areas, particularly in the estuarine conditions of the Corantijn, Coppename and Commewijne rivers. Mangroves can be considered poor habitat for otters in Suriname, whether on the wider rivers such as the Corantijn or Commewijne where the tides are very strong or on the smaller creeks and canals radiating from them.

Behind the mangrove belt there are open swamps and/or ridge forests. On the ridges, shrubs, palms and small stands of trees predominate. On the creeks, which may broaden into swampy areas with floating vegetation mats composed of *Nymphaea, Limnobium,* or *Ipomoea,* the banks are lined with swamp scrub or swamp forest (Beard, 1955). The water may be brackish or, further inland, tainted brown by the peat layer present. Stands of mokomoko or arum lilies *(Montrichardia arborescens)* lining the banks are characteristic of swamp forest.

2) *Interior* : While swamp forests are found quite far from the sea, particularly along the creeks of the Corantijn river (Winana and Kaboeri creeks, for instance), other vegetation zones also exist. The savannah swamps with isolated patches of gallery forest are typical of two giant otters areas : the upper stretches of Nanni creek and the upper Coesewijne river. Savannah swamps, which are flooded or boggy year around are called floating meadows (e.g. the surrounds of Nanni Lake) and are characterized by *Cyperus articulatus* and *Montrichardia.* In the Coesewijne savannah swamp *Eleocharis interstincta* is present.

Vegetation along the banks of rivers and forest creeks can be divided into the following categories, bearing in mind that there may be a succession or mosaic of vegetation types along a single creek, spaced sometimes only a few kilometres apart.

1) *Riverbank high forest.* The rain forest grows to the river's edge and is not affected by seasonal flooding. Broadleafed forest grasses and small bushes cover the ground while palms *(Astrocaryum)* are in the understory. This type of forest is common in the interior below 5°N.

2) *Swamp forest.* The soil is damp to wet year round in this floodable forest type. The thick clay soil is poorly aerated and litter decomposes very slowly, accumulating to form a peat layer (Mittermeier, 1977). Swamp forest can reach 20 m in height with palms *Bactris* and *Euterpe* predominating in the understory. *Triplaris surinamensis* (Polygonaceae) is the predominant tree. Giant otters use this habitat only during the dry season.

3) *Marsh forest.* Also floodable, but usually the soil drains well as the ground is above the water table (Beard, 1955). The herb layer is well developed *(Ischnosiphon, Ravenala, Diplasia, Olyra, Helosis)* (Lindeman & Molenaar, 1959) and *Montrichardia* does not occur as it does in swamp forest. *Maripa* palms are common. This is good otter habitat as it dries out seasonally.

4. The Aquatic Environment

The aquatic environments of Suriname are divided into two groups : 1) running water or lotic environments such as the forest streams and broad rivers ; and 2) standing water or lentic environ-

ments such as savannah swamps, ponds and lakes. The larger rivers like the Coppename and the Corantijn can be subdivided into regions : 1) the swift flowing upper reaches below 5°N with torrents and rapids with stony, boulder-strewn bottoms ; 2) the rivers become broader and slower as they emerge from the foothills of the interior and have sandy-silty bottoms ; and 3) the rivers broaden still further and gain in organic matter as they near the lower tidal reaches near the sea with larger forested islands and sand bars present. These lower areas are characterized by long estuarine reaches where the freshwater zone above the brackish zone may still be affected by tides 180 km upriver.

Lowe-McConnell (1975) has pointed out that in tropical rivers such successions between swift-water, calm-water and the widely spaced intervals between falls act as ecological barriers and help to explain the very rich freshwater fish fauna, often numbering several hundred species. In South America, the Characoid and Siluroid fishes which are the dominant types, flourish and show great variation in body form with a high degree of endemism (Roberts, 1972). Gery (1969) recorded 364 species from the Guianas which is peripheral to the richest freshwater fish fauna in the world : the Amazon Basin with more than 3000 species, 85 % of them Ostariophysi (i.e. Characoids, Gymnotoids, Cyprinoids, Siluroids). Roberts (1972) stated that in the Amazon 43 % of the fish are Characoids, 39 % Siluroids and 3 % Gymnotoids.

The fish communities are very unstable and fish predators are numerous including many piscivorous fishes of which the piranha *Serrasalmus* is the most notorious. Other predators include reptiles such as the caiman, birds and mammals, including otters. Fish migrations coincide with floods during the rainy season. The Characoids move upstream at the start of the high waters and some species have two migrations and spawning periods during both long and short rainy seasons (Meschkat, 1960). The constantly changing water level as the waters rise and fall drastically alters the faunal composition and this must also have an effect on the predators as well.

Chemically the Suriname water system includes both dark and white waters, but *Pteronura* are found usually in dark, clear waters. The blackwater rivers and creeks predominate in the forested central area where this study took place. Blackwater rivers carry only small amounts of suspended matter and even though stained a dark sepia color are clear, the transparency ranging from 60 cm to 1.8 m in creeks with white sandy bottoms. The pH ranged from 2.9 to a high of 4.9 due to the humic acid decomposition of the tree debris and leaf litter. Not surprisingly such acid creeks lack primary production of plankton and aquatic insects (Janzen, 1974). The decomposing vegetation further reduces the oxygen content of the water and the fish are dependent on

allochtonous forest debris dropping into the water such as flowers, fruits, leaves, insects, frogs and small birds (Marlier, 1967). The pile of leaves and sediment covering the bottom of slower stretches provides food and shelter, alternating with faster stretches of bare sand and boulders where rock crevices and roots provide cover for nocturnal Siluroids and Gymnotoids. Even though blackwater streams have low primary production, fish species are remarkably abundant, from 30 to 50 species exist, probably because few have specialized on any particular food and many are piscivorous or commensals of other fish (Lowe-McConnell, 1975).

The rainfall has been discussed but should now be reviewed in the context of its influence on the aquatic environment. The seasonality of rainfall leads to annual lateral flooding of the river and creek banks. The flood regime may be further complicated by rains which vary from year to year and can even be very local in effect. A good deal of information is now available about the annual cycle of events and its influence on fish communities in seasonal rivers (Lowe-McConnell, 1964).

The lateral flooding leads to temporary lacustrine conditions in the forest along the low-lying banks of larger rivers and forest creeks. The flooded forest floor, darkly stained and heavily particulate, provides a warm, marshy habitat suitable to fish spawning. Both lentic and lotic conditions may exist with small stagnant pools slowly drying up only a few meters from rapids along the larger, rocky rivers such as the Upper Coppename. Fish have adapted to the drastic seasonal changes in water level by moving about a great deal and, on the whole, confine their breeding to when the water is at its highest level shortly after the onset of the rains (Lowe-McConnell, 1975).

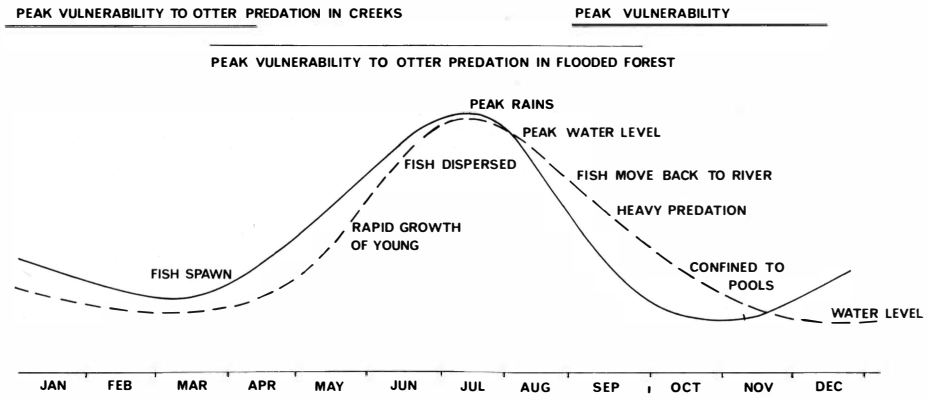


Fig. 4. — Seasonal fish cycle in relation to precipitation (Adapted from Lowe-McConnell, 1977.)

Seasonal fluctuations in water level have profound effects not only on the feeding, reproduction and dispersal of fishes (Matthes, 1964) but also on the movements of their predators. During the high water when more space and hence more food is available, fish make use of the ideal spawning habitat in the flooded forests, and as a result both fish and giant otters are widely dispersed during the rainy season (Fig. 4).

Forest streams overflowing in the wet season may be reduced to a trickle or dry up altogether during the dry season so that the fish must leave or withstand extreme variations and possible dessication. Some, like *Hoplias,* a preferred prey of otters, have adapted to deoxygenation and dessication by burying themselves in the leaf litter where they are particularly prone to predation.

The seasonal fluctuation mean that certain habitats exist only during a given portion of the year. Even though the length of the rains and height of the water level may vary from one year to the next, the rains are a predictable annual phenomenon, thus increasing the effective environmental heterogeneity — and increasing species diversity (Roberts, 1972).

C. The Study

1. Material and Methods

A 12 m dugout canoe of a 4 m Zodiac inflatable boat equipped with a 25 HP outboard motor were used on large rivers and along the coast while a 4 m aluminum canoe with a 4 or 6 HP outboard engine was used to visit narrow creeks and swamps. A local guide and a boatman were hired for the duration of the project. I was able to establish the presence of otters by direct sightings and secondary evidence while visiting a wide variety of habitats.

An aerial survey was attempted using a single engine Cessna 182 high-wing aircraft. I flew along the coastline and over major river systems at an altitude of 250-300 m at an average forward speed of 70-80 knots. One observer was seated on each side of the plane, resulting in an effective survey path of 2 km wide approximately. This technique was used during a manatee *(Trichechus manatus)* survey (Duplaix & Reichart, 1978) but proved useful in establishing accessibility to the upper reaches of poorly mapped rivers in the interior, and the extent of flooded savannah swamps and marsh forests. While well-used otter sites in open areas were visible from the air I was unable to spot dark giant otters in the black water, a difficulty complicated further by the forest canopy masking the creeks in many places. I logged 21 hours of flying in 7 flights.

Questioning local people living along the rivers proved a useful method in acquiring local information, even though not always

reliable, on the abundance and whereabouts of giant otters. Neither Carib Indians and Bushnegroes while keen hunters and fishermen shoot and eat *bigi watra dagoe* (big water dog) as they call *Pteronura* (Mittermeier, 1977 & pers. obs.).

The otters were usually observed with the naked eye or the aid of 10 × 40 binoculars at a distance of 20 to 200 m from the boat whose movement made the use of a spotting scope impractical. Habituated animals in the study area in Kaboeri (1) creek were approachable to within 5 m or less. I usually motored or paddled along a river until an otter was spotted and then either stopped and watched it and/or attempted to follow it. Observational conditions varied considerably depending on the season, the river and the response of the otters to my presence. The emphasis of the study during the rainy season when the otters retreated to flooded forest shifted to the larger rivers where the banks were not flooded and to surveys of the interior on foot.

Recordings were made of the otters on a Uher 4000 IC and a Nagra ISD tape recorders using a Sennheiser 415 directional microphone with a wind baffle. Otters were recorded at a distance of 20 m or less on Kaboeri creek for 3 hours 42 minutes and the best results were obtained from January to March 1978 once the animals had become habituated. These recordings were later analyzed (see Vocalizations) using a Kay Sonagraph which was kindly lent to me by the Department of Zoological Research, National Zoological Park in Washington, D.C.

2. Study Phases and Results

a) *Preliminary survey*

The study was divided into two phases. During the preliminary survey phase from mid-July to September 1977 six major rivers, fifteen large tributaries, 41 creeks and one lake were visited, some of them several times during 212 days in the field. This allowed me to gather a general impression of *Pteronura*'s habitat requirements and its seasonal cycle. During that survey I saw 102 otters for a total of only 4 hours 29 minutes as I was unable to maintain observations for long periods, the longest being 50 minutes, the average being 10 minutes per sighting (Table I).

b) *Intensive study*

The second phase, from September to November 1977 and 13 January to 11 March 1978 was devoted to a full time study of the resident giant otters of Kaboeri Creek, an eastern tributary of the Corantijn river, north of Washabo, a Carib Indian settlement (Fig. 5).

(1) Sometimes spelt Kapoeri (Duplaix, 1980).

Fig. 5. — Kaboeri creek entrance seen from the air. The Corantijn river and Kaboeri island are on the right.

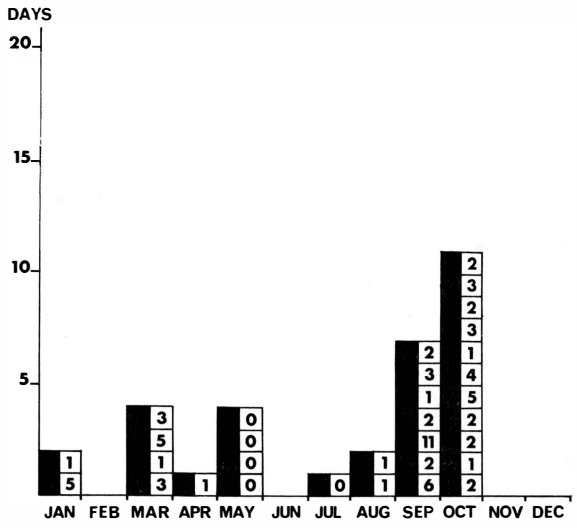


Fig. 6. — Number of sightings per day spent on Kaboeri creek in 1977. In black, number of observation days on the creek.

Previously, 74 sightings had been made on Kaboeri while monitoring the activities of the 23 resident otters every six weeks from January to 18 October 1977 (Fig. 6), and three groups totalling twelve otters became partially habituated to the observer.

By the end of the study, 188 giant otter sightings had been made totalling 252 individuals of which 97 were seen more than once. Total direct observation time was 108 hours 54 minutes during 297 days in the field. During the rainy season (May to July peak) the otters were difficult to follow and observe when they deserted the open creeks retreating deep into the flooded forests or wide open rivers with numerous islands ; only 16 sightings of 34 otters for 52 minutes were made from April to the end of July 1977 versus 139 sightings of 56 otters for 100 hours 46 minutes from August to April 1977, the majority of observation hours being devoted to Kaboeri creek animals.

Census and recognition of individual otters was possible as the patterns of white spots and blotches on the necks varied individually and were easily seen as the otter bobbed its head and neck up and down while investigating the observer.

TABLE I

List of rivers and creeks visited July 1976 - March 1978

		Visited	*Sightings*	*Evidence*	*Reports*
A.	*Corantijn River*	+	+	+	+
	Nanni Creek	+	+	+	+
	Nanni Lake	+		+	+
	Kaboeri Creek	+	+	+	+
	Kauri Creek (Kabo creek)	+	+	+	
	Matapi Creek	+	+		
	* Kabalebo River	+			+
	* Lucie River				+
	Zuid River	+	+	+	+
B.	*Nickerie River*	+	+	+	
	Arakonie Creek	+			+
	* Maratakka River	+		+	+
	Takomara Creek	+		+	
	Suake Creek	+		+	
	Oude Savannah Creek	+		+ +	
	Tokotoko Creek				+
C.	*Wayombo River*	+	+	+	
	Pierre Creek	+		+	+
	Omossé Creek	+		+	
	Arawara Creek	+		+	+
	Pereko Creek			+	+
D.	*Coppename River*	+			+
	* Coesewijne River	+	+	+	+
	Goliath Creek	+	+		
	Seekoe Creek				+
	* Tibiti River	+	+	+	
	Kabo Creek	+			
	Kalabash Creek	+			
	Kwama Creek	+	+		+

TABLE I (Continued)

	Visited	*Sightings*	*Evidence*	*Reports*
* Tangnimama Creek	+	+	+	+
Bofroe Creek	+		+	
Kodjo Creek	+		+	
Himkar Creek	+		+	
Hoof Falls	+		+	+
Tonken Falls	+		+	
Gran Soela Falls	+	+	+	
Foengoe Island	+	+		
Adampada Creek	+	+	+	
* Recter Copename River	+			
* Linker Coppename River	+		+	
* Midden Coppename River	+		+	
E. *Saramacca River*				+
F. *Suriname River*				+
* Para River				+
Kroebara Creek				+
G. *Commewijne River*	+			+
* Cassewenica Creek	+		+	+
Matapica Canal	+		+	+
Herstelling Creek	+		+	+
Caramaca Creek	+			
Mako Creek	+			+
* Mapana Creek	+			+
Mot Creek	+		+	+
Penninica Creek	+			
Hendrickson Creek	+			
Djaki Creek	+			
* Cottica River	+	+	+	
* Perica River	+	+	+	+
Ricanau Creek	+			
Barbakoeba Creek	+			
Gado Creek	+			
Koopmans Creek	+	+	+	
Orange Creek	+			
Mido Creek	+			
Boekoe Creek	+			
* Coermotibo River	+			+
Pikiensanti Creek	+			
Koemboe Creek	+			
Christoffal Creek	+			
Wane Creek	+			+
H. *Marowijne River*	+			+

* = main tributaries

A record of each otter's marking was kept and only two or three sightings were necessary to memorize the pattern (Fig. 7).

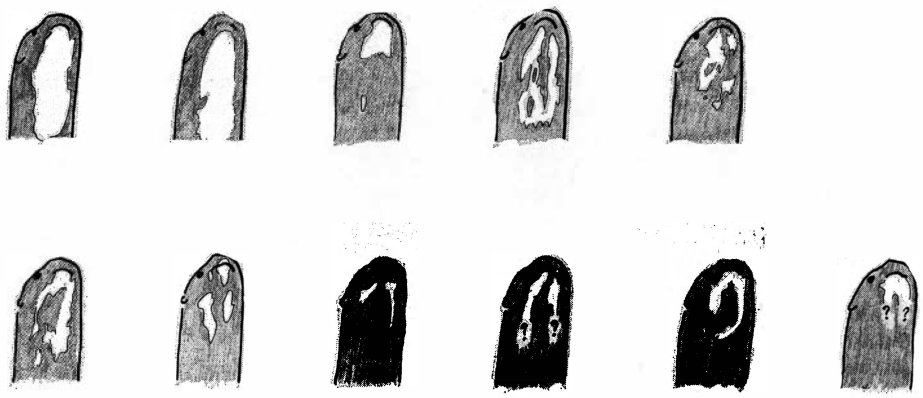


Fig. 7. — Neck patterns of *Pteronura* on Kaboeri creek.

Age classes could be distinguished readily with practice : adult males had a noticeably thicker neck and head than adult females. Subadults or cubs usually swam in the middle of groups, flanked by the adults. It was not possible to identify the sexes of subadults or cubs and they can be confused with adult females. To pinpoint each otter's movements along the Kaboeri creek, the banks were marked every 100 m for 12 km. I also used names given by the Carib Indians to certain areas of the creek and added, of course, many of my own.

D) The Species

1) Morphology

One of the largest carnivores in South America, *Pteronura brasiliensis* is a primarily terrestrial mustelid which has become extremely well adapted to using an aquatic environment as a source of food. Adult males reach a total length of 1.5 to 1.8 m and weigh 26-32 kg ; females are only marginally smaller measuring 1.5 to 1.7 m but weigh less, 22-26 kg. These are tentative data as the actual size of the " giant " otter has raised much speculation — reports of individuals measuring 2.2 m (Cabrera & Yepes, 1940) and even 2.4 m (Santos, 1945) are not uncommon. Perhaps *Pteronura* in Suriname is smaller than its Brazilian counterpart based on my observations and the measurements based on the descriptions available in the litterature (Table III).

The tail measuring 50 to 70 cm is thickly muscular at the base becoming dorso-ventrally compressed in its median to distal portion with a noticeable bilateral flange, giving it a sword blade appearance. The tail tip is rounded.

TABLE II. *Giant otter sighting data*

LOCALITY	MAIN RIVER	DATE	TIME	LENGTH OBSERV. (min.)	SEX/AGE CLASS (no repeats) ♂	♀	sub/cub	?	NUMBER of sites	SPRAINTS collected	
Koopman's C	Cottica R.	27 Jul 76	1200	4	1	1					♂ charges boat
Kwama C.	Coppename R.	13 Aug 76	1400	4	1	1	1				♂ charges, subadult
Tangnimama C.	»	16 Aug 76	1105	3	1	1	2				shy sunning on log,
Tangnimama C.	»	18 Aug 76	0840	20	1	1	3				shy
Hoof Falls	»	12 Oct 76						evidence			
Foenge Is.	»	25 Aug 76	0815	1				1			shy
Adampada C.	Up. Coppename	3 Oct 76	1335	2	1	1					shy
Gran Soela	Coppename R.	4 Oct 76	1110	2	1	1	1				shy, retreat up creek
Maratakka R.	Nickerie R.	7 Nov 76						evidence		16	
Commonada C.	Maratakka R.	8 Nov 76						evidence			
Tapoeripa	Nickerie R.	12 Nov 76	0935	28	1	1	2				♂ charges, shy
Corantijn R.		19 Jan 77	1320	11	3	2	2			6	3 ♂♂ come close
Tibiti R.	Coppename R.	25 Jan 77	1745	2				1		4	shy
Kabo C.	Tibiti R.	26 Jan 77	1118	32	2	2	3			15	♂♂ joined by ♀♀ and cubs from forest
Kabo C.	Tibiti R.	26 Jan 77	1150	10	1	1					
Coesewijne R.	Coppename R.	3 Feb 77	1345	1	1	1	1				shy
Coesewijne R.	»	3 Feb 77	1445	3	1	1					
Coesewijne R.	»	3 Feb 77	1725	1	1	1					
Coesewijne R.	»	4 Feb 77	807	8	1	1					
Coesewijne R.	»	4 Feb 77	1044	4		1	1				
Goliath C.	Coesewijne R.	5 Feb 77	1145	4	1	1	5				same as on 19 Jan and 2 new cubs ?
Corantijn R.		10 Mar 77	0912	25	2	2	4				feeding on sand bar
Kauri C.	Corantijn R.	10 Mar 77	1331	1				1			shy
Kauri C.	Corantijn R.	13 Mar 77	1052	1				1	7		shy
Perrica R.	Cottica R.	12 Apr 77	1245	3	5	5	6		1		♂♂ charge, retreat into mangrove swamp
nr. Nanni L.	Corantijn R.	6 May 77	1538	14	1	1			3		bold
Zuid R.	Lucie R.	15 Jul 77	1145	4	2	2	3				shy, retreat into forest
Zuid R.	»	15 Jul 77	1155	2	1	1	3		18	23	
Zuid R.	»	26 Jul 77	1351	29		1					
Corantijn R.		25 Sep 77	1535	50	1	1					fishing

N observations = 27 ; N otters seen = total : 102 ; by sex : 30 ♂♂, 31 ♀♀, 37 cubs/subadults, 4 ? ; N minutes of observation = total : 269 min.

R = river ; C = creek ; L = lake

TABLE III

Measurements and weights of single Pteronura *specimens.*

HEAD & BODY (mm)	TAIL (mm)	TOTAL LENGTH (mm)	WEIGHT (kg)	SEX	SOURCE
967	457	1424			Desmarest, 1817
864-890	330-356	1200			Schomburgk, 1840
1000	450	1450			Gervais, 1855
1092	610	1702			Gray, 1869
		1600			Brown, 1876
		1800	30		Kappler, 1887
720	500	1220		Sub. ♀	Nehring, 1900
		1800 +			Quelch, 1901
		1830 +	34.2		Fountain, 1902
1020	575	1595		Ad. ♂	Allen, 1910
1000	530	1530		Ad. ♀	Allen, 1910
1230	650	1880			Pohle, 1920
1200	1000	2200		Ad. ♂	Cabrera & Yepes, 1940
1400	1000	2400			Santos, 1945
1050	575	1623	24	Ad. ♂	Sanderson, 1950
1160	420	1580			Vieira, 1952
1090	580	1670			Vieira, 1952
	550-1000	1480-2200			Mondolfi, 1970
1200	700	1900			Trebbau, 1972
			24.5	Ad. ♀	Autuori & Deutsch, 1977
1000	579	1579		Ad. ♂	Husson, 1978 [1]
815	443	1258	26	Sub. ♂	Husson, 1978 [2]

1 - Collected on Kaboeri creek, Suriname (Husson, 1978).

2 - Collected on Maratakka River, Nickerie district, Suriname (Husson, 1978).

While the broad head is flattened, the blunt, sloping muzzle is so short that the otter's head seems globular. The dark, round eyes and nostrils are placed forward on top of the head and the rhinarium is haired. The small round ear pinnae are set high and well back. Numerous long mystical, supraciliary and gular vibrissae are present. The long neck is thick and muscular and often as broad as the head in adult males. The feet are large, the thick webbing extending to the end of the five clawed digits.

The fur is short, the guard hairs not much longer than the thick underfur, giving the otter a brown velvet-like coat when dry, changing to a shiny black chocolate color when wet.

The lips, chin, throat and chest may be spotted with creamy white to buff which can be virtually absent or form a large white bib on the throat. These white markings were found to be highly variable and individualistic, making the recognition of individual animals straightforward.

The dental formula is I 3/3, C 1/1, P 4/3, M 1/2 = 36. The lower premolar may be absent in some cases.

2) Taxonomy and Distribution

Pteronura, while a large and very distinctive animal, was initially the subject of much confusion, probably because specimens were not available in Europe until 1899 (Harris, 1968). First described by Margrave in 1648 it was confused with the tayra *(Eira barbara).* Later, Linnaeus (1758) made *Pteronura* synonymous with the Pacific sea otter *Enhydra lutris,* assuming that since both were the same size they must be closely related. This mistake was corrected by Zimmerman in 1777 and 1780 and, later, Gray coined the genus *Pteronura,* the Spade-tailed Otter (1837).

Only two subspecies are described : *Pteronura brasiliensis brasiliensis* (Gmellin, 1788) is the subspecies found in Suriname and *P.b. brasiliensis* occurs across the Guianas, southern Venezuela and Colombia, eastern Ecuador and Peru, Bolivia, Paraguay and Brazil. *P. b. paranensis* (Rengger, 1830) of doubtful value, is described from the Paraguay and Parana rivers and occurs in Brazil, northern Argentina and Uruguay.

II. ECOLOGY

A) Habitat selection

1) General habitat survey

The major rivers and creeks of northern Suriname were surveyed to determine the habitat preferences of *Pteronura* and *Lutra enudris.* Usually, rivers were surveyed from their mouth

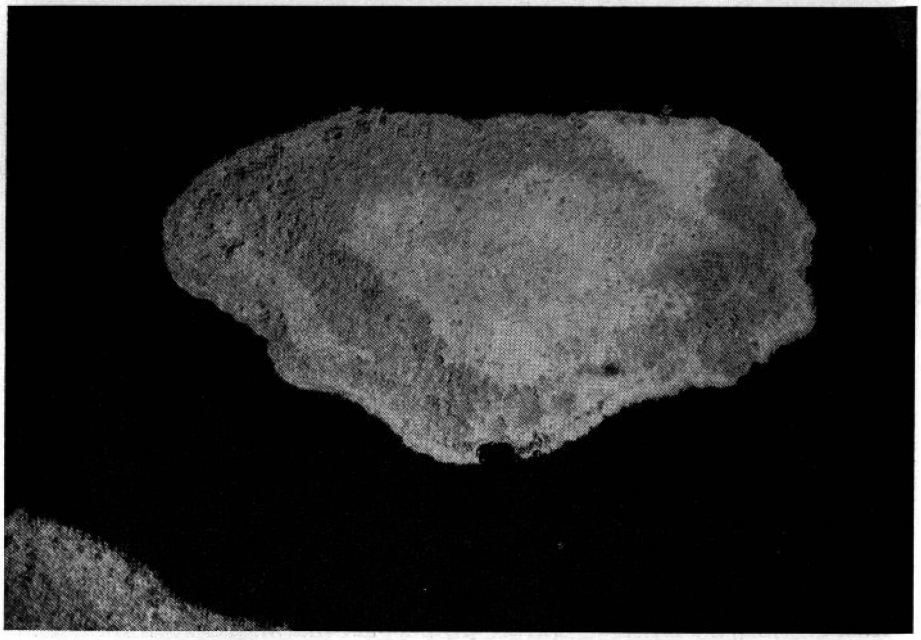


Fig. 8. — Islands on Nanni Lake seen from the air. The indentation marks a campsite along the edge. The site is visible as a thin black mark extending on either side.

up to the point where boats could go no further or until logistical problems made it impractical. Most, if not all, of the larger creeks on either bank were also explored. Locality data for *Pteronura* and *Lutra* were obtained from my own field data and from first-hand observations made by four other biologists well acquainted with the Suriname fauna. Data on habitat preference were based on my own observations.

2) Significant parameters of habitat choice

Pteronura appears to prefer slow-flowing creeks and rivers which indicate an assortment of criteria :

a) *Creek vs. river.* Due to the seasonality of preferred habitat, it is difficult to generalize on habitat types which vary during wet and dry seasons. *Pteronura* was sighted five times on large rivers like the Coppename, Nickerie and Corantijn. Three sightings were of otters crossing large rivers or feeding near creek entrances, remaining close to shore as they did so. Twenty-one sightings were made in smaller rivers or creeks where marsh forest, swamp forest, *Mauritia* palm swamp and high forest were the predominant vegetation types along the riverbanks. Mangrove

swamps seem to be avoided and *Pteronura* is not often reported in the coastal areas of Suriname, but whether this is due to unsuitable habitat and/or human disturbance is unknown. *Lutra,* on the other hand, appears to be frequently found in coastal savannah swamps and in scrub forest behind the mangrove forest lining the banks (Fig. 9).

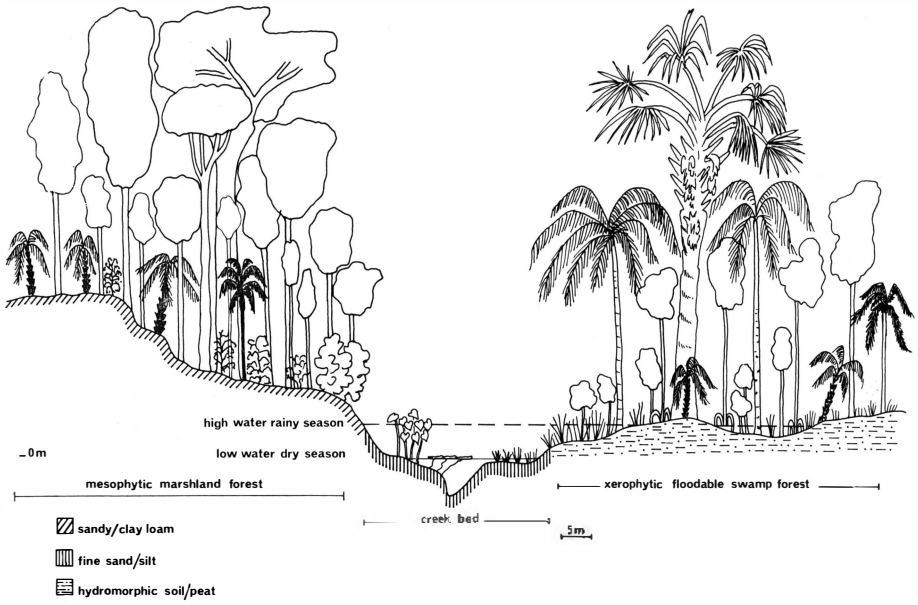
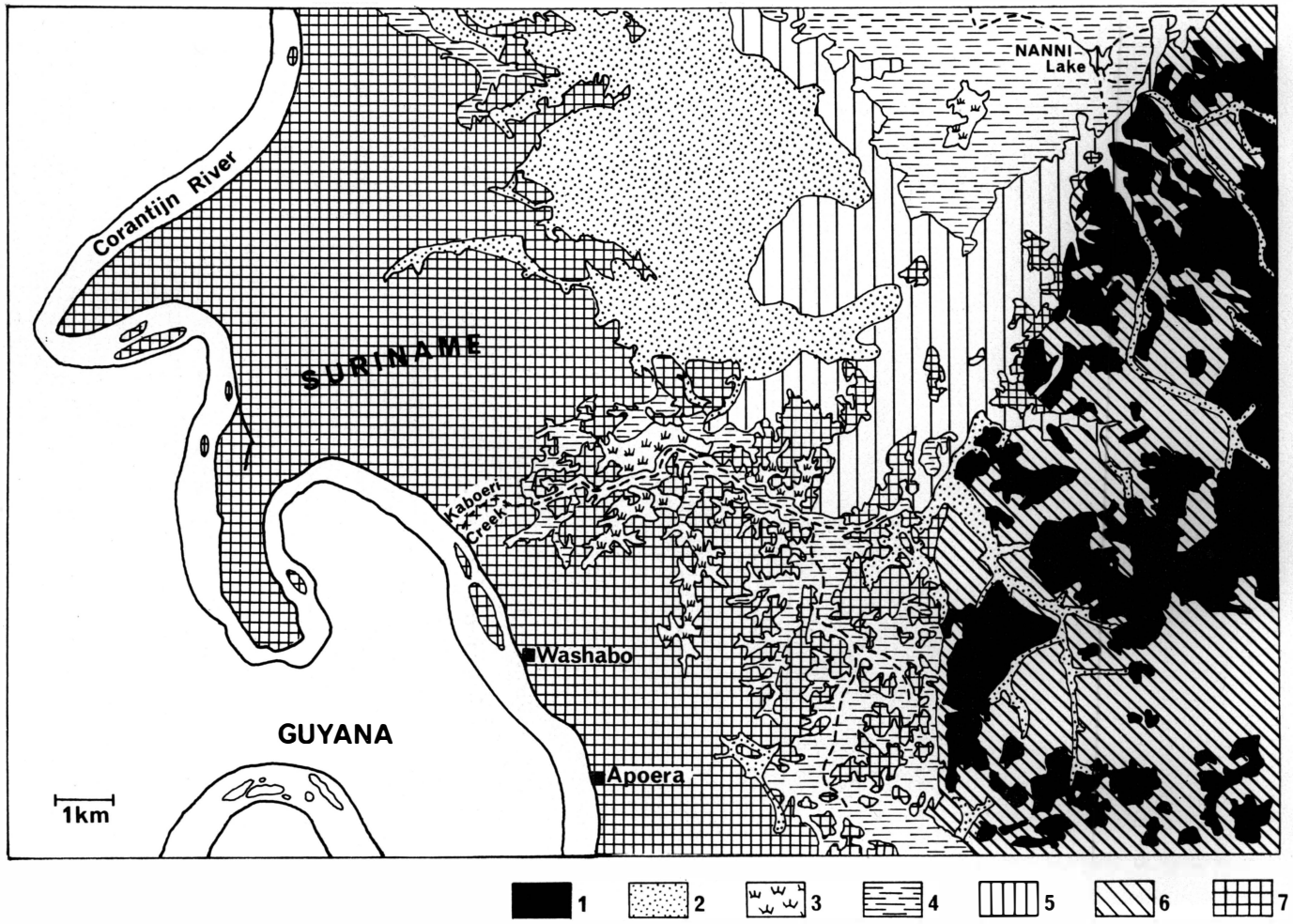


Fig. 9. — Kaboeri creek section 8 km from mouth.

b) *Bank types and cover.* These were varied and did not appear to be decisive factors. *Pteronura* were seen in wide open falls areas with little vegetation among the boulders, save for widely spaced midstream islands. Marsh and swamp forest offered a dense cover down to the water's edge with bushes and usually a curtain of *Montrichardia. Mauritia* palm swamps were more open but usually were followed by marsh or swamp forest where sites would be located. High forest usually meant high banks with relatively little undergrowth and the otters preferred lower-lying areas found along the creeks nearby. Floating vegetation mats (usually composed of *Ipomoea reptans*) were frequent on the Tibiti and Coesewijne rivers and along upper Kaboeri creek. These grass-edged sections were favored by *Pteronura* as fishing areas if they were located in shallow portions because the fish seek shade and cover under the floating vegetation (Fig. 10).

c) *Water and related aspects. Pteronura* seemed to be often associated with black water creeks with sandy or rocky bottom whereas silty, saline and white waters did not coincide with fre-


NANNI
Lake
Corantijn River
SURINAME
Kaboeri
Creek
Washabo
GUYANA
Apoera
1km
1
2
3
4
5
6
7

quent sightings. Such dark waters are common in forested areas. Marlier (1973) has explained that the dark brown color is due to the humic substances derived from decaying vegetation and humus in the forest soil. Black waters usually originate from flat land covered with swamp or marsh forests which are inundated during the rainy season. Particulate matter, either suspended or on the bottom, is present where the water flow is slowest or at slack water in tidal blackwater creeks, such as Kaboeri. The transparency may be up to 1.8 m or more if there is a sandy bottom giving a better reflection.

d) *Food availability.* *Pteronura* appears to favor these shallow creeks particularly during the dry seasons, preying heavily on the piscivorous Characoid *Hoplias* and smaller catfish (Siluroids) which lie still on the bottom. The shallower the water the more vulnerable the fish, and giant otters were observed charging through lilypads at low tide and catching small *Hoplias* at depths of 20 cm to 1 m at most.

The key factors in habitat choice are : 1) food availability with an abundance of readily available and vulnerable prey such as *Hoplias* in relatively shallow waters ; 2) low sloping banks with good cover and, preferably, easy access to small forest creeks or swampy areas and, in broader rivers, access to shallower areas such as rapids or waterfalls with pools and ponds between boulders and sandbars. Both key factors must also coincide with crucial seasonality factors affecting fish populations. The otters follow the fish during their seasonal movements, exploiting them mainly in shallow areas, the location of which vary considerably. The biomass of prey species, for instance, is greatest at the end of the rainy season, when huge numbers of small fish and crustacea are crowded together in the rapidly shrinking waters (Lowe-McConnell. 1969), whereas a few weeks later the water may have dried up completely and the fish either have been eaten or moved to deeper waters. Such rapidly changing conditions, with falls becoming calm pools in a matter of days, mean that predator-prey conditions are continually fluctuating and that habitat type preference must center mainly on accessibility to good fishing areas year around encompassing a wide spectrum of water levels. These parameters coincide with creek forest, marsh forest, swamp forest and portions of high forest vegetation types. Sometimes there are successive vegetation types along a given river or creek (such as Kaboeri) and while most of the banks might be flooded during

Fig. 10. — Vegetation map of the Kaboeri creek area. 1. Xerophytic dry forest ; 2. Hydrophytic flooded swamp forest and creek forest ; 3. Herbaceous swamps with scattered scrub and tall grass ; 4. Xerophytic floodable swamps forest and floating meadows (Nanni lake) ; 5. Xerophytic floodable palm swamps and forests. ; 6. Mesophytic dry land forest ; 7. Mesophytic dry and marshland forest. Adapted from P. Teunissen, 1978.

the rains, other higher areas of creek forest remain dry and usually coincide with large perennial otter camp sites.

B) Food and diet

1) Fish abundance and species richness

The ecology of the fish populations in the Guianas has been outlined above and the importance of the seasonal fluctuations in water level and its impact on prey species has been discussed.

The abundance of fish species and their variability within the three major orders (Characoid, Gymnotoid and Siluroid) make the study of the food ecology of *Pteronura* particularly challenging. For instance, the Characoids make up 40 % of the South American fish fauna and represent one of the most extreme and complex cases of evolutionary adaptive radiation among vertebrates (Weitzman, 1962). In 1912, Eigenmann collected 70 to 90 species in one haul of a seine net in the Essequibo river in Guyana and another 60 species in a small creek a few hours later. Characoid reproductive biology is governed by seasonal flooding ; many of them move long distances into the flooded forest to spawn during the rains. The rainy season is the main feeding and growing time for these fishes but little is known about their biology because they are so difficult to catch at this time (Lowe-McConnell, 1969). We determined that, in the study area at least, Characoids made up the bulk of *Pteronura*'s diet.

Lowe-McConnell (1975) noted that on large rivers the fish stock were poor but that the density increased near the banks on beaches. Accumulations of fishes also occur at confluents and near the entrance to smaller creeks as well as in the creeks themselves, where the current is slower. These observations coincide with my findings — *Pteronura* in large deep rivers like the Corantijn, Nickerie, Coppename were seen fishing near the banks or among the boulders and near sandbars on the plateaus. My most frequent sightings of predation took place on creeks but there is considerable bias since I spent most of my observation hours in creeks with otters habituated to our presence. I watched the subadult KI pair fishing near the entrance of Kaboeri creek around Kaboeri Island and further upstream in the Corantijn river opposite Apoera. The first 1.5 km section of Kaboeri creek is 20 m wide in places, and presents the same fishing conditions as found on the Corantijn near Kaboeri Island.

2) Direct observation of predation

It was possible to make 202 direct observations of prey capture by 4 individuals (2 pairs) on Kaboeri creek dring the dry season from 13 January to 11 March 1978.

	N Days Obs.	*Hrs. Observ.*	*N of Fish Captured by Otter*
H ♂	**19**	74 h 01	157
H ♀	**4**	14 h 34	**25**
KI ♂	**6**	11 h 20	**10**
KI ♀	**6**	11 h 20	**10**

The discrepancy between the days of observation of ♂ H and ♀ H was due to the fact that she disappeared on/or around 19 January during a territorial dispute with the neighboring S group of 7 otters. The KI subadult pair which moved into the first 1.5 km of the creek after the S group had begun to move upstream into the H pair's territory became habituated by the end of January and was observed feeding on 31 January, 26, 27, 28 February and 2, 8 March. The longest number of hours observation and direct prey capture sightings were made with ♂ H who was completely habituated and could be observed for up to 5 hours continuously as close as 3 m.

I tried to determine the size and type of prey taken. This was usually straightforward as only 11 species of fish were captured (Table IV) belonging to 4 orders (Characoids, Siluroids, Percoids and Gymnotoids). Characoids and *Hoplias malabaricus* in particular, were the favored prey ; the H ♂ caught it 83 times out of his 157 captures (53 %) but there may have been a bias as he nearly always fished in a small area of the creek called Arawaboo Pond where this species was particularly abundant. A Gymnotoid, the nocturnal logologo *Gymnotus carapo,* a close relative of the electric eel *Electrophorus,* was the species least favored : it was caught only at the beginning of the creek by the KI pair on 3 occasions out of their 20 observed captures (15 %), which represents 2 % of the total 202 captures by the 4 individuals. Both Siluroids (catfish) and Percoids were caught nearly as frequently : ♂ H 39 (24.8 %) and 28 (18 %) respectively and ♀ H 3 (12 %) and 1 (4 %) respectively (Fig. 11). The KI pair were not observed catching Siluroids which may have been harder to find in deeper water at the entrance of Kaboeri as these fish are nocturnal and hide on the bottom or in crevices during the day.

It was not possible to identify the species in 15 instances (7.4 %) either because the otter swam with the prey underwater and ate it hidden in the overhanging vegetation near the bank or consumed it with its back turned towards the observer.

The size of the prey caught varied with the type of fish taken. *Hoplias* measuring 17-22 cm were caught 38 times (34.2 %) whereas those measuring 10-15 cm were caught 21 times (19 %) and 25-

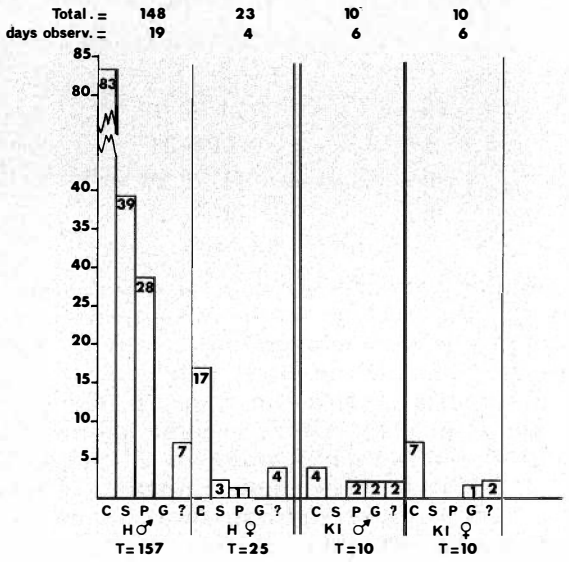


Fig. 11. — Prey categories, overall frequency of take by individual otters on Kaboeri creek. C, Characoid ; S, Siluroid ; P, Percoid ; G, Gymnotoid ; ?, Unidentified.

28 cm 19 times (17 %). This species which usually lies immobile on the bottom and partly hidden in the leaf litter is one of the most voracious Characoids (Lowe-McConnell, 1975). *Pteronura* catches it easily because of its habit of lying still until the very last minute and its preference for shallow water.

Small Siluroids of 10-15 cm were also easily caught in the shallows under lily pads or floating reeds. I recorded 26 small catfish being eaten (62 %) but the largest prey, the tiger catfish measuring 50-60 cm was caught twice (5 %) by the ♂ H and his 1976 subadult cub also caught one in October 1976 (not recorded in these data).

Small Percoids again were the predominant size taken, 24 (77 %) measuring 10-15 cm whereas two peacock bass (6 %) measuring 35-40 cm were captured by the KI ♂.

In reviewing these data I would like to stress that my findings reflect only a short time period during the dry season in one creek and cannot be interpreted as representative of what percentage of a given prey species contributes to *Pteronura*'s diet. From my direct observations and in keeping with most Carnivora, *Pteronura* is an opportunistic predator exploiting the available prey categories which are caught the most quickly and easily. It is both specialized enough in exploiting shallow water fish spe-

TABLE IV

List of species of fish observed being taken by four otters in 187 direct observations.

NAME	FAMILY	ORDER	NATIVE NAME	N	%
Hoplias malabaricus	Erythrinidae	Characoid	Pataka	95	50.8
Hoplias macrophthalmus	Erythrinidae	Characoid	Anoejmara	1	0.5
Brycon falcatus	Characidae	Characoid	Moroko	12	6.4
Hoplorythrinus unitaeniatus	Erythrinidae	Characoid	Warapa	2	1.1
Leporinus friderici	Anastomidae	Characoid	Wanakoe	1	0.5
Trachycorystes galeatus	Doradidae	Siluroid	Noja	16	8.6
Rhambdia quelen	Pimelodidae	Siluroid	Djaki	9	4.8
Pseudoplastystoma fasciatum	Pimelodidae	Siluroid	Spigrikati	2	1.1
Hoplosternum thoracatum	Callichthyidae	Siluroid	Kwikwi	15	8.1
Cichlasoma bimaculatum	Cichlidae	Percoid	Krobia	14	7.5
Cichla ocellaris	Cichlidae	Percoid	Toekoenari	2	1.1
Tilapia mossambica *	Cichlidae	Percoid	Congo	15	8.0
Gymnotus carapo	Gymnotidae	Gymnotoid	Logologo	3	1.6
				N = 187	99.9 %

* Introduced in Suriname in 1950.

cies and flexible enough to take even small prey and, in certain area, freshwater crabs. It would be interesting to have comparative data for other habitats in other parts of South America and a broader spectrum of seasonal prey species to see just how flexible *Pteronura*'s diet really is. I saw the ♂ H feeding on two unusual items : he went ashore twice in two days to gather tapir *(Tapirus terrestris)* dung and returned to the water to eat it. On four occasions the ♂ H surfaced with his snout covered in mud and chewed an unidentifiable crunchy item which may have been of crustacean or insect origin. He returned to the same place in Arawaboo pond and appeared to find the same item on all four visits.

It is clear that much work remains to be done on the predatory habits of *Pteronura* and that this is only a beginning. I was at both an advantage and a disadvantage in having habituated four otters which could be observed feeding at close range both because the sample was not large enough to eradicate the otter's possible individual preferences and the creek too small to have a broad enough sample of potential prey species.

3) Spraint collection and analysis

The analysis of spraints (scats) which has provided so much useful information on *Lutra* and *Aonyx* species (*L. lutra* : Erlinge 1967 a, 1967 b, 1969 ; *L. canadensis* : Greer, 1955 and others ; *L. maculicollis* and *Aonyx capensis* : Rowe-Rowe, 1977) was an unsatisfactory method in the case of *Pteronura,* at least for such a short study. I located 225 single spraints and collected 126 and another 65 samples were taken from 119 communal latrines. Two problems made detailed analysis difficult : 1) the huge diversity of the prey species available making identification below the order level speculative and 2) the rapid decomposition of the spraint through the combined action of temperature, humidity, sunlight, fungus and the destruction by termites and ants leaving only the scales and crab exoskeletons. Further, on communal latrines, the otters themselves spread their spraint and mix it with mud which accelerates decomposition of any softer material such as invertebrates or vegetation which might have been consumed along with bulkier prey.

Table V records where the spraint samples were collected and the superficial analysis which was conducted on the spot. As I have discussed elsewhere (cf. Home Range), *Pteronura* leave single spraint in only two types of habitats, falls areas on large rivers and small forest creeks with boulders and fallen logs where communal sites were uncommon. One could advance the theory that communal campsites are used in well-established territories in the core of the range whereas single scats are left during seasonal visits to outlying fringes of the home range.

TABLE V

Number of spraint seen and collected on various Suriname rivers and creeks, with rough analysis of contents.

CREEK/ RIVER	RIV. SYSTEM or LOCATION	DATE	N OF SITES	SPRAINT SEEN	SPRAINT COLL.	FISH ONLY N	FISH ONLY %	FISH/CRAB N	FISH/CRAB %	CRAB ONLY N	CRAB ONLY %	OTHER N	OTHER %
Coppename R.	Tonken Falls	Oct 76	29	118	43	9	20.9	25	58	9	21		
Coppename R.	Raleigh Falls	Oct 76	19	33	22	7	31.8	9	41	6	27		
Maratakka R.	Nickerie R.	Nov 76	18	17 + 1 (L)	16	15	93.8		—		—	fish and 1 mammal ?	
Nickerie R.	nr. Tapoeripa	Nov 76	4	4 (L)	3	3	100.0		—		—		
Kabo C.	Corantijn R.	Nov 76	7	9 + 1 (L)	6	3	50.0	2	33		—	amphib. ?	(16.7 %)
Coesewijne R.	nr. Biggi Poeka	Jan 77	11	16 (L)	10 (L)	10	100.0		—		—		
Kabo C.	Tibiti R.	Jan 77	16	28 (L)	15 (L)	15	100.0		—		—		
Tibiti R.	S. of Bitagron	Jan 77	6	11	4	4	100.0		—		—		
Corantijn R.	nr. Matapi	Jan 77	2	7	6		—	6	100		—		
Kaboeri C.	Corantijn R.	Jan-Sep 77	51	68 (L)	40 (L)	40	100.0		—		—		
Zuid R.	Up. Lucie R.	Jul 77	23	30 + 1 (L)	26	6	23.1	10	36	10	36		

N.B. Only single spraints were collected. (L) indicates a communal latrine where sample was taken.

I found that fish were the main prey of *Pteronura* in 112 spraint samples (58.6 %) whereas spraint containing a mixture of fish and crab appeared to be more seasonal, being found in October on the Coppename river, July on the Zuid river, November on Kabo creek on the Corantijn and January on the Corantijn near Matapi. Fifty-two spraints (27.2 %) contained a mixture of fish and crab, and 25 (13.1 %) contained crab only. Two unusual prey items were found in spraint, decomposed remains of an amphibian and broken bones of a mammal but both were unindentifiable further. It is interesting to note that fish was the only prey item found in communal latrines in three areas : Kaboeri creek, Kabo creek (Tibiti) and the upper Coesewijne river. Whether there is a bias in communal latrines due to the feces spreading procedure which might eliminate crab exoskeleton by breaking

TABLE VI

Possible competitors and predators of Pteronura *and* Lutra *in Suriname.*

	COMPETITOR		PREDATOR	
PISCES	*Pteronura*	*Lutra*	*Pteronura*	*Lutra*
Larger Siluroids	+++	+++	?	+
Larger Characoids *	+++	+++	+	+
Larger Gymnotoids	+++	+++	?	?
REPTILIA				
Caiman crocodylus	++	++	?	+
Paleosuchus trigonatus	++	++	?	+
Eunectes murinus	+	?	cubs?	+++
AVES				
Anhinga anhinga	++	++		
Ardea cocoi	++	++		
Pilherodius pileatus	+	++		
Phalacrocorax olivaceus	++	+		
Hydranassa tricolor	?	+		
Tigrisoma lineatum	?	+		
Pandion haliaetus	?	+		
Ceryle torquata	?	?		
Chloroceryle amazona	?	?		
MAMMALIA				
Procyon cancrivorus	—	++ (crabs)	—	—
Panthera onca	+	++	+	+++
Puma concolor	?	?	?	++
Sotalia guianensis	++	?	—	—

* In the Amazon 40 species of Characoids are primarily/exclusively piscivorous (Roberts, 1972).

Key : + possible, ++ likely, +++ certain, ? unknown.

them up into small particles or whether *Pteronura* does not prey on crabs in these areas because they are not available, is unknown. I scrutinized the communal latrines carefully in my search for prey items. Crabs were found in spraint in Kabo creek, another forest creek on the Corantijn about 15 km upstream from Kaboeri creek, and near Matapi about another 40 km upstream from Kabo.

4) Possible competitors and predators

As I have stated elsewhere (cf. Predation and Human Conflict) *Pteronura* is not preyed upon frequently by any animal I could determine with the possible and occasional exception of jaguar, puma and anaconda. On the other hand, there are a great many competitors for the food categories that both species of otter exploit in Suriname (Table VI).

Some of the Siluroids which are found in brackish water at the mouth of the larger rivers can reach a very large size of 120 kg or more and are strictly piscivorous. While the biomass of the fish ingested can not be determined with any accuracy it may represent a significant competition to *Pteronura* weighing only a fraction of that. Estuarine conditions may prevail up to 100 km upriver on the Corantijn, Commewijne and Suriname rivers and even though this is a marginal habitat for *Pteronura,* the possibility of direct competition could exist if the Siluroids were present in sufficient numbers. A more direct competitor might well be *Pteronura*'s favored prey, the Characoids of which, in the Amazon, at least 40 species are primarily or strictly piscivorous (Roberts, 1972). *Hoplias macrophtalmus* can grow to quite a large size ; the average weight was 5.6 kg (N = 11) on the Zuid river and 6.1 kg (N = 8) on the upper Coppename. At the beginning of the dry season, when trapped in pools in forest creeks they are particularly voracious as their available food supply rapidly dwindles and there are confirmed unprovoked attacks on the feet of humans wading across creeks (F. C. Bubberman, pers. comm.). It seems not too farfetched to speculate that *Lutra,* if not *Pteronura,* might be preyed upon by a larger specimen whose mouth opens easily to 30 cm in diameter.

Birds which prey on small and usually surface feeding fish which represents marginal competition to *Pteronura* preying on larger species resting on the bottom. *Pteronura* was never seen to attempt to catch the numerous water birds on Kaboeri creek which allowed the otters to get quite close at times. These include the wattled jacana *Jacana jacana,* the sunbittern *Europuga helias,* the sungrebe *Heliornis fulica,* the least grebe *Podiceps dominicus,* the anhinga *Anhinga anhinga* and the cormorant *Phalacrocorax olivaceus.*

Of the mammals only the freshwater dolphin *Sotalia guianensis* which was observed on the Corantijn all the way up to Apoera

where the tidal influence is still felt, can be considered a possible competitor of any importance. It is also reported in the mouths of the other larger rivers (Husson, 1978). The jaguar is said to catch fish along riverbanks and may exploit *Hoplias* in creek pools in the forest but its direct competition is probably occasional and insignificant. I observed a jaguar on the lower Zuid river resting on the bank.

One mammal which may compete directly with otters is the crab-eating raccoon *Procyon cancrivorus* which is coastal in distribution. While this is a marginal habitat for *Pteronura,* the coastal swamp and mangrove forests are favored by *Lutra* which would prey also on the various species of ghost crabs and mangrove crabs. I collected scats of *Procyon* which are different in odor and in appearance to those of otters ; they contained tiny fragments of crab, sometimes fruit and beetles. A dead *Procyon* was collected on the road to Coronie, running parallel to the coast where *Lutra* have been sighted (P. Teunissen, pers. comm.).

C) Possible competition with *Lutra enudris*

1) The species

The Guiana otter *Lutra enudris* Cuvier 1823 occurs also in Suriname but was seen only 11 times (13 individuals) with no repeats for a total of 23 minutes observation (Fig. 11 and Table VII).

Externally *Lutra enudris* differs from *Pteronura* by its size which, on average, is 1 m to 1.3 m total length and 5-12 kg in weight ; the adult males being a third larger than adult females (Table VIII). The tail is conical and tapers to a point. It has an overall auburn to chestnut brown color with no distinctive white markings on the neck although some may be present on the lips. The guard hairs are much longer than the thick underfur. The interdigital webbing is thin and does not extend to the nailed digits. The dental formula is I 3/3, C 1/1, P 4/3, M 1/2.

Two subspecies are recognized in Suriname, *Lutra enudris enudris,* the larger subspecies which is distributed throughout the Guianas and northern Brazil, and *Lutra enudris mitis,* a smaller more coastal subspecies from the Guianas and eastern Brazil which has a slightly different rhinarium shape (pers. obs. ; Harris, 1968).

2) Behavior and habitat preference

Lutra is a much shyer otter than *Pteronura.* While it may be seen during the day in the uninhabited interior, it is reported to be crepuscular or nocturnal in habit (Husson, 1978). All my observations were made during the day but I never observed it feeding. It favors a wide variety of habitats from small, shallow creeks deep in the high forests of the interior to open, marshy savannah areas near the coast where *Pteronura* was not found.

Table VII

Sightings of Lutra enudris *1976-1978.*

LOCALITY	RIVER SYSTEM	DATE	HOUR	NUMBER	LENGTH OF OBSERVATION	REMARKS
Cassewenica r.	Commewijne r.	23 July 76	0755	1:1	glimpse	Marshy habitat, dived into water
Midden Coppename	Coppename r.	29 Sept 76	1355	1	glimpse	Forest creek, went ashore
Omossé creek	Wayombo r.	1 Nov 76	0855	1:1 + 2 cubs	15 min	Forest creek, went into forest
Maratakka r.	Nickerie r.	5 Nov 76	1125	1	glimpse	Floodable forest, in water
Maratakka r.	Nickerie r.	7 Nov 76	1510	1	glimpse	Floodable forest, in water
Paru river	(Suriname/Brazil)	17 Dec 76		(1)		Cub purchased in Indian Village
Kaboeri creek	Corantijn r.	15 jan 77	1145	1	glimpse	Forest creek, dived into water
Kabo creek	Tibiti river	25 Jan 77	1245	1	glimpse	Forest creek, in water
Kabo creek	Corantijn r.	10 Mar 77	1125	1	glimpse	Forest creek, dived into water
Kabo creek	Corantijn r.	5 July 77	1215	1	glimpse	Forest creek, dived into water
Upper Zuid r.	Lucie r.	14 July 77	1625	1	glimpse	Forest creek, on log, dived
Kaboeri creek	Corantijn r.	27 Feb 78	1320	1	glimpse	Forest creek, in water

TABLE VIII

External measurements and weight of Lutra enudris.

HEAD & BODY (mm)	TAIL (mm)	TOTAL LENGTH (mm)	WEIGHT (kg)	SEX/AGE	LOCALITY	SOURCE
660	**427**	1087	7	♂	Suriname : Oost river (Lucie R.)	Husson, 1978
740	**570**	1310	11.5	ad. ♂	Suriname	Sanderson, 1949
575	**453**	1028	3.86	subad. ♀	Suriname	Sanderson, 1949
609-740	457-570	1066-1310	—	—	Guianas	Harris, 1968

Geijskes (quoted in Husson, 1978) is mistaken in thinking that *Lutra* and *Pteronura* are never found in the same habitat. They are sympatric seasonally, if not year around on at least five major rivers systems in Suriname. In some areas, such as the creeks flowing into the Corantijn, Tibiti, upper Coppename, Wayombo and upper Zuid rivers, both species occur and leave spraints on midstream boulders or sloping logs (cf. Territorial behavior). The diameter (± 1 cm) and length (± 5 cm) of the spraint is different enough not to confuse the two species. On the upper Zuid river near the Kaiser mountains in Central Suriname I saw *Lutra* and *Pteronura* along the same stretch of creek during the rainy season. During the dry season both species exploit the pools where crab and fish are stranded as the waters recede in the falls areas of the upper Coppename river.

Usually when sighted, *Lutra* races for cover ashore or, when in the water, submerges after a quick glimpse and is not seen again. A pair of *Lutra* and their two cubs were observed on the Omossé creek (Wayombo river) on 1 November 1976. The cubs became separated from the parents, and gave distress chirps in the tangled undergrowth as the adults swam near the shore ; eventually they found their cubs and retreated into the forest.

One can speculate that *Lutra* also has cubs at the onset or during the long dry season from September through February or March like *Pteronura*. Another cub, about 6-8 weeks old, was purchased in December 1976 from Trio Amerindians living near the Sipaliwini savannah in southern Suriname on the Brazilian border. It had been caught on the Paru river by chasing the mother and her two cubs ashore where one was easily overtaken on foot. I visited the Indian village two days later on 17 December and found the male cub weighing 1500 g in reasonable condition although it has not eaten for 48 hours. That day it accepted chopped raw fish and later whole fish 4-8 cm long. Three days later it ate raw tortoise meat *(Geochelone carbonaria)* and white-collared peccary *(Tayassu tajacu)*. It died a year later, killed by an anaconda *(Eunectes murinus)* (cf. Mortality factors).

3) Competition and conflict with Pteronura

I found no evidence of direct conflict or apparent competition between the two otter species even when they shared the same habitat and food resources. Both piscivorous predators have well-defined niches, but feed on fish and crabs of different sizes, and probably visit the same tide pools during the dry season but at different times of the day, *Lutra* being possibly more crepuscular and nocturnal when sympatric with *Pteronura*. The greatest differences between the two species centers around their degree of sociality.

a) *Cohesiveness*

There is a high degree of pair bonding and group cohesiveness in *Pteronura.* Family members travel and fish together, seldom straying out of sight or calling distance from one another. Allo-grooming takes place frequently and mated pairs sleep in contact with one another.

The apparently much more solitary *Lutra* was seen alone eight times ; a pair and family only once respectively.

b) *Communication*

Pteronura large family groups are made conspicuous by their barrage of snorts and screams. Group cohesiveness is enhanced by vocal communication and *Pteronura*'s vocal repertoire is varied and complex. Furthermore, the role of olfactory communication as evidenced by the use of communal latrines in territorial spacing, should not be under-estimated.

The more discrete *Lutra,* while possessing a wide range of vocalizations does not have the intergradations of *Pteronura*'s repertoire based on my earlier captive studies of *Lutra.* In the wild, *Lutra* was only heard to snort in alarm when sighted and, on one occassion, calling to its cubs. Their intra-specific communication system seems to be based on the olfactory through single spraints left at conspicuous intervals in their home range, in keeping with many other solitary, nocturnal carnivores.

c) *Group permeability*

Pteronura family groups did not appear to exchange members with other resident groups in the area or transient individuals passing through their home range at least during my short study. Territories are patrolled and expanded but direct conflict is actively avoided. The fact that no direct encounter between groups was ever observed, indicates the stability of a group's composition from one year to the next.

Whether *Lutra* choose the same mate from one year to the next in Suriname is not known.

d) *Integration and differentiation of sex roles*

Male *Pteronura* actively defend family groups from human intruders and both sexes defend the group in intraspecific encounters, at least in captivity (pers. obs. ; Trebbau, 1972). The female(s) regulate the pair's or group's movements, initiating activities and rest periods.

Lutra appears to devote only a small portion of the year to close contact social behavior. It must be noted that the solitary habits and small size of *Lutra* are an advantage when inhabiting open savannah swamps or small forest creeks. Large noisy

groups would be remarkably conspicuous but not as vulnerable to attack as the smaller, solitary *Lutra* when it becomes more terrestrial on forest creeks from large predators such as jaguar *Panthera onca* (Schaller and Vasconcelos, 1978) and puma *Puma concolor*. A single small *Lutra* can also find sufficient food in small forest streams, eating fish 5-15 cm long on average, whereas this would hardly sustain a group of *Pteronura* for long.

Il is tempting to speculate, although I have no direct evidence to support it, that *Lutra* is more sedentary in habit than *Pteronura* which follows its prey's seasonal cycle, utilizing a wide home range.

Basic differences between the two species' social systems exist, but apparently *Lutra* and *Pteronura* do not compete for habitat or prey categories in Suriname at least. More extensive and elaborate field studies are necessary to further evaluate the relationship between the two species, using telemetry and habituated animals which can be monitored closely during their complete annual cycle.

D) Mortality Factors and Human Conflict

1) Mortality factors

Although there is no direct evidence, it has been postulated that the jaguar *(Panthera onca)* and the puma *(Puma concolor)* are the only terrestrial predators of the giant otter (Desmarest, 1817). While potential aquatic predators are present in Suriname rivers no interaction between them and the otters was ever observed. There appears to be no conflict between *Pteronura* and *Caiman crocodylus,* a fact that was also noted by Santos (1945). Piranhas *(Serralsamus)* may be uncommon in black water creeks, preferring more open waters (Roberts, 1972) but manatees are reported to be vulnerable to attacks from piranhas (Bertram and Bertram, 1973) and the same may hold true for *Pteronura.* Several adult otters had scars on the sides and tips of their tail as if small bites had been taken out of them. Large fish, when hooked on a fishing line were sometimes attacked by piranhas and clean bites had been taken similar in shape and size as those observed on giant otters. But whether in fact the otters had scars from piranha attacks rather than intraspecific aggressive encounters is conjectural.

Young cubs are liable to stray soon after they emerge from the den and are probably the most susceptible to predators. Schaller and Vasconcelos (1978) report jaguar preying on *Lutra* in Brasil and a pet adult male *Lutra* was attacked and killed by an anaconda *(Eunectes murinus)* on the banks of a plantation canal (Jenkins, pers. comm.). The size of an adult *Lutra* (c. 1.3 m and 10 kg) corresponds to that of a juvenile *Pteronura* of 4 to 5 months, so the possibility of this mortality factor should not be dismissed.

Other potential causes of mortality could be the stingray *(Potamotrygon)* and electric eel *(Electrophorus)* : the latter tend to congregate in shallow water under vegetation mats and deeper pools where otters feed during the dry season. Otters investigating such pools could accidentally dislodge a stingray buried in the sandy bottom. Large electric eels measuring up to 1 m in length are common in most rivers and creeks but their nocturnal habits (like most Gymnotoids) make encounters less likely. Once, thirty-two electric eels were flushed from under a single boulder at Raleigh Falls during the dry season.

I was unable to establish whether *Pteronura* suffered frequent mortality from accidental causes or direct predation. It appears, in Suriname at least, that there are no predators which prey with any regularity on *Pteronura*.

2) Men and otters

The indigenous population of Suriname presents no direct threat to *Pteronura* or *Lutra*. Neither species is hunted for food or for its fur although it is reported that *Lutra*'s soft fur may be used for making slippers (Husson, 1978). I never saw otter pelts being offered for sale or used in making artifacts by either Bushnegro or Amerindian craftsmen. Sometimes otters are caught as cubs by amerindians and kept as pets.

While many mammals and birds are shot for food by Surinamers, Javanese farmers on the coast, Bushnegro tribes and Amerindian tribes in the interior, none considered the otters as a game animal. Mittermeier (1978) interviewed a cross-section of 42 native Surinamers as to their food habits and examined kitchen middens near villages for skeletal material and never recorded otters being taken for food or any other purpose.

In Apoera on the Corantijn river, the two cubs of the H pair in my study area were taken by an Arawak Indian shortly after they emerged from the den. In his own words Samuel made the following report : " On Christmas week around the 19th or 20th (1977) I went out fishing in the Kaboeri creek, traveling upwards. Somewhere around the duck pond square I met parents water dogs and their babies two. The parents were hunting caught a fish and went ashore in a hole feeding the babies maybe. I then saw they both came out the hole with the two babies. They were very beautiful and I decided to take the babies. I look at them and get a chance rush to them. The parents were afraid and jump in the water, also the babies but maybe young enough they couldn't swim nor even dive longer than about two or three minutes (sic) and so I get hold of the two babies. I take them home minding them for two days. I gave them milk with a nursing bottle and they did suck on the first day. The second day I caught some small silver fishes and gave to them, seeing if they could eat the fishes

and they ate also. I was glad seeing them eating and drinking knowing won't die, and liking them very much. In the third I was warned by police that if I don't set them free I would be charge and would be in trouble for it is against the law to keep these animals. And so I was very sad but still I have to lose them both in the river watching them going away swimming and diving a little until are out of sight ". This statement shows the feelings of the Indians towards small animals and it allows one to better appreciate why giant otters appear to hold a reasonably safe position in creeks near Indian settlements even today. The H cubs were never seen again and their loss had a profound effect on the H pair — they lost their territory to the encroaching S group down stream. The H female and the subadult born in 1976 disappeared from the creek shortly thereafter in January 1978.

Not all Indians are so tolerant however. On 26 February the H male, now living alone on Arawaboo pond, a favorite fishing spot for both otters and Indians was seen with a 20 cm crescent-shaped wound on his right flank behind the shoulder. The clean edges of the wound would indicate a machete cut which was probably inflicted when this habituated otter swam too close to a fisherman's dugout. The deep wound healed rapidly in five weeks and the otter showed no discomfort after 10 days, fishing normally.

I received reports of otters drowning in the nets placed across the entrance to small forest creeks during the dry season. Fishermen on the upper Coesewijne and Commewijne reported such incidents and also that otters had been trapped in *boxitas*, a spring trap used to catch *Hoplias*. I noticed that the otters became much shyer on the Coesewijne between my visits in November 1975 and February 1976 after a commercial fisherman had purchased a license to exploit the fish. Such evident results of conflicts between fishermen and otters are rare, and tolerance is the rule towards both otter species in Suriname.

3) Consequences of development

The possible effect of polluted waters could only be inferred by the absence of otters from areas where they would normally occur and was not established from carcass analysis. Segments of the larger coastal rivers of Suriname are now devoid of resident populations of otters immediately around the towns of Paramaribo, Nickerie and Moengo probably as a result of a combination of factors : high human population with its attendant pollution and constant river traffic with large barges and maritime cargo ships.

4) Large scale habitat destruction

The largest and most irreversible habitat destruction which has so far occurred in Suriname is the damming of the Suriname

river for the building of a hydroelectric power plant. This project flooded 2,250 km² forming in 1964 the Prof. Dr. Ir. W.J. van Blommestein Lake known more conveniently as Brokopondo Lake (Walsh and Gannon, 1964). The otters probably suffered the least of all the fauna which was displaced or drowned during the rising waters.

Another similar hydroelectric dam project is planned on the Kabalebo river, a tributary of the Corantijn, south of Matapi. This dam will furnish the power necessary to build a large town on the present site of Apoera, for a projected 60,000 people. A railway is currently nearing completion there to serve as a link between Aporea and a bauxite mine 92 km inland.

Siltation from the clearing of the rain forest for the railway, road and housing development has created new sandbars which impede river traffic. The river traffic carrying fuel and heavy machinery chugs upriver and docks at Apoera, the backwash eroding the mudbanks and sandy cliffs. The population of Arawak Indians in Washabo and Apoera increased from 200 to 600 between January and October 1977 as relatives from Guyana arrived, anxious for well-paid jobs. Kaboeri creek, 10 km downstream is easily accessible by boat even though its narrow course is littered with fallen logs. So far only Arawak Indians and a few Europeans visit the creek regularly but distractions are few in Aporea and it can be a matter of months before the situation changes.

" Il you shoot a gibbon, you leave seven lonely rivers ". This saying of the Shaw Karen tribe in northern Thailand quoted by E. O. Wilson (1975) could be easily transposed to *Pteronura*. We hope the rivers in Suriname will not become too lonely too soon.

III. — BEHAVIOR

A) Behavioral Repertoire

1) Senses

Sight : Pteronura is entirely diurnal ; it emerges from its den or campsite shortly after dawn and returns to it to sleep at dusk. Its strictly diurnal activities would indicate that it is a predominantly visual animal. Indeed it hunts by sight, chasing and cornering fish even in muddy waters. Tansley (1965) describes the enormous sphincter muscle in the iris which squeezes the anterior part of the lens when it contracts. She further states that their vision is comparable to that of the cormorants (*Phalacrocorax* sp.). Indeed while fishing, and sometimes while swallowing, the otter's eyes would appear to bulge in a very noticeable way (Fig. 21). The otter can recognize conspecifics and the human

observer at a distance of some 50 m. The habituated otters of Kaboeri creek recognized me both in the inflatable boat and the aluminum canoe and would resume their interrupted activity after sometimes only a brief glance whereas all other humans were avoided.

Hearing : As in other otter species, *Pteronura*'s hearing is acute (pers. obs.). An adult pair sleeping on shore heard an Amerindian canoe being quietly paddled upstream long before I did and, before it came into view, dived into the water. Sound location, however, may be poor with such small ear pinnae.

Smell : The sense of smell is excellent as indicated by the presence of well developed scroll bones in the nasal chambers of the skull. The snout is provided with a generous supply of nerve endings. Extensive use of the two anal scent glands is made when marking. Furthermore, the presence of communal latrines prove that scent must play a dominant role both in social behavior and when recognizing conspecifics at closer range and evaluating their sexual state. When investigating or walking on land the otters would frequently smell the substrate. Nose to nose contact was made when two family members met even after a brief separation of only a few minutes duration.

Touch : The sense of touch and its sensitivity were difficult to evaluate at a distance and must be reduced with such thick interdigital webbing. The otters manipulated twigs and stones. However, the use of forepaws let alone single digits to investigate objects with their gaze averted, so often seen in *Aonyx* and *Amblonyx* (pers. obs.), was never observed in *Pteronura*.

Vibrissae : A special mention must be made of the vibrissae which are extensions of the sense of touch. Radinsky's (1968) investigations of the somatic sensory specialization in otter brains indicate that *Pteronura* possesses an abnormally enlarged coronal gyrus corresponding to an increased sensitivity of the facial vibrissae which are noticeably long, stout and abundant in this species. This adaptation is of great advantage in prey location in muddy water when vision is impaired.

2) Locomotion

a) *Terrestrial locomotion and postures*

As in most other mustelids, the otter's body is long and low, with short legs and plantigrade feet. The pelvis is broad and muscular while the shoulders are narrow giving *Pteronura* a hunched appearance on land.

Walk : It walks with head held low, back hunched. The paws are moved singly in a diagonal pattern and the distal third of the tail is curved slightly upwards, not touching the ground. The gait with large and thickly webbed paws is clumsy on land.

Trotting : The shortness of the legs in relation to the size of the feet made trotting particularly difficult and it was seen only briefly during the transition between walking and bounding.

Gallop-bounding : When galloping the back is arched even higher after the hindfeet leave the ground simultaneously and are set down next to, or in advance of the forefeet. Bounding is a more rapid form of the gallop and is used when fleeing in alarm. It is a noisy gait ; the slap of the hindfeet as they land on muddy banks is audible some distance away. Even at high speed, *Pteronura* could be overtaken by a large dog (pers. obs.), and the otter would then turn back and race to the water.

Jumping : Was never observed in *Pteronura* whether over an obstacle or across a ditch.

Climbing : The otters scaled vertical banks slowly, ventral surface pressed to the substrate, feet moved alternately and in a diagonal.

Sliding : Along the ground was seen while rubbing to dry the fur (cf. grooming). Sliding down banks at cross-over points was observed. This was done cautiously head first and limbs extended stiffly forward. It was not repeated during play bouts as had been reported in other otter species (Harris, 1968). When possible *Pteronura* skirted vertical banks, preferring shallow inclines for entry and exits into the water. Trebbau (1972) reports a captive *Pteronura* climbing a 2 m high fence and falling to its death.

Tripod sit or stand : Standing or sitting on the plantar surface of the hindpaws using the tail as a brace for added support was observed in captive *Pteronura* (pers. obs.) but was seldom seen in the wild, probably because this investigatory posture was replaced with periscoping in the water. It was used, though occasionnally, during campsite clearing when pulling down overhanging vegetation.

In conclusion, *Pteronura* while neither fast nor agile on land, must cover considerable distances in flooded swamp forests during the rainy season and when using cross-over points connecting creeks. *Pteronura* appeared to keep land travel to a minimum and used the shortest distance overland between two creeks ; these well-worn cross-over paths could be easily followed and had probably been used for many years.

b) *Aquatic locomotion*

Entering and leaving the water : In undisturbed circumstances, *Pteronura* enters and leaves the water slowly keeping its ventral surface close to the substrate. When entering the water, the otter reaches down with its forepaws, flexes them and slides smoothly into the water. The head may be submerged or kept above the surface as the forepaws and chest submerge first. The

back and tail remain awash or just below the surface. When leaving the water, the otter reaches up with its forefeet before hauling its body up the bank. Sometimes the otter smells the bank while doing so. Slow ripples are seen in the water when entering or leaving the water in this manner.

When alarmed, the otter crashes headfirst into the water, neck and paws stretched forward, hitting the water with a loud splash and making waves. An alarmed exit is equally rapid, the otter scrambling, then bounding up the bank and under cover, leaving muddy waves in its wake. The types of wave or ripple is a good secondary sign for the observer as to the presence of otters in the vicinity and usually, after a short wait, a sighting can be made as the otter also returns for a second look.

Swimming : Immediately after entering the water, the otter will dog-paddle, using its paws alternately, its chin raised or resting on the surface. The paws are thrust backward alternately but not in diagonal. Dog paddling is also used when an otter cranes its neck above the surface while swimming or when stationary (Fig. 12). It is relatively slow and the jerky movements are characteristic.

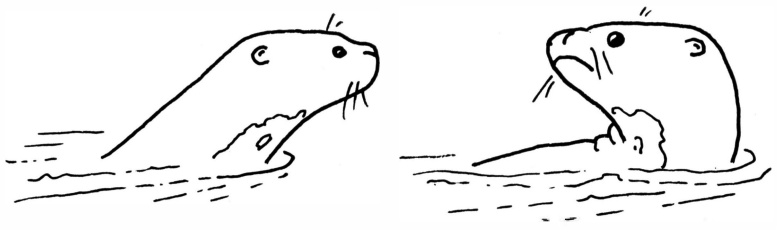


Fig. 12. — Swiming postures. Left, male dog-paddling and craning neck forward. Right, otter glancing back, keeping in visual contact.

The otter normally propels itself in the water after a strong initial thrust of both fore and hindfeet, by flexing its body and tail dorso-ventrally. The large flat tail of *Pteronura* is probably a morphological adaptation to its body size but also presents a net advantage in the water. At top speed the limbs are hardly used except singly to assist steering with the tail or when grasping prey with the forepaws.

Periscoping : While stationary the otter can crane its neck and head straight out of the water while paddling with its forepaws, bobbing in place up and down (Fig. 13). This is the usual posture used when investigating a human in a boat or when trying to locate a conspecific swimming at a distance ; if alarmed, it will suddenly submerge like a periscope with a "plop !" sound and

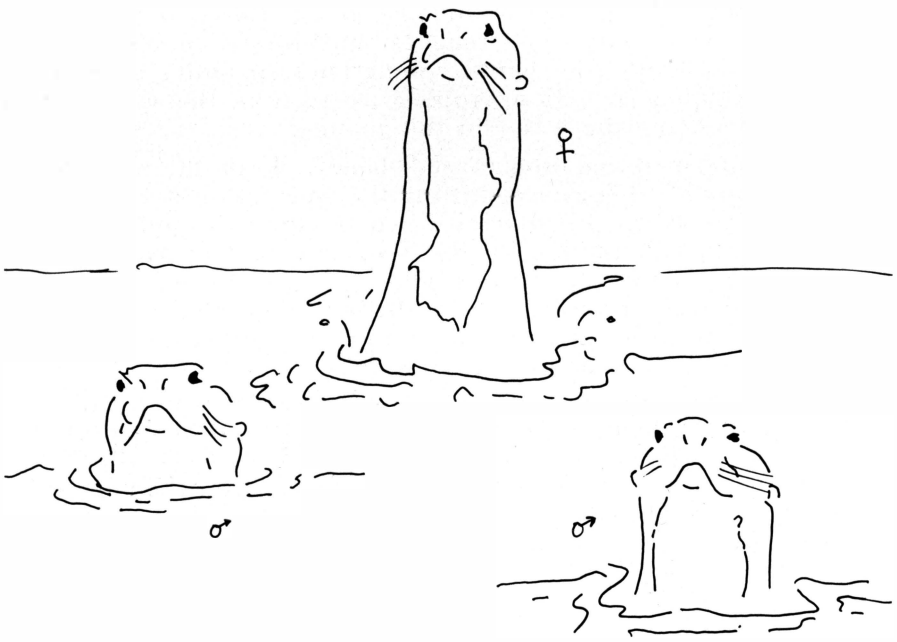


Fig. 13. — Periscoping posture.

swim away submerged. Cubs usually do not periscope well, probably because their swimming musculature is not yet fully developed ; their heads remain close to the surface, making them easily identifiable as juveniles in a group.

Breathing and duration of dives : The nares and the pinnae are valvular and constrict as soon as the otter submerges, effectively closing the nostrils and ears under water. The length of time spent suhmerged is proportional and correlated to the type and state of activity. The depth of the dives varied from a few cm to approximalety 3 m in large rivers.

1. *Normal swimming pattern* : While swimming quietly alongside the banks of both large rivers and creeks, otters surface and dive at regular intervals. One has the impression of a fluid sequence of movements : surfacing for *circa* 5 seconds, raising chin and opening mouth just above the surface, inhaling ; chin then head submerge and body rolls forward, porpoises, submerge for *circa* 20 seconds and surface again 20 to 50 m away (Fig. 14). Pairs travelling together surface and submerge synchronously, the lead otter sometimes surfacing and submerging a few seconds before its mate. No sound is heard and very few ripples are seen. A minimum of effort appears to be expended in this rythmic

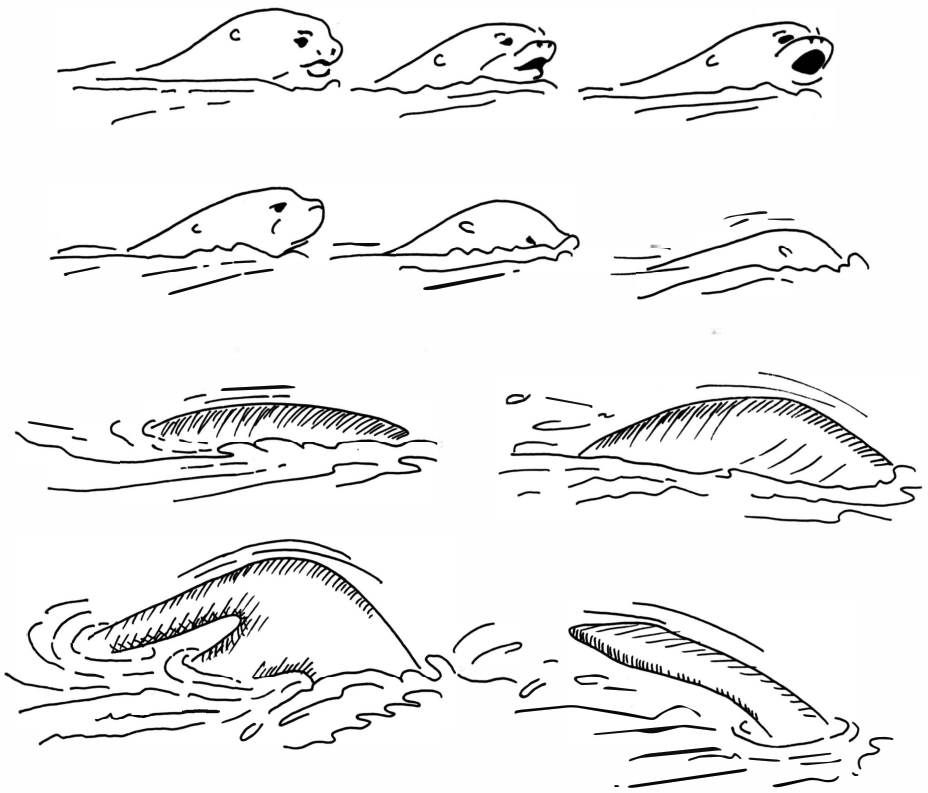


Fig. 14. — Diving sequence (from top to bottom, and left to right).

surfacing-submerging sequence which is used when the otters are travelling and not hunting. When large family groups are seen, like the S group (2:2 + 3 cubs) surfacing and submerging is not as noticeably synchronous although the progress of the group remains the same. Not enough data were gathered, but it was my impression that cubs surface more frequently than adults.

2. *During hunting bouts or when alarmed,* the surfacing is sudden, the inhalation is forceful and audible as one or two sharp gasps of breath which may be confused with the HAH ! vocalization. At these times the otter is usually swimming fast and swiveling under water surfacing with a loud splash and waves, but the duration of the dive is of similar length if not usually shorter, *circa* 10-11 seconds.

3. *Length of dives* : The actual length of the dive is much more variable during hunting than when traveling quietly but I never recorded a dive over 72 seconds long. Longer dives are sometimes erroneouslly recorded because the otter surfaced under vegetation

or behind the boat, particularly when alarmed. In the beginning of the study I recorded much longer dives, of two minutes or more and, while this may be possible, later in the study when I was better able to anticipate and follow the otters' movements, these abnormally long dives were not observed. As a general rule, otters submerged for shorter periods as their activities became more strenuous or in fast waters.

The following sequences illustrate the variations in diving length correlated with activities.

I. *25 September 1977 : 1535-1625. KI pair (1:1). Corantijn River (opposite Apoera)* seen swimming together downstream on the rising tide. They were observed for 50 minutes. Length of dives of male : 32-33-29-18-*36*-11-22-23-22-30-25-16-24-26-29-30-20-28-18-19-*6*-15-23-28-30-20-34-21-7-8. N = 39. $\overline{X}$ = 22.5 s. Range = 6.36 seconds.

II. *26 Jan. 77. 1118-1200 Adult ♂ Kabo creek (Tibiti river).* Swimming alone but was later joined by 2 ♀♀ and 3 cubs. Traveling downstream.

Length of dives (seconds) . 17-12-14-16-16-25-*10*-14-18-72-58-60-12-10-11-13-18-10. N = 18. $\overline{X}$ = 22.55 s. Range = 10.72 s.

III. *10 March 1977 0912-0924. Family group : 8 otters (3:3+2 cubs). Corantijne River.* Above Kabo Creek along sandbar. Water depth 60 cm. Fishing sequences of one individual.

Length of dive : 4-5-4-4-6-5-7-8-4 N = 9. $\overline{X}$ = 5.2 s. Range = 4.8 s.

IV. *24 Jan. 1978. 1056-1140. Ad. H ♂ Kaboeri Creek — Arawaboo Pond.* Solitary fishing sequence under floating vegetation mats and in creek.

Time : 1056 Dive : 18-23-6-13-24. T = 84. N = 5. $\overline{X}$ = 16.8 s.
Time : 1104 Dive : 6-5-6 T = 17. N = 3. $\overline{X}$ = 5.6 s.
Time : 1105 Dive : 15-2.6-1.7-13. T = 32.3. N = 4. $\overline{X}$ = 8 s.
Time : 1108 Dive : 7-26-5.8-18-7.6-5.4-9.5-4-7.5. T = 90.8. N = 9. $\overline{X}$ = 10 s.
Time : 1112 Dive : 17-9.7-20-7-10.8-17.3 T = 99.6 N = 7 $\overline{X}$ = 14.2 s.
Time : 1118 Dive : 16.6-17.8-6.7-16-10-8.3-8.3-25.3-3-18-12-11. T = 153. N = 12 s. $\overline{X}$ = 12.75.
Time : 1123 Dive : 9.3-10-15-17-8.8-7-12.5 T = 79.6 N = 7. $\overline{X}$ = 11.37 s.
N = 47 Dives 47 Dives totalling 9 min 27.3 s.
Average length : 11.83 s. Range = 2.6-25.3 s.

V. *26 July 1977. 1351-1420. Znid River.* ♀ Swimming downstream becomes alarmed as I follow her in boat.

Dives : 12-13-14-13-13-7-9-11-7-16-6. T = 121. N = 11. $\overline{X}$ = 11 s.
On surface between dives : 6-8-4-1-10. T = 29. N = 5. $\overline{X}$ = 5.8 s.

The top speed during a dive was observed in a subadult ♂ on Kauri creek (Corantijn R.) which when alarmed covered 100m underwater in 26s or 14 km/h.

3) Comfort activities

a) *Grooming*

Pteronura spends a large portion of its time ashore engaged in grooming activities. The otters dry themselves immediately after leaving the water by rubbing and rolling against the substrate. They also groom their fur using their incisors and the fore and hind paws.

1) *Rolling and rubbing.* The venter, thorax, chin, neck, flanks and dorsal surface were the main areas involved in rubbing. Rubbing apparently functions to dry the guard hairs and press the water from the underfur. Rubbing is energetic and thorough, the otter first rubbing its neck and thorax by pressing them against the ground and rubbing the body back and forth or in a sideways snaking movement. The otter then rolls over on its back with the back of its head and neck pressed against the ground and repeats the process.

The substrate may or may not be scratched prior or between rubbing bouts. The rubbing is so vigorous that particles of dirt and vegetation cling to the fur like sawdust after the otter has dried itself. Rubbing areas are recognizable on sites — they are smooth, freshly scratched areas which sometimes form slight depression indicating frequent and repeated use.

Rubbing may last 4 to 11 minutes continuously, based on 8 observations.

2) *Scratching.* Scratching of the fur with the hindpaws was seen both on land and in the shallows. After hunting and feeding, the otter might pause briefly to scratch, or nibble its fur or yawn before swimming off again. The flanks, shoulder, neck, head and lips were areas groomed by a hindpaw. The otter would roll its body laterally and scratch with slow or vigorous movements of the hindleg, digits curled downward, neck arched.

In captivity I observed an adult female scratching and nosing under her tail simultaneously but this was not observed in the wild.

3) *Fur nibbling.* Fur nibbling involves the use of the incisors, lips and perhaps tongue (Fig. 15). It is both used in solitary and social grooming. The otter, lying in a prone position, arches its neck and buries its muzzle in its fur and with its incisors combs through the fur with rapid biting movements. The fur is then nosed down and licking may take place but it is impossible

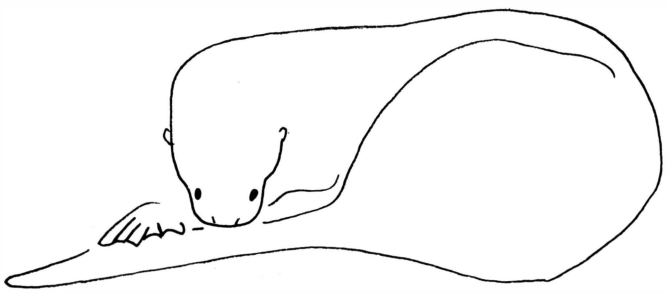


Fig. 15. — Autogrooming : adult female fur nibbling her tail.

to see from a distance because of the thickess of the lips. Fur nibbling was often observed in the shallows, occuring as a break during fishing sessions. The H ♂ observed continuously for 4 hours 25 minutes, fur-nibbled 6 times between 1055 and 1144 and rubbed 3 times on shore between 1207 and 1520 prior to resting.

Large portions of the body are accessible to nibbling : flanks, back, limbs, venter and tail. The head, face, neck and shoulders are the areas nibbled during allo-grooming, complementing solitary grooming patterns.

4) *Using of forepaws.* The heavily webbed forepaws are used, digits fanned, to further rub down portions of the fur after rubbing and rolling on the ground or against a log. The paws may also be rubbed over the eyes and muzzle and behind the ears as a final part of the drying-out process. Individual digits of the forepaw may also be used to remove particles of food lodged between the teeth. This was observed in a adult male lying on its back in the shallows ; it then rubbed its muzzle with both forepaws in conjunction.

5) *Stretching and yawning. Pteronura* was never observed stretching, probably because this is accomplished during rubbing sequences. Upon waking it might roll and rub briefly, for instance.

Yawning, the mouth opening wide, was observed after feeding while the otter rested in the shallows and ashore after rubbing and prior to resting. It was once observed while the otter scratched.

6) *Head shaking.* Head shaking was observed twice. Once while resting in the shallows, an otter raised its head and shook it rapidly and once after leaving the water it shook its head prior to drying itself.

b) *Resting and sleeping postures*

1) *Low-sit.* The fore and hind limbs are flexed, the ventral surface and tail resting on the ground. This posture is used while ashore when alert and immobile.

Fig. 16. — Otter in curled resting position.

2) *Resting.* *Pteronura* were seen dozing ashore during the day after swimming and fishing. Once ashore, the otters rub themselves dry, scratch the ground and lie down. The entire ventral surface from chin to tip of tail rests on the ground, or the otter may lie stretched on its side. Sometimes the head is propped up against a log or sleeping companion, chin over nape or rump. A curled or half-curled position was also seen, the chin resting on the tail or the extended hindpaws (Fig. 16). The H pair would usually rest side by side (Figures 17 and 18), sometimes a forepaw

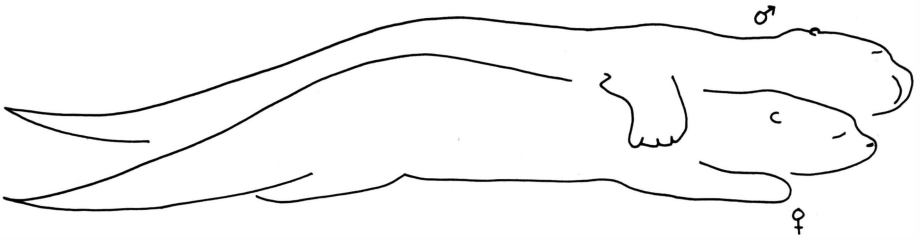


Fig. 17. — Pair resting side by side.

draped over the partner, whereas the subadult KI pair, probably 1976 cubs which had not yet mated, were never observed sleeping in close contact, usually lying 2 m or more from each other (Fig. 19). No one position appears to be used more consistently than another.

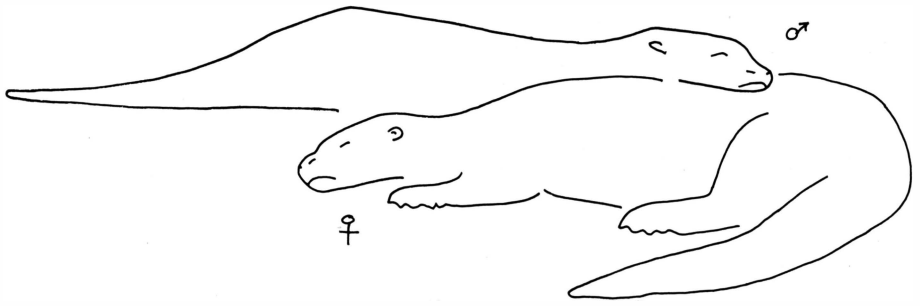


Fig. 18. — Pair resting end to end.

3) *Sleeping.* The postures used appear to be the same as in resting but the breathing is deep and regular, the exhaling longer than the inhaling. A limb may twitch. A solitary male was heard humming, a social vocalization, once while sleeping. Sleeping periods were difficult to differentiate from resting as the

Fig. 19. — Subadult KI female sleeping on a camp site with subadult male companion resting 2 m to the left (out of sight).

otters would wake up suddenly particularly if sudden splashes were heard or when biting insects became too insistent. Usually only the head and neck were raised, the otter pausing to listen or nibble its fur before dozing again. The KI subadult pair rested ashore, once for 50 minutes continuously. The H ♂ rested for 23 minutes after rubbing himself dry (cf. Activity Budget).

c) *Elimination*

Pteronura urinates and defecates (spraints) on land. The otters defecate in a given area which is used often repeatedly by an individual and other group members. Urination and defecation can occur simultaneously.

1) *Defecation.* The otter leaves the water, locates the communal latrine or another chosen spot such as a log or boulder, carefully smelling the area before turning and backing up. The tail is lifted, the pelvic area is arched and the stiffened hindpaws lifted alternately in a shuffling movement. The head may be bobbed once or twice up and down. Two or three abdominal contractions can be observed before the feces is passed. The stream of urine arches backwards, landing beyond the mucoid feces

which drop directly below the anus. Circling movements with the forepaws, digits spread and pressed to the ground, may be seen during and after defecation as the otter begins to spread the feces present on the latrine, mixing its own in the process. The hindpaws may continue to shuffle as the weight is shifted from one side to the other, the otter circling or moving ahead. The tail may wave sideways and up and down before, during and after defecation (Fig. 20).

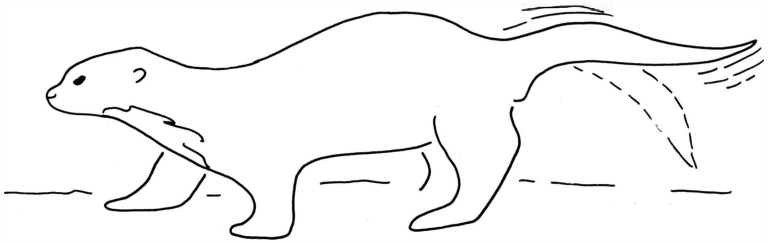


Fig. 20. — Otter tail-waving defecation.

Both males and females were observed spreading feces in this manner. Once a pair with their juvenile cub each came ashore separately to defecate, the female first followed by the male 4 minutes later. They defecated, urinated and spread their feces 14 minutes later in the same place and again the male followed the female, this time immediately afterwards. The juvenile did not follow its parents ashore on either occasion but waited for them in the shallows at the base of the site.

2) *Urination.* Urine may be passed during defecation and also dribbled over a larger area while scent-marking. The smell of fresh urine is strong, a mixture of fish odor and ammonia. The scent from the subcaudal scent glands, constricted during defecation, is mingled in the spraint.

It was not possible to determine how long urination lasted during scent-marking because of the thickness of the vegetation. However, the back was kept arched and the forepaws and hindpaws held stiffly during shuffling for 3 to 12 minutes of continuous scent-marking.

4) Maintenance activities

a) *Feeding*

Pteronura were only observed to capture fish on Kaboeri creek and they hunted by sight. They were seen hunting alone, in pairs and in family groups. The otters swam usually side by side, diving and surfacing at regular intervals, in close proximity

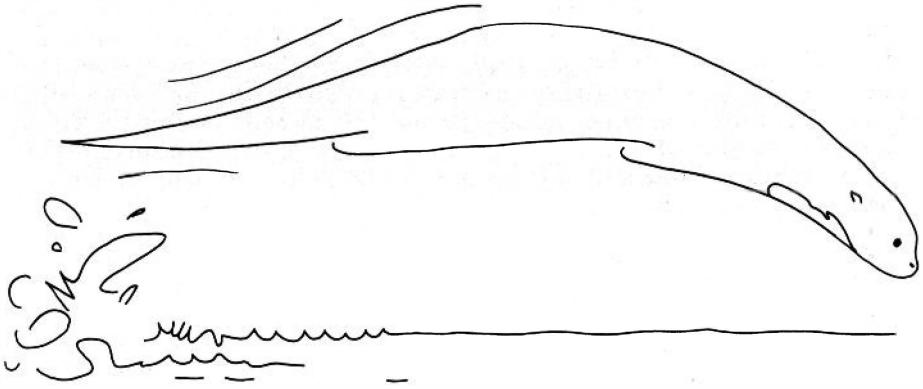


Fig. 21. — Otter diving in search of food.

Fig. 21). The feeding behavior sequence begins with active aquatic locomotion when a fishing area has been reached, usually associated with shallow areas of 50 cm to 2 m in depth. The otters search the bottom and dive under floating vegetation, surfacing among the mats for a quick gasp, pushing the head out of the water only long enough to open the mouth wide to breathe, submerging almost immediately. Underwater chases are very rapid and, in the shallows, create great turmoil as several otters splash through the water in pursuit until the fish is seized. A chase ending in capture is not always dependent on the velocity of the pursuit but on other factors such as a sudden change in direction or interception of the fish's flight path. A fish in deeper water will elicit a single dive whereas in shallow water it may entail several dives and lunges. Perhaps this is due to the reduced mobility of the fish in shallow water glutted with vegetation whereas in deeper, more open water, the fish can escape more easily or the otter abandons the chase more quickly.

The prey is rushed from above or below, the otter swiveling or turning at the last instant to seize it in its jaws, usually close behind the head dorsally or ventrally. No head shaking is observed.

On Kaboeri creek a complete hunting sequence with the H pair is summarized below.

1259. Both in water after resting ashore. ♀ in lead heading upstream.

1302. ♀ catches small fish 10 cm long in the shallows. Eats it immediately.

1305. ♀ catches another small fish and eats it on a log headfirst.

1306. ♂ catches 18 cm *Hoplias* and eats it on log beside her. Both dive into water and resume hunt.

1308. Fish under reed bed.

1316. Two Indians pass headed upstream in canoe. Both snort and watch them pass by.

1318. They leave reed bed and head downstream.

1319-1322. Both go ashore and mark vegetation.

1322. Both go into water but the male turns back and goes ashore to rub while ♀ hums (a low threat sound) in the water.

1324. Both in water again and they head upstream again.

1329. Fishing in reed bed.

1330. Male catches 20 cm *Hoplias* and eats it headfirst in shallows.

1331. Female catches 34 cm *Hoplias* and male gives excited squeals as she drags it ashore, holding her head sideway as it flops against her neck. He lies in shallows 10 m away and nibbles his fur while she eats the whole fish, starting headfirst.

1338. She displaces male as she approaches him with about 5 cm of the fish's tail end in her mouth. He hum-growls but makes no attempt to steal it.

1342. When she finishes they head upstream.

1345. Start fishing near bank among lilypads. Enormous turmoil and muddy waves as they charge through shallows. Male completely clears water as he lunges forward. Both miss.

1351. Again a miss by both of them.

1353. Male catches a *Brycon* 15 cm. Swims to log and starts eating headfirst and then switches to shallows. As usual, the rapid crunching is noisy and thorough, the otter twisting its head from side to side as it shifts the mouthful from the molars on one side to the other.

1355. Male catches another *Brycon* 10 cm. Eaten headfirst in shallows.

1359. Male again misses a fish.

1400. Female catches a 10 cm *Brycon*. Male squeals after she catches it. He was in the lead during the chase.

1404. He catches a small fish.

1405. Turn back downstream and swim steadily down, the female going briefly ashore to rub and autogroom for less than a minute at 1420.

1424. Female catches a *Hoplias* 17 cm. Eats it headfirst in shallows.

1426. Male catches a *Hoplias* 20 cm. Eaten in shallows.

1428. Female catches a large *Hoplias* 28 cm and again the male squeals as she carries it to the shallows. She starts to eat it, then stops halfway at 1431 and crosses creek to finish it ashore opposite at 1435. The male stays within 5 m of her and hums in the shallows.

1436. Male catches *Hoplias* 25 cm and eats it while female autogrooms in shallows until he finishes at 1439. He hums as the female comes up to him when he's finished.

1440. Male catches *Hoplias* 20 cm and eats it on log. Female rests beside him in shallows and yawns twice. She nibbles the fur on the male's rump for 8 seconds while he feeds, apparently unaware. She leaves him and noses around the shallows until he's finished at 1444.

1444. They continue upstream.

1447. Go ashore in floodable forest.

This hunting sequence is typical and illustrates a number of points : 1) each otter catches its own prey and consumes it immediately near the point of capture ; 2) the fish is eaten headfirst firmly clasped between the forepaws (Fig. 22). The otter chews rapidly and noisily, swallowing a mouthful after eight to twelve bites ; 3) there is no food sharing or hoarding and parts of the prey

Fig. 22. — Feeding posture in shallow water. Fish are always eatem head first, the forepaws firmly grasping the prey, elbows resting on the bottom. Note that the left eye is slightly exorbited. The sphincter muscle in the iris squeezes the anterior part of the lens giving the eye a bulging appearance, an adaptation to underwater vision.

are not discarded after being partly consumed ; 4) the partner waits for its mate until the eating is over and does not wander off on its own ; 5) there are few misses and the chase is rapid, lunging and twisting through the shallows. Garbled screams and snorts may be heard, particularly in larger groups with juveniles present.

In this sequence the female caught 7 fish, the male 8. From my data on the size and weights of *Hoplias* and *Brycon* caught by fishermen in Kaboeri I can estimate that the female consumed 880 g of fish, the male 730 g. Meals of up to 3200 g per hunting session have been observed when a tigercatfish weighing c. 2.8 kg was caught and consumed entirely. One can extrapolate the amount of food ingested per day per otter as follows : up to four fishing sessions per day were observed. If the average intake was 700-1000 g of fish per otter per session, this would represent approximately 2800-4000 g of fish consumed per day. Since a subadult female *Pteronura* consumed 2041 g of fish in captivity (Zeller, 1960) this estimate is probably reasonable. Carrying speculation further a pair of otters would consume 42 to 56 kg of fish per week and the 19 otters residing on Kaboeri ate 57-76 kg per day, 400 to 532 kg per week, 20,800 to 27,664 kg per year.

The rapidity of the digestion must also be noted here. From experiments made on captive *Pteronura,* I established that one meal could pass through the digestive tract in 35 to 40 minutes. In the wild, otters defecated about 50 minutes to an hour after their postprandial rest period.

Small prey of 10 cm or less can be consumed while swimming, the otter treading water and holding the fish between its palms (Fig. 23) while it swallows it in two of three bites. Larger prey are seized near the head and held in the mouth while the otter swims close of, or on shore (Fig. 23) to eat it.

After feeding the otter may pause briefly in the shallows and even shut its eyes for a few seconds. Fur nibbling or scratching or allogrooming may occur. The ♂ H lapped water holding his snout just above the surface and then dunking his head. While resting thus, the otter may look underwater swinging its head from side to side before submerging. It was difficult to establish what it was searching for — predator or prey.

Once a pygmy kingfisher *Chloroceryle aenea* darted down and retrieved small fish scales dropping into the water as the ♂ H continued to eat a fish and ignored this scavenger's swoops right past his nose (28 Jan. 77, 1120).

Earlier authors also noted *Pteronura*'s feeding habits. Brown (1876) relates " I shot a large female water-dog, which, being busily engaged eating a cartabac (?) on some rocks, and snarling at her husband, who wished to deprive her of it, did not observe my approach. " Beebe's (1917) account is a more accurate : " The water dog or otter, has learnt to fish where shallows meet the deep. (...). Should one hear an uproar of conflicting cries — turara, turara, turara, turara — these is no need for alarm, though, through the forest the noise is, at first, startling. A family of otters is expressing its delight over some fine fish which has been brought to bank by father or mother otter. " These " turara " sounds are the wavering screams associated with a high level of excitement or, when more plaintive and whining, with the cub's " food begging " vocalization.

Schomburgk (1840) usually so careful in his descriptions, comes to the wrong conclusion when he states " they seize (the fish) at

Fig. 23. — Otters feeding on small fish while swimming or treading water.

once by the belly and drag them on shore, where they are deposited while they continue their pursuit" and "they have certain haunts, where, when they have been successful, they devour their prey, leaving the heads, tails, and fragments of fish which infects the environs with an insupportable smell." I never observed *Pteronura* to cache fish or to abandon a prey except when suddendly frightened while feeding ashore, and refectories were not seen. The areas described are more akin to the mound of scales found in old communal latrines. However, Schomburgk unlike Brown has correctly noted that "none of them showed any intention to share the prey with the successful hunter or to dispute its possession".

According to Hershkovitz (1969) the giant otter uses a cooperative diving technique very effectively — a group driving fish into a shallow back-water where they are easy prey. It is hard to tell how concerted or intentional the effort is. I have observed a group of eight otters abreast fishing near a sandbar on the Corantijn. They would porpoise in the shallow water 30 cm - 60 cm deep and several came up with small fish which they consumed while treading water and keeping up with the group. There are of course definite advantages to group hunting even when a "to each his own" system prevails — a fish running such a gauntlet has little chance of escape. But a fish being actively pursued by one otter may be intercepted by another which should be viewed as accidental, opportunistic cooperation rather than a concerted action of chase and intercept.

5) Social Activities

1) *Communication*

a) *Visual*

Pteronura possesses limited expressive movements or postures that seem consistent or ritualized enough to function as signals. Perhaps a longer study will reveal this statement to be false. Giant otters possess no erectile hair, very small and virtually immobile ears and short limbs which would enhance visal signals. Their vocal and olfactory communication systems are highly complex and sophisticated which probably compensates for the lack of visual cues.

A recognizable visual signal is usually of short duration for instance a sudden jerk of the head upwards in alarm, but other visual signals not directly related to an individual's movement can also have lasting properties, *i.e.* when the environment has been altered in a noticeable way, scratching a bank or tearing the rotting bark of a tree stump. Communal sites are visual clues which will be discussed as part of olfactory behavior; and scratching, because the otter may impart some of its scent to the

substrate while scratching, will also be regarded as primarily olfactory in intent.

b) *Olfactory*

Olfactory behavior and scent signals in particular play a very significant part in *Pteronura*'s social activities.

There are various possible sources of scent :

1) *The anal glands* : two subcaudal anal glands are situated under the skin with short ducts opening from inside the anus. They secrete a dark brown viscous fluid with a powerful musky smell. The glands can be contracted volontarily or in an apparrently reflex action when the otter is suddenly alarmed at close quarters. This was observed once on Kaboeri creek when the ♂ H was suddenly awakened by the crash of a large tree 15 m from where he was lying. The air was filled with a strong musky odor from the apparent discharge of these glands.

2) *Feces.* These have a characteristic odor derived from a combination of glandular secretion and fishy smell. They also play an important role as a long-distance signal in scent-marking lasting several days or more.

3) *Urine.* Urine is used while scent marking and trampling vegetation. It may also be passed with the feces and kneaded into the substrate with the forepaws and hindpaws.

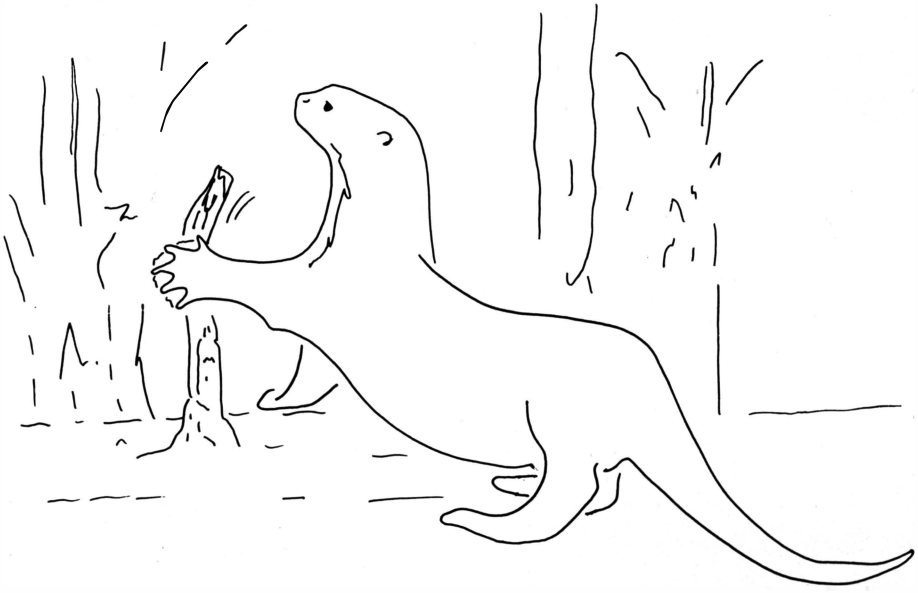


Fig. 24. — Male otter knocking over thin sapling during marking sequence.

As I have established (cf. Home Range), visual signals in the shape of well-defined landing sites on the banks, are not randomly distributed in the home range. They are set on riverbanks, along what is the otter's most frequented "pathway" and are visited at variable intervals.

Scent is deposited and spread during comfort activities and also when clearing sites. The sequence below is typical :

14 January 1977 : the ♂ male goes ashore at 1037 and starts clutching armfuls of twigs and leaves by rearing up on his hindpaws and grasping small branches to his chest. He pushes them down his chest between his legs and begins to trample them. The ♀ comes ashore, watches him for a minute and returns to water after sniffing the substrate. The ♂ enters water at 1046 after greeting the female with a snort and they swim upstream to fish briefly from 1057 to 1059. They then go ashore and rest until 1135. The male rises and knocks over a thin sapling with his extended right forepaw, digits fanned, and passes it under his body (Fig. 24). He defecates. The ♀ starts rubbing her forepaws on the ground and also knocks down a sapling 1.5 cm in diameter and defecate over it. Both resume kneading the substrate for a minute before slipping into water.

The smell is strong and rank, and the muddied vegetation is bedraggled, the leaves having been trampled deep into the ground. Urine and feces are difficult to distinguish in the oozing mud. Both otters seemed to be very concentrated on their individual task, circling with arched back and tail waving up and down and from side to side. The palms are pushed backwards and forwards as well as sideways in a stiff-legged, almost jerky fashion. The gaze may be averted when a branch is clasped and drawn down the chest (Fig. 25).

Fig. 25. — Adult H male rearing out of water to grasp overhanging vegetation (*Pithecellobium adiantifolium*, Mimosaceae) and mark it by rubbing it over his body.

This sequence lasted 2 minutes but longer ones have been recorded, e.g. two lasting 16 minutes. That day the H pair marked on three separate areas within 50 m of each other towards the top end of their territory at 1040, 1135, 1145, 1157, 1205, 1250 ; two sequences lasted one minute only.

Marking was observed on Kaboeri creek during the dry season at various times and did not seem to be related to the sexual state of the animals. The H pair marked just as feverishly while they had young cubs in a den, leaving them for up to four hours to do so and to fish. And later in January when they no longer had cubs they continued to mark as related above. The S group marked small areas on the river bank while moving their territory up-stream, using well-defined sites or just trampling an area near the water which was never visited again during the study.

It was difficult to assess what factors made the otters choose one spot rather than the other. The appeal of a well-defined site that needed to be cleared of fallen leaves and debris and re-saturated with scent was fairly obvious but the choice of an area which would not be visited again seemed to involve a great deal of expended effort for no apparent reason. Perhaps the otters by repeatedly marking insignificant portions of their territory in a quick and apparently casual manner eventually spread their scent at close intervals along both banks between larger and better defined sites. I visited areas which had not been used in months and the fish scales strewn over the latrines were still evident ; by scratching down among them one could detect a faint *Pteronura* smell, attesting to the long-lasting properties of feces and scent combined and trampled into the substrate.

While urine is often dribbled during vegetation marking and site clearing, it may convey a more expanded message. Otters rubbing the substrate cover themselves with the scent they are spreading and, later, while resting they rub themselves against the ground and against each other until a composite scent characteristic of a pair or even a group may evolve. It would be interesting to speculate how this complex system of scent saturation of individuals and territory evolved.

The following functions of scent marking can be surmised : 1) delineating territorial boundaries to warn transients or neighboring groups ; 2) to communicate information concerning the identity, sex, sexual state, receptivity and time elapsed between scenting visits. Presumably an old mark would not be as much of a signal as fresh ones. Sites and their communal latrines are both visual and olfactory marks, which are further prominently enhanced by trampling the surrounding vegetation and the substrate. One system complements the other — advertising and informing other *Pteronura* who may pass by. Whether this extreme form of unusual scent marking is restricted to the dry

season is not known with certainty, but one can postulate that on Kaboeri creek, scent marking during the dry season (which coincides with the cub-rearing season, perhaps an important factor) occurs frequently. In other areas visited during the rains, single scats and, in some areas, communal latrines were used in conjunction.

c) *Vocal repertoire*

Pteronura vocalize frequently. They respond to various situations with complex and extensive vocalizations, which, in turn, elicit fairly predictable responses from conspecifics. The nine basic vocalizations can be subdivided endlessly if small pattern differences are taken into account. Eight of the nine distinct vocalizations were recorded but each has many gradations, intermediates and juxtapositions linking them to one another. At first, one is confused by the bewildering variety and subtleties and, for that reason, I restricted myself in the analysis to basic categories. My previous experience in observing and recording river otters in captivity was particularly useful as regards vocalization interpretation in the wild. When the otters were still too shy to be observed continuously it was already possible to interpret tentatively their activities, while they remained out of sight in the undergrowth along the riverbank, by listening to their vocalizations. Pairs will hum, coo and chortle quietly to each other and to their cubs as they swim on the surface and rest ashore. While hunting, an otter may scream in apparent peevish frustration when a group member catches the fish it has been chasing. Thus, giant otters could never be called discrete or quiet, traits more characteristic of *Lutra*. Even when alarmed by a human observer they will snort loudly and emit a wavering scream as they chase through the water towards the boat. Not surprisingly it is these agonistic calls which are referred to most often by early explorers and naturalists (Schomburgk, 1840 ; André, 1904 ; Hingston, 1932 ; Sanderson, 1950).

I have listed the vocalizations in the following order : 1) agonistic, 2) affiliative social contact (hum, coo, whistle) and 3) parent-cub sounds ;

a) *HAH !* — A startled otter will emit a sharp HAH !, a discrete sound given with the mouth partly open in a sharp exhalation. It can be interpreted as a question mark, indicating the lowest level of alarm or interest. It usually stimulates alertness in other group members who will momentarily stop their activities to look for the source of alarm or uneasiness (Fig. 26). While surfacing an otter may HAH ! before submerging or a parent may give it when re-entering the den where the cubs are lying. When the observer is first sighted the otter will HAH ! and if the level of alarm increases a snort (alarm), a long-call (contact), a hum

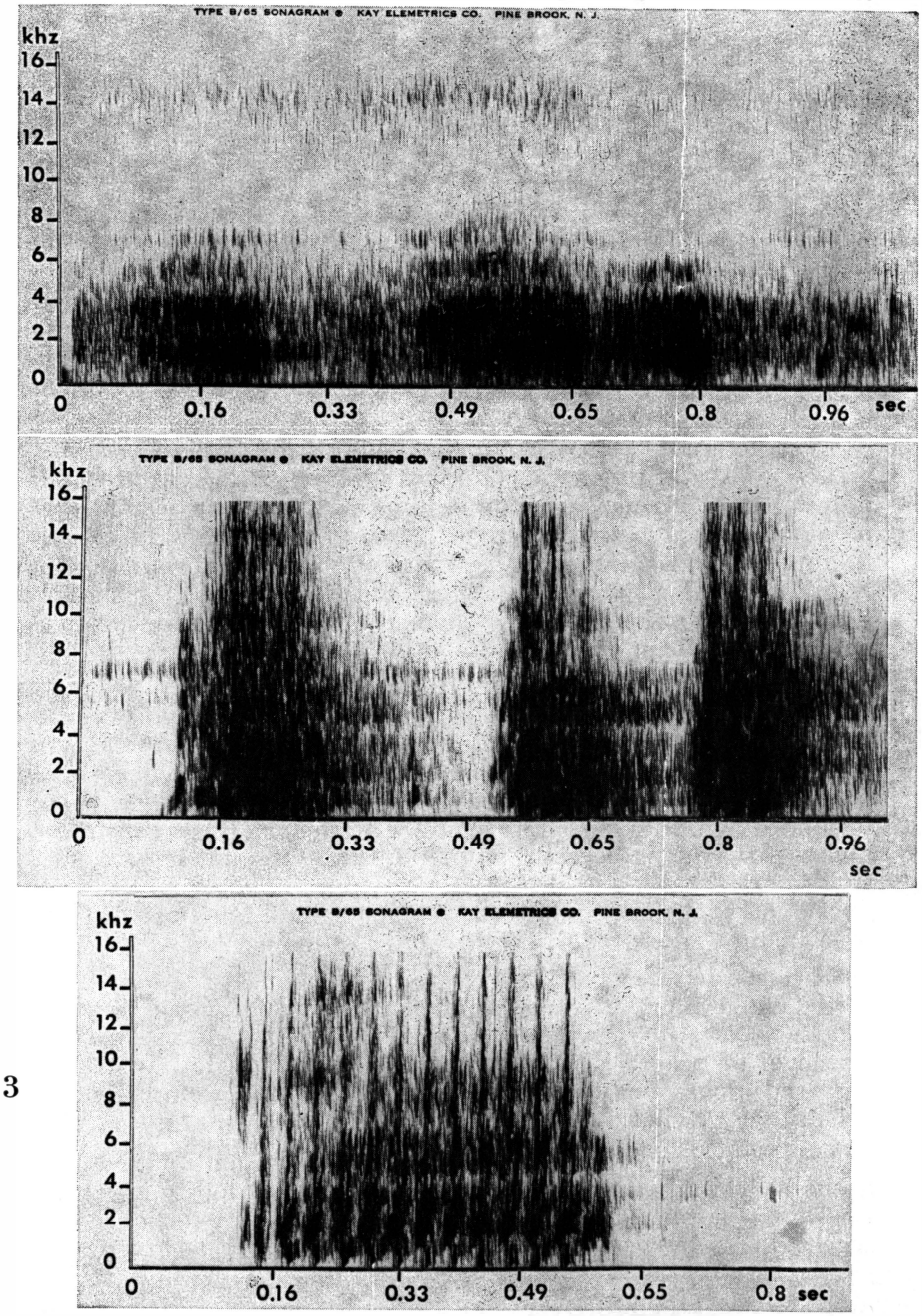


Fig. 26. — Sonagrams of giant otter vocalizations. I. From top to bottom (1) Three short HAH !s made by two adult otters ; (2) Three short snorts ; (3) One long snort showing separate pulses.

(re-assurance to a conspecific) or a growl (threat) may be given afterwards. The HAH ! rarely occurs in a rapid series, the otter pausing for several seconds between each one but several otters may HAH ! in rapid succession, one after the other.

b) *Snort.* An explosive snort is given when the otter is suddenly alarmed or when facing a source of potential danger. Snorts immediately attract the attention of all group members who stop their activities and regroup, the males together and the females and cubs behind. Shy otters would always snort when first sighting the boat, a fact also frequently referred to by other naturalists. "Whenever they saw the boats coming they would raise their heads above the water and snort loudly" (André, 1904). Snorts may also be given during hunting sequences when the level of excitement is high, but more usually it indicates high intensity alarm.

For example, on the Zuid river in July 1977, my attention was first attracted by a snort and while trying to locate the source, an adult male swam by, dogpaddling, and glancing repeatedly in my direction, snorting each time. A female and three grown cubs followed 10 m behind, giving whine-long calls to the male. They regrouped and periscoped, all HAH! ing and snorting for 2 minutes, then turned and continued downstream as I followed behind before they disappeared ashore into a swampy area.

Snorts may not always be followed by immediate departure. In July 1976, on Koopman's creek, my attention was again attracted by a snort and I snorted back. A male swam out quickly from under the overhanging vegetation lining the bank where he had been observing me. I snorted back and forth as he periscoped up and down, making short charges at the boat to within 2-3 m, giving a wavering scream, with mouth open. A female, out of sight, started calling to him and then swam into view and they cooed to each other, turned and dived, disappearing into a narrow flooded area in the undergrowth. The whole sequence lasted 4 minutes.

Snorts can be given singly or in short bursts of two or three (Fig. 26 b). Long wavering snorts where each pulse is audible (Fig. 26 c) are heard when the otter is watching intensely or when the level of alarm is on the wane. Others snorted just as they surfaced, on several occasions, which gave the sound a peculiar echoing quality.

c) *Wavering scream.* This vocalization mentioned above is a harsh, whining scream which may be modutated and wavering. It usually is given during a bluff-charge towards the observer or when other otters are heard or thought to be heard on the river.

For instance, in January 1977, the boatman spotted an otter on Kabo creek (Tibiti river) and I gave a long-call. A male swam out from where it was hiding near the bank and he HAH'ed and

snorted, periscoping rapidly and suddenly with a "plop"; he started calling and we could hear similar calls being answered in the forest 100 m away followed by scrambling in the underbrush. Another male, two females and two cubs entered the water and swam across to the male. They all snorted and HAH'ed and the two males charged the boat with loud wavering screams. The cubs herded between or immediately behind the adults. This scream during a bluff charge is given only by shy otters and does not occur and cannot be provoked in habituated animals.

The scream is a common vocalization of an excited *Pteronura* and can also be given during a prey capture sequence. It can be wavering and long or truncated and so short, it sounds almost like a bark. Sanderson (1950) mentions that *Pteronura* "barks loudly, the sound being akin to that emitted by a sea-lion *(Zalophus)*". This does describe the harsh and loud quality of the scream, which is usually longer and more modulated than the bark he describes.

Schomburgk (1840) gives a very accurate description of the wavering scream and how the otters respond to a human's imitation of the sound by charging closer. "We saw first only one, swimming like a dog, with the head and neck out of the water, but more and more made their appearance, until their whole number amounted to about twelve. They were approaching our canoes, now raising themselves partly out of the water, accompanying this motion with a loud snore (sic) or an angry growl, or diving rapidly under water, and reapearing a few moments after some distance behind our canoes. Our Indians commenced a shout, striking repeatedly with the hand against their throat, by which a sound not unlike to the growl of the otter was produced. This attracted their curiosity; and ranging themselves in a line, they came nearer, and were within the reach of the gun."

d) *Growl.* This is a low intensity offensive threat which can merge into a *staccato scream,* a high intensity threat or into a low hum-growl given with mouth closed (Fig. 27). I heard an adult female giving a *hum-growl* while watching me from a patch of mokomoko where she was hiding with her cubs while the three other members of group S snorted and HAH'ed nearby.

When my Doberman dog once surprised the S pair and two subadults ashore in March 1977, I heard a *snarl-bark* as they paused and faced the dog before racing into the water. Snarls are louder variations of the growl while the bark was a truncated scream-snort combination — a sequence showing the extreme intergradations of basic vocalizations when conflicting motivations exist.

e) *Hum.* Hums are reassurance close contact sounds made between individuals traveling together. They may be modulated

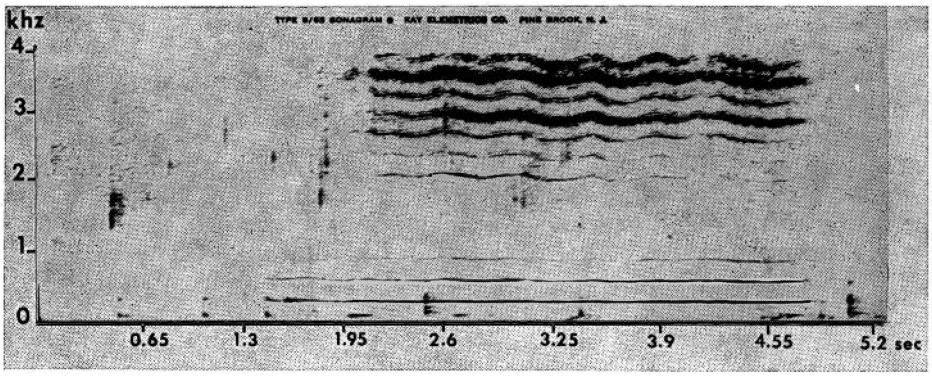


Fig. 27. — Sonagrams of giant otter vocalizations. II. A long hum-growl.

and last for several seconds before a pause and then resume, for minutes on end. The H pair hummed almost continuously together with their grown cub and they were then called " The Hummers ". When the observer moves too close, hums may be interspersed with HAHs and, sometimes, a snort. Whereas a HAH ! indicates an alert otter a hum typifies a relaxed situation. While resting ashore an adult pair will hum and coo. I noticed that humming might sometimes become more rapid or insistent immediately prior to the departure of a pair or group from their resting place. Hums were also used in conjunction with coos when a pair was reunited after a brief absence during a fishing sequence or when one individual approached another just before touching noses (Fig. 28).

f) *Coo.* The coo is associated with a close contact situation between individuals of a pair or parent-cub interaction. It may immediately precede a reunion and can also be termed an excited friendly greeting. In allogrooming sessions, the otter being groomed might hum and coo. Adults often cooed to their cubs. This short chevron-shaped falling note call is discrete and can only be heard at close range of a few metres (Fig. 28).

For instance, on 15 March 1977, I watched the H pair and their cub swimming across a pond glutted with lilypards. The cub became separated from its parents three times, appearing to lose them when they submerged in the shallows (1 m or less). It would surface, crane its neck, look underwater from side to side, raise its head again and give the plaintive cub lost whine (Fig. 29) which was immediately answered by the wavering scream of the parents 20 m away who raced towards the sound. They submerged and all three surfaced close together with mutual nose touching and repeated coos before resuming their swim downstream.

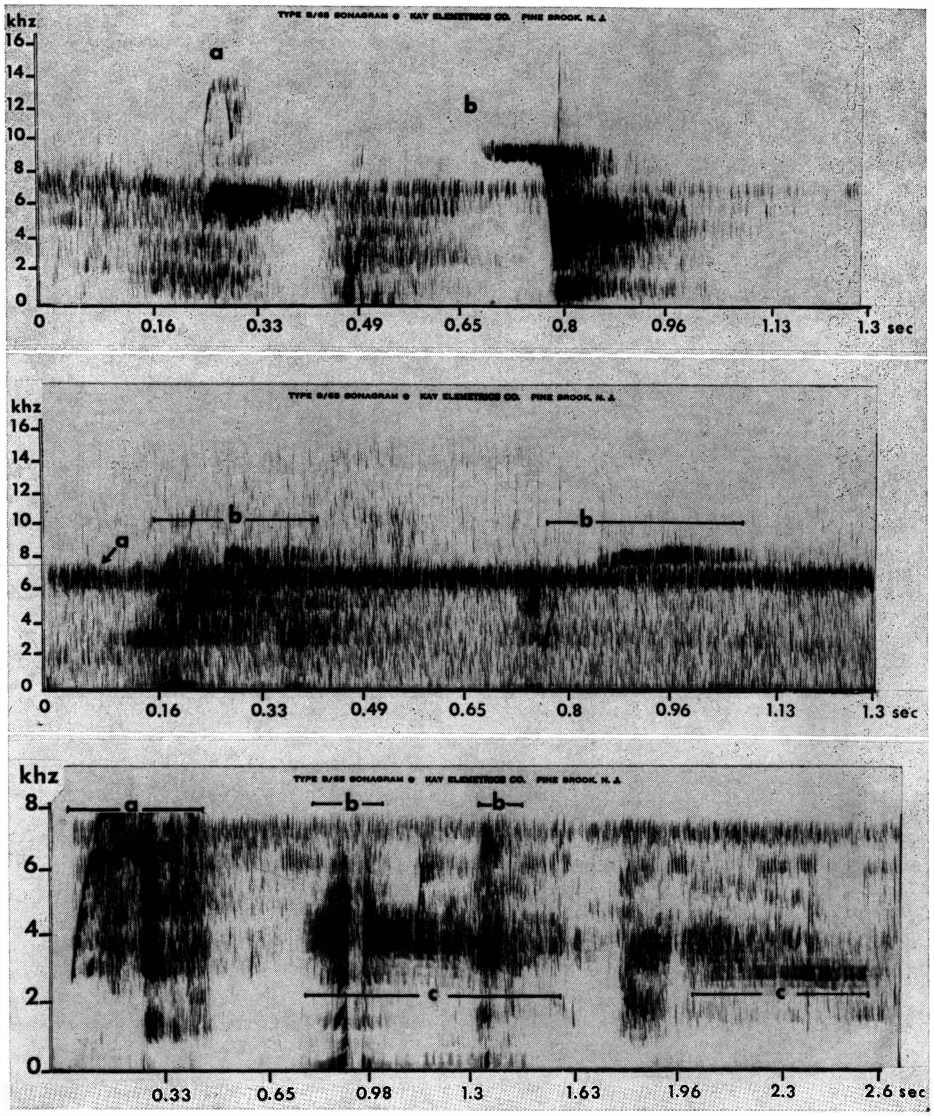


Fig. 28. — Sonagrams of giant otter vocalizations. III. From top to bottom : (1) Adult coo (a) followed by a cub long call (b) ; (2) Adult hum (a) and coo (b) ; (3) Cub call (a) and adult coos (b) and hums (c).

The coo can also be given in a hum-whine-coo sequence which indicates growing excitement and is a longer distance social contact sound than the coo by itself. Such a sequence probably promotes group cohesion and when the whine becomes louder

Fig. 29. — A cub-lost sequence. From left to right : The cub looks for parents, bobs up in water (low " periscope "), pears under water, and gives the lost call.

still can serve as a friendly rallying call. One adult may hum to a cub, for instance, while another will coo, and they each may reverse the process. (Figs. 28 1-3). Cubs will usually cease their calls or whines when the parents appear to calm and reassure them with hums and coos.

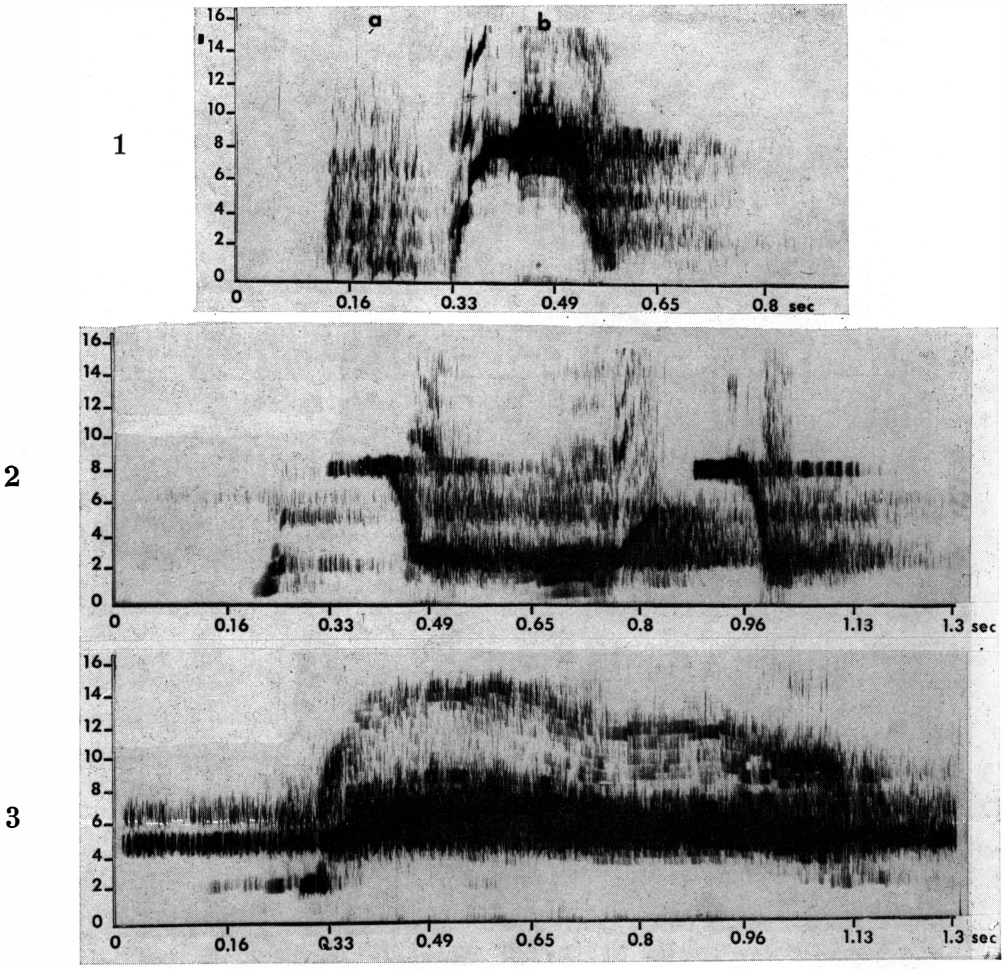


Fig. 30. — Sonagrams of giant otter vocalizations. IV. From top to bottom : (1) Snort of adult (a) and cub call (b) during an hunting sequence ; (2) Repeated food begging calls by cub during an hunting sequence ; (3) Long plaintive, modulated cub food begging call.

g) *Whistle.* This pure tonal sound with none of the harsh nasal overtones of the usual intragroup whines and screams was heard only once when a group of 7 otters approached a bend in Kabo creek, and started whistling before turning into a creek. They were answered by the same sound and a minute later another adult pair swam out from the bank's undergrowth at the bend where they had just disappeared — there was no physical contact between the two groups, only these pure whistles. This may be an intergroup contact call denoting friendly intent and not territorial invasion but it appears to be used only in this specific instance and is therefore heard very rarely as intergroup contacts are uncommon.

h) *Newborn cub squeaks.* On 2 October 1977 while the H female was transporting her cub from den to den, it gave repeated loud squeaks (Fig. 31 a) which sometimes became shrill squeals. This was the only time cubs were heard to make such

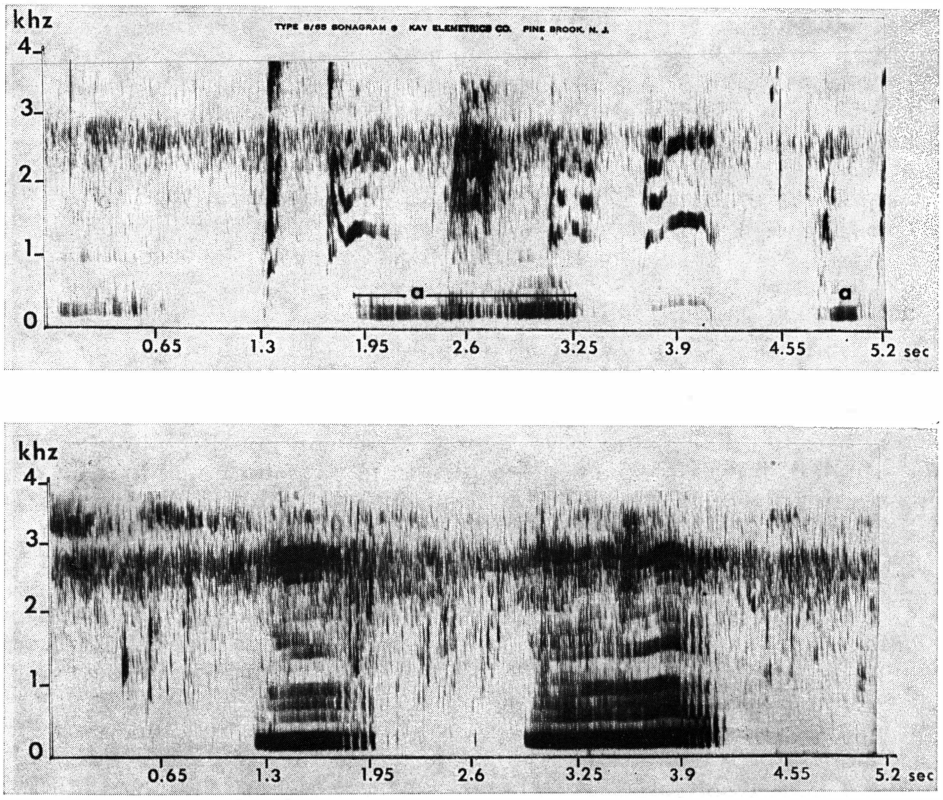


Fig. 31. — Sonagrams of giant otter vocalizations. V. Top : Newborn cub squeak and female's purr (a). Bottom : Rattle purr, female to cub.

loud vocalizations, and it appears to disappear from the repertoire after a few days. The parents both gave an unusual purr (Fig. 31) in response, a low rattling hum sounding like a soft purr. It was only directed towards very young cubs and appeared to be replaced later by the hum or coo sounds.

i) *Cub whines and wails.* When the cubs began to join in group activities when aged about three or four months, they could be distinguished from the adults by their whines, sometimes emphatic and shrill becoming a garbled scream. Schomburgk (1840) when describing two pet otter cubs says " their cry when angry or in pain was most plaintive, sometimes piercing and disagreeable " which describes the quality of these sounds. Zeller (1960) compared a captive subadult female's call as resembling that of a buzzard (*Buteo* sp.), also a long rasping note sounding harsh to the ear. For instance, while the S group hunted, if a cub repeatedly missed its prey, it would stand by a feeding adult and give a long piercing scream (Fig. 30,1) which I termed *food-begging.* The parent would carry on eating and food-sharing was not observed. These calls were very variable in intensity and length (Figs 30,2-3), but maintained an initial chevron shape characteristic of a chirp - whine, sometimes increasing to a wavering scream which was much more shrill than the adult's. These nasal whines appeared to be used for all levels of defensive annoyance or pain, but rather than inhibiting approach they would help the parents in locating lost cubs or attracting attention to them. But it attracted only the parents's attention whereas the wavering scream of the adult immediately rivet the attention of the whole group and sometimes appears to stimulate cooperative action such as charging or retreat.

Non-vocal sounds such as coughs, sneezes and hiccups were very rarely heard, usually while the otters were resting alone or together in the shallows or ashore.

The adaptive value of *Pteronura*'s vocal repertoire should be evaluated, however sparse these preliminary findings. In many cases, for instance, I was under the impression that a given vocalization elicited an almost automatic response from another group member. For instance, a snort and sudden periscope dive by an individual would cause all the otters to disappear before the cause of the alarm had been investigated further even though when they sufaced again, individuals and adult males in particular would approach and investigate. A cub's wail was calmed with a hum-coo, or investigated or simply ignored which does not imply that the cub was sending a specific signal, but merely that the parent evaluated each call before responding to it, quite unlike the snort which is a negative alarm signal. A positive, affiliative sound like a contact hum or coo became negative when its intensity was increased, changing into a hum-growl interspersed with HAHs.

The number of affiliative sounds used in contact situations and in appeasement certainly reduced the aggression level and I never observed physical violence between group members.

The low degree of hostility, the cohesiveness within the group as well as the cooperation among group members during a presumed " attack ", as provoked by the observer initiating the aggressive wavering scream, all point to the high degree of sociality of the species.

2) *Agonistic and friendly behavior*

a) *Affiliative*

I have very little data on affiliative behavior and all of them based on the H pair which was observed in 1976 for a total of 2 h 3 min with a juvenile cub and as a pair, rearing young cubs, in September and October 1976 for 13 days and a total of 4 h 36 min. In January 1977 a three day period yielded 14 h 28 min of observations.

As a pair and a family group, the H individuals kept very close together and actively sought their cub when it strayed on four occasions. When approaching one another they each would touch noses briefly, the vibrissae angled forward, and coo once or twice. It was apparent that they sought each other's company ; the near constant hums, coos, chortles and purrs were all variations of contact enhancing vocalizations. While resting, the male and female would be in close contact, lying parallel head to tail or head to head, and often one would drape a paw over the other or rest its chin on the nape or rump of the other.

The closeness of the pair bonding was illustrated by the length of the allogrooming sessions. Allogrooming took both the form of nibbling the fur on face, neck, rump of the other as well as rubbing up against it with the neck or flank (Fig. 32). In a continuous observation of 4 h 12 min, the pair allogroomed for 4 min 16 s versus 2 min of rubbing on the bank in autogrooming. During the time, the male allogroomed the female for 3 min 46 s discontinuously while the female returned the favor for only 30 s. On another day the male groomed her for 7 min 22 s in a 16 min period on the neck and shoulders while lying side by side on a log, and on a third day he groomed her for 1 min 55 s and she nibbled him for a perfunctory 8 s. It would have been interesting to determine whether these affiliative grooming sessions were in any way related to her sexual state. She has lost her cubs a month earlier and might have been coming into estrus. Unfortunately, this could not be determined as she disappeared four days later and was never seen again during this study.

The H female appeared to initiate certain activities often after humming repeatedly and increasingly to the male. After a rest

Fig. 32. — Allogrooming posture. The female grooms the male's shoulder.

period she entered the water first and swam around the shallows, peering under water until the male joined her. Another time the H male began to get impatient and repeatedly tried to coax her from her resting position while sunning on a log until he gave up and joined her again. When he had yawned, stretched and settled down, she abruptly got up and dived into the water. During marking sessions the female initiated the activity, by going ashore, defecating and beginning to spread the spraint ; the male followed suit and often spent longer marking than the female.

Overt affiliative behavior such as partner play or chasing was not observed on land or in water. However, earlier naturalists describe forms of play which may in fact have been hunting or grooming behavior patterns. Waterton (1812-1824) mentions that " In going through the overflowed savannas, which have all a communication with the river, you may often see a dozen or two of them (otters) sporting amongst the sedges before you." While in British Guyana, Guppy (1973) saw " on a sandy beach, a family of giant otters leaped and rolled and played — until they saw us, stopped, pointed their noses into the air for a minute, and trotted out of sight ".

b) *Agonistic*

As the otters appeared to actively avoid intraspecific and/or intergroup agonistic encounters it was not possible to observe any. When the S group started moving into the H territory, the H pair retreated into the forest as soon as they heard the otters calling in the distance, usually screams and snorts as the otters fished. Once the H male dashed into the underbrush, an action which was explained by the arrival of the S group in Arawaboo Pond 2 minutes later but I had heard nothing heralding their arrival.

3) *Investigation and Alarm*

a) *Investigation*

Pteronura is extremely inquisitive and very aware of its surroundings — a single noise out of place in the constant background sounds of insects and birds will cause it to lift its neck and try to locate the source. This alert posture (Fig. 33) is seen very often and, in the water, is replaced by periscoping, i.e. bobbing up and down while treading water. If the object being inspected visually appears alarming, the periscoping otter may suddenly submerge straight down with a "plop" rather than rolling forward and submerging head first.

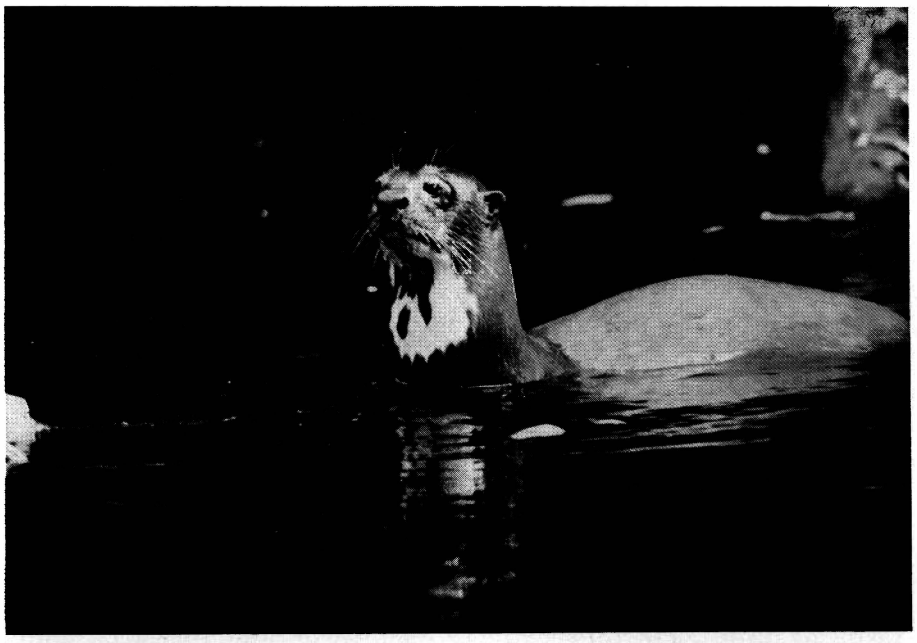


Fig. 33. — Alert posture of the subadult KI female in shallows.

While investigating a conspecific or the substrate, the otter stretches its neck forward and sniffs, vibrissae angled forward. In a situation of potential alarm the limbs are slightly flexed in a approach-withdrawal crouch position. While investigating a 35 mm camera which had been left on shore the H male advanced, retreated and when the automatic release triggered the motor drive mechanism he HAH'ed, then snorted and recoiled backward suddenly.

In investigating small objects such as a fish remain floating on the surface the otter scoops it towards its chest and muzzle with a circling movement of a forepaw, digits fanned.

b) *Alarm*

Alarm was only observed in relation to other groups as in the example mentioned above and towards human observers.

When sighted ashore, the otters would crane their necks, peering from side to side through the undergrowth and then one or several would HAH! and/or snort and they would dart for the water, diving in one after the other, or if the banks were clear, all at once. Different otters reacted in different way. The S group was always alarmed by my presence even after 91 sightings whereas the H pair was allowing me to follow already a year earlier in March 1977. Outside the study area, some individuals would immediately retreat into a creek or flooded swamp where I could not follow on foot or in the boat, while others watched me for minutes and then allowed me to follow them at a respectable distance of 15 m or more.

The threat and attack charges were not seen in single individuals but only in pairs or in groups. The male or males would give a wavering scream as I called to them, detach themselves from the groups and charge across the water sending up a wave ahead of them and diving in the last few meters from the boat or periscoping and continuing to scream. A male might appear to give a solitary charge but in the two instances where this was observed the female and the family group joined him shortly afterwards.

Early authors also refer to this charging approach in situations of high intensity alarm. Hingston (1932) relates, " Swimming and diving they approach a boat uttering peculiar snorts and barks and exposing their rows of teeth." Quelch (1901) describes periscoping and bluff charging : " They are often met with in flocks of a dozen or more, and they will rise, head and neck out of the water, at a short distance from the boat, as though to get a thorough good look at the disturbers of the peace. Frequently they will respond to the calling cry of the boatmen ,and rise momentarily at quite close range, diving backwards and forwards, and breaking back again when pursued, as though in actual trifling

with the hunter." Finally, Smith (1943) described a mildly alarmed otter on Kaboeri creek and already then they seemed inclined to accept the presence of an observer ! " Abruptly, ripples broke the glassy surface of the water, a few feet from the canoe. A strange round head rose from the stream, regarded us for a moment with sorrowful eyes, and then, having given us the once-over, sank away from sight." ..." As I recalled the creature's face, which had gazed into mine from so close a distance, I could not help remembering a Great Dane which I had once owned, back home in California. The mournful look in his eyes had been exactly like that of the otter."

6) Reproductive behavior

1) *Seasonality and correlation with rains*

Nineteen sightings of groups with subadults or cubs were made and young cubs were observed on three occasions. A pair was seen with two newborn cubs on 2 October 1977 on Kaboeri creek. A pair of approximately one month-old cubs was donated to the Paramaribo Zoo on August 1976 but did not survive. A female with a cub aged 3-4 months was seen in a den on the Upper Coesewijne river on 4 February 1977. Altough the data are scanty (Table X) it would appear that cubs are normally born at the beginning of the dry season, from late August to early October after the otters return to their dry season home ranges.

It is possible that there may be a second birth season later in December, March or April if the first litter fails, as may have been the case with the cubs brought to the zoo, but this seems to be uncommon in the wild as the group structure data show.

Evidence supporting multiple births during a year due to litter mortality is provided by the observations of Autuori and Deutsch (1977) of captive *Pteronura* at the Sao Paulo zoo in Brazil. The data are summarized below :

Date of mating	*Gestation* (days)	*Date of Birth*	*N of cubs & sex ratio*	*Comment*
—	—	8 Sept. '70	2	eaten by ♂ Day 1 ?
27 Dec. '70	65	10 March '71	5 (3 ♂ : 2 ♀)	died of suffocation in den
16 July '71	70	24 Sept. '71	2	eaten by ♀ Day 1
8 Oct. '71	65	10 Dec. '71	2 (1 ♂ : 1 ♀)	♂ cub died May ♀ cub survived

Rengger (1830) reports that mating occurs in July-August, which coincides with our data, but goes on to say that cubs are born " early in the year " which is incorrect, given the 60-day gestation period, but should be September-October. Warden (1819) reports parturition in March.

2) *Mating*

I did not observe *Pteronura* mating in the wild but again reports are available from captive studies which can provide basic information until better data are available from field studies.

Trebbau (1978) observed a pair copulating in the Parque del Este Zoo (Caracas, Venezuela). The male grabbed the female by the neck and copulated ventro-ventrally, tails loosely intertwined (Fig. 34). The pelvic thrusts were rapid and lasted 5-10 seconds but

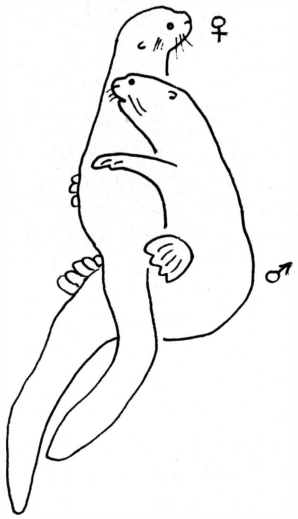


Fig. 34. — Copulation posture of *Pteronura* in captivity. Redrawn from Trebbau, 1978.

were repeated several times, the pair remaining joined for 10 minutes. The female pursued the male after copulation and they copulated again 5 minutes later. This was followed by play and feeding. They copulated again later that day and mating contacts were observed for three days.

Autuori and Deutsch (1977) reported that the male pursued the female for 30 minutes before copulation, the female trying to escape by rolling and scuffling in the sand. The male forced her into the water and mounted her dorsally, her whole body was submerged except for the head. Copulation lasted only 1 minute in the water. Sexual activities lasted 10 days.

These two reports may not necessarily be conflicting but complementary, several postures being used. The role of male and female will require better observations to determine whether it is one sex or the other which elicits copulation attempts.

3) *Parturition*

Litter size appears to be 1 to 3 cubs based on 19 sightings (see Group size) but other authors mention up to 5. Autuori and Deutsch (1977) report five cubs born in captivity which suffocated in a small den. It has been reported that litter size may be correlated with food abundance in larger carnivores (Stevenson-Hamilton, 1954) but I found no direct evidence of this. My observations of small litters, usually seen as juveniles or subadults in a group might indicate early mortality. The female has only four nipples placed low and close together on her abdomen ; a fifth cub might not survive in the wild.

Litter size	*Gestation* (days)	*Locality*	*Source*
3-4	—	Brazil	Warden, 1819
2-3	—	Paraguay	Rengger, 1830
1-5	—	Guyana	Quelch, 1901
2-5	—	Suriname	Penard & Penard, 1905
2-3	70	Caracas Zoo, Venezuela	Trebbau, 1972
2-5	65-70	Sao Paulo Zoo, Brazil	Autuori & Deutsch, 1977
1-3	?	Suriname	Duplaix, this study

The cubs are born furred and blind in a small den, usually close to a fishing area. Both parents remain with the cubs in the den where the squeaking of the cubs and the coos of the adults can be heard from the outside. Cubs may be transferred to other dens in a pair's territory. This was observed only days after the birth of two cubs on Kaboeri creek when the female swam out of the den with a cub held crosswise in her mouth, gripped across the midsection. It squeaked and struggled at first as the female dogpaddled with her head above the water, the male close by her side. Both parents gave the rattling purr, which was only heard with young cubs, and coos, a re-assurance vocalization. She returned 14 minutes later to retrieve the second cub and also swam with it, submerging and surfacing at regular intervals. She remained submerged for up to 6 seconds and the cub showed no apparent discomfort although it spluttered and squeaked loudly when she surfaced. The female was never seen carrying both cubs at once and the male did not carry them et all.

Weight and measurements of five newborn cubs which died of accidental suffocation two days after birth are given by Autuori and Deutsch (1977) :

Sex	*Weight* (g)	*Total length* (cm)
♂ 1	213	33.5
♂ 2	193	33.5
♀ 3	161	31
♀ 1	230	33.5
♀ 2	209	32.5
	average = 201.2 g	average = 32.8 cm

Fig. 35. — Pair of emaciated six-week old cubs at the zoo in Paramaribo. They died shortly afterwards.

I was not able to obtain measurements of cubs in the wild but made measurements of two emaciated and moribund cubs aged approximately six weeks at the Paramaribo zoo (Fig. 35).

Sex	*Weight* (g)	*Total length* (cm)
♂	1400	55
♀	1200	52.5

It was not possible to retrieve these cubs and hand-rear them, and they died a few days later and were disposed of without a post-mortem examination.

Lactation and weaning

I was not able to determine the length of lactation. The nipples of the H female remained enlarged and conical until her disappearance in mid-January, approximately a month after her cubs had been taken from her. The female of the S group was never habituated to my presence enough to observe the condition of her nipples but two of her three cubs were observed catching fish and eating them on 23 February 1978, approximately four months after birth.

This coincides with the observations of Autuori and Deutsch (1977) who report that a cub born in captivity was seen eating a fish 90 days after birth which the mother had caught and placed next to it. Seventeen days later it caught its own fish in the water and dragged it ashore before eating it tailfirst. The cub was observed to eat its fish tailfirst whereas the adults always eat fish headfirst, an observation which coincides with my findings in the wild.

7) Ontogeny

Solitary

It was not possible to follow the development of individual cubs closely as they were never seen by themselves but always with their parents and, supposedly, elder siblings. Young cubs remain out of sight in a den for the first three weeks and may be seen only briefly if and when the mother transports them to another den.

Social :

As soon as they learn to swim, cubs travel and eventually fish with the group members and lead virtually an adult's existence.

When the cubs begin to join in a group's daily activities they measure approximately 2/3 the adult length, as can be seen when they race to cover ashore. Their coat color is lighter than the deep brown of the adults but the white spots or blotches on the neck and chest are present from birth. In the water, cubs can be recognized in a number of ways : 1) their head and neck are smaller than a female's ; 2) their ears appear to be larger, probably because the pinnae are not pressed flat to the side of the head ; 3) they do not periscope when they dogpaddle but keep their head and chin just above the surface, appearing to swim much lower in the water than an adult ; 4) they swim close to the other cubs and close to females who usually flank the cubs on either side, giving the impression of a cluster of heads next to an adult's, whereas adults swim at regular intervals of 1 metre or less.

Autuori and Deutsch (1977) report that a female taught her cubs to swim in captivity, starting at three weeks of age. She

submerged them individually two or three times a day until they could keep afloat vertically ten days later and then swim in a horizontal position shortly after that. The eyes open between Day 28 and 30 during this period of initiation to the water.

The mother and group members keep a close watch over cubs, a point already noted by Quelch (1901) when his boatman removed a cub from a " nest in the grass of the savannahs " where four others were squealing. By causing the cub to squeak this " soon brought into close proximity quite a family of adults which kept on making their characteristic cry, and one or more of which made repeated attacks on the paddles in the water, savagely biting pieces from the blades ". When returned to the nest, the others had been removed, presumably by one or both of the parents. Brown (1876) also reports a similar incident in Guyana when he found a cub stranded, unable to scramble up the bank to its den. " We then placed it higher up near the mouth of the burrow, just as its mother came swimming down river. Seeing us and hearing the cries of her young, she hurried up within twenty feet of us, diving and coming up repeatedly in a most anxious and excited state. When we pushed off from the spot she landed, seized her infant in her mouth, and disappeared with it into her burrow. Presently, to our surprise, she appeared on the top of the bank, a few yards off, having evidently left her house by a back door ".

Parents are most anxious when a cub strays out of sight while swimming. Both the adults and the cubs call to one another, look underwater, periscope and glance from side to side. When they do locate the cub, they give a long call, submerge and surface next to it cooing, humming and touching noses. Normally the pair swim side by side, cub in the middle. In larger groups, the male(s) swims ahead, followed by the cubs flanked by one or more females with an adult male in the rear. The cubs sometime appear to become separated when the adults stop to investigate and the cubs keep on swimming. Their marked anxiety not only testifies to the strength of the parental bond but also to the fact that a cub swimming alone is probably far more vulnerable to predation than when with a larger group. The only potential predator of cubs swimming might be a large caiman *C. crocodylus,* and piranha a remote possibility ; but a cub could easily be lost from sight in a narrow winding creek filled with fallen logs and once out of hearing range, become difficult to retrieve. This latter threat rather than the imminent danger of predation would probably explain the parents' anxiety.

Cubs were observed playing together only once in the wild. The S group had come ashore and two of the three cubs remained in the shallows. One cub reared up, forepaws raised, and fell on the cub next to it, biting its neck (Fig. 36). The cubs both rolled

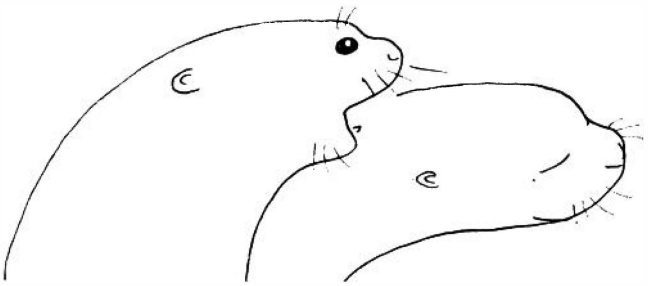


Fig. 36. — Intention play bite by juveniles.

over with the open-mouth play-face typical of play behavior observed in captivity in other species (pers. obs.). Social play was not observed in cubs elsewhere or in the S group again. This may be due to the shyness of the group, the otters fleeing in alarm or remaining on the alert and not relaxing. In captivity, otters spend a major portion of their waking hours in social, bond-strengthening activities (pers. obs.), and the only explanation of their absence on Kaboeri creek is that groups with cubs were not habituated enough to my presence, inhibiting normal activity patterns.

The cubs showed great excitement while fishing with the group. I observed the S group fishing on 3 occasions in Kaboeri creek. The 4 adults barged through the lilypads in the shallows churning up the mud while the 3 cubs nosed in the water, dived and chased with screams and snorts. One cub consistently missed and all 3 cubs missed catching fish far more often than the adults who showed greater economy of movement. The cubs would give the wavering food-begging call when an adult caught and ate a fish near them but no sharing or stealing was observed. It has been stated that an animal while growing up " learns to take those foods which its repertoire of behavior patterns and structure permit it to exploit most efficiently " (Hinde, 1958) and even though the cubs were not adept at catching fish they chased them with agility, swiveling and porpoising in the water.

Cubs were never observed exploring their environment either alone or with other cubs. The parents and sibling kept too close to them to allow them to stray very far and it was not possible to observe them resting ashore.

B) Group structure and movements

The *Pteronura* observed in Suriname fall into two basic categories : *residents* usually living in family groups which remain on small creeks during at least the dry season, returning to this

same area in their range every year ; *transients* usually solitary individuals which apparently lead a more nomadic existence and do not appear to be linked with an established resident group in the area. Perhaps the latter category applies to 1) subadult animals splintering away from a family group after they reach two years of age or 2) a member of a pair which has lost its mate. Both categories do not appear to be rigid or exclusive but may be normal stages in a giant otter's life cycle.

1) The group

Pteronura sighted in an aggregation of two or more individuals was called a group.

a) *Size and composition*

Early naturalists appear to agree on one point : *Pteronura* is often seen in groups ranging up to 20 individuals (Table IX). We noted group sizes of 3 to 16. In the 26 sightings made outside the study area, single individuals were seen 5 times (19 %), pairs 9 times (35 %), trios 3 times (12 %), four together twice (8 %), seven 4 times (15 %), eight once (4 %) and sixteen once (4 %). This largest group may have been two groups traveling together in April moving from their dry season range to their rainy season habitat.

If one is to discount sightings of 2 minutes or less which may bias towards a smaller group size as all the individuals might not have been sighted, the following percentages of 18 sightings are obtained : pairs 7 times (39 %), seven otters 4 times (22 %), four otters twice (11 %) and once for otters in groups of 3, 5, 8, 16 or alone (6 %). One can see that the smaller the group, and single animals in particular, the more difficult it is to maintain observation for a reasonable length of time.

Table IX

Reports of group size in Pteronura.

Group size	*Locality*	
12 +	Guyana	Waterton (1812-1824), 1973
20	Paraguay	Rengger, 1830
12	Guyana	Schomburgk, 1840
12 +	Guyana	Quelch, 1901
12-15	Venezuela	Mondolfi, 1970
5-10	Venezuela	Trebbau, 1972
8-15 (4-6 norm)	Venezuela	Mondolfi & Trebbau, 1978
7-16 (4-8 norm)	Suriname	Duplaix, pers. obs.
3-20 (3-5 norm)	Peru	Terborgh, pers. comm., 1980

Pairs were sighted five times in January and February when presumably they might have been rearing cubs whereas the larger groups were seen in January, February, March, April, July and August when family groups were coming together when and after the parents had cubs reaching the juvenile stage of 4 months of age and, later, when moving to or in their rainy season range.

After I observed the habituated otters of Kaboeri creek on a daily basis it became apparent that group composition was very stable. As individuals were recognizable it was possible to establish that at least three of the five resident groups returned to the creek after their absence during the dry season and that the same individuals were present in each one ; the individuals in the other two groups were too shy to determine this with certainty.

The larger groups of 4 or more otters consist of 2 adult animals (a pair), one or more subadults and one or more juveniles ; an observation already noted by Schomburgk (1840) : " Thus much is certain ; ..that in the same community there are otters of all sizes, and apparently of three or four successive generations. " The age classes are sometimes difficult to distinguish unless the whole group can be viewed for 5 minutes or more at less then 20 m. The adult females have a noticeably thinner neck and smaller head than adult males but subadult males can be confused with adult females. However, males tend to remain together and the females stay close to the cubs so that one can, with practice, make an educated guess of age classes.

Because of the three age classes present in each large group and my observations of the groups on Kaboeri creek allowing the cubs of 1976 to remain with the group and cubs of 1977, I think that the group structure in *Pteronura* is based on the family unit or pair. I do not know how long subadults stay with the parents, but the fact that I never saw more than 3 cubs in my sightings of large groups may indicate that they leave prior to or at sexual maturity to start a family unit of their own (Table X).

b) *Sex ratio*

In my 27 observations of groups outside the study area I saw 30 males, 31 females ; 37 subadults or cubs and the sex of four could not be determined (Table II). Only the sex of adults can be determined with any confidence in the water. When a group is observed on shore, the nipples or the scrotum of subadults can be seen while resting on their side.

The evenness of the sex ratio of adults would support my theory that the family unit is based on a pair. The extra female recorded was sighted alone with her cub in a den. It is not known what the sex ratio is at birth save for the pair of moribund cubs brought to the Paramaribo zoo and the findings of Autuori and

TABLE X

Sightings of groups with subadults and/or cubs.

LOCALITY	RIVER SYSTEM	ADULTS ♂	ADULTS ♀	SUB-ADULTS	CUBS	DATE	ACCURACY OF AGE CLASS IDENTIFICATION BY OBSERVER
Kwama Creek	Coppename R.	1	1	1		13 Aug 76	good
Tangnimama C.	»	1	1	2		16 Aug 76	good
Tangnimama C.	»	1	1	3		18 Aug 76	poor
Gran Soela	»	1	1	1		4 Oct 76	poor
nr. Tapoeripa	Nickerie R.	1	1	2		12 Nov 76	good
nr. Apoera	Corantijn R.	3	2	2		19 Jan 77	3 ♂♂ good ; poor ♀/subadult sighting
Kabo Creek	Tibiti R.	2	2	3		26 Jan 77	good
Coesewijne R.	Coppename R.	1	1	1		3 Feb 77	good
Coesewijne R.	»		1	1		4 Feb 77	good
Goliath C.	Coesewijne R.	1	1	2	3	5 Feb 77	good of cubs ; poor of ♀/subadult
nr. Apoera	Corantijn R.	2	2	2	2	10 Mar 77	good
Perica R.	Cottica	5	5	6		12 Apr 77	poor ♀/subadult sighting
Zuid R.	Lucie R.	2	2	3		15 Jul 77	good
Zuid R.	Lucie R.	1	1	3		15 Jul 77	good, repeat of above ?
STUDY AREA :							
Kaboeri C.	Corantijn R.	1	1		1	Mar 1977	habituated H group
»	»	1	1		2	Mar 1977	S group
»	»	1	1	1	2	Oct 1977	H group
»	»	1	1	2	3	Oct 1977-Mar 1978	S group
»	»	1	1	3	2	Jan-Mar 78	U group- upper Kaboeri
»	»	1	1	?	?	Jan-Mar 78	F group- upper Kaebori, dens in use

Deutsch (1977) on breeding in captivity (cf. Reproductive Beh.). They observed two litters of 3 males : 2 females and a pair which would indicate that the sex ratio is probably even at birth.

c) *Transients*

Solitary individuals or transients were observed 5 times in 27 observations outside the study area and four transients were seen on Kaboeri creek. Transients are otters which had not been seen before or which did not belong to a resident group and were either passing through the area and or were so shy that they actively avoided the observer.

d) *Group cohesiveness*

Already at first glance a group of otters swimming abreast gives the impression of a well-coordinated, closely-knit group (Fig. 37). Indeed, most of the activities carried out during the day are done by individuals in close proximity to one another. A single individual, usually an adult female, may initiate a group movement, such as going ashore or heading towards a fishing area, or an activity such as grooming, resting ashore or marking and the other group members will invariably follow suit within

Fig. 37. — Family S group. From left to right : 2 adult females, 1 adult male (with open mouth snorting), 3 three-month old cubs, and one adult male.

a few minutes. Group cohesiveness is strong as evidenced by the observation that group members do not normally splinter from the group and wander off for days at a time. The only time that subadults did not remain with their parents was during the time cubs were being reared in the den. As I have stated, the male plays an active role in rearing his cubs, never straying far from the female.

The role of adult males in the group is to maintain this cohesiveness and integrity by warding off transients and intruders. When a human observer is first sighted, the male or males will often be the ones to approach the closest, charging the boat and giving the open-mouth wavering scream. Such charges can be provoked by imitating this call and while they may not be fooled a second time, they come to within 3 to 10 m of the boat to investigate. Such a fearless charge may be made under the mistaken apprehension that unknown otters are threatening their group rather than motivated by consuming curiosity. When a group of 16 otters was spotted in April 1977 and called to in this manner, five adult males veered towards my boat and charged while the females remained with the cubs 20 m away.

No competitive or aggressive encounters between group members of same or opposite sex were observed which does not mean that they do not occur. Each otter caught and ate its prey without a group member attempting to take it away through intimidation, regardless of age, class or sex. No disputes were observed and even play fighting was observed in cubs only once. Whether there is in fact a rank order in a group based on sex and age is not yet certain.

e) *Seasonality and influence of habitat on group size*

It was not possible to observe the movements of the giant otters in my study area during the complete annual cycle but I was aware that the residents had moved into the flooded forest and swamp habitat on either side of the creek from mid-April to late August.

Observation of group size show that variability in group size is usually related to the presence of young cubs in the den when only the parents remain with them ; 6 weeks to 2 months later the subadults rejoin the family group again. I found a discrepancy between the S pair with 2 subadults and the H pair with one offspring. When the S group had cubs in September 1977 the subadults stayed in close proximity and the parents were often seen with them while the cubs were still in the den. However the H subadult was not seen close to its parent but remained in their territory until the female disappeared in late January 1978. Whether this group structure change during cub rearing is the general rule in *Pteronura* is not known.

It was not possible to determine whether habitat type affected group size in any way. Generally, in the falls areas of larger rivers sightings were rare, but in the creeks radiating from them I saw family groups. Group size and habitat type apparently have no bearing on each other.

C) Activity budget

1) Daily activities

Pteronura in Suriname is strongly diurnal. The groups are active during most of the daylight hours from 0630 to 1830 hours approximately and retire at night to their campsites or a den within their established territory or home range. During my 212 days and nights in the field I never saw or heard a giant otter on the river at night. Sometimes I would camp near a site where otters had retired in order to be able to follow them the next morning. Once on the Coesewijne the reverse occurred and a pair of otters spent the night near my campsite and I saw them at 1725 in the evening and again at 0807 the next morning. On Kaboeri creek I was able to keep virtually continuous contact with the semi-tamed H and KI pairs for several continuous days merely by returning to the area of their territory where I had left them the previous evening.

Of course, activity occurs before the otters leave their sleeping sites in the morning. Grooming, toilet activities and resting occur before the otter(s) enter(s) the water. My earliest sighting was at 0747 and my latest at 1741 on Kaboeri.

2) Kaboeri creek

I will confine my remarks on daylight activities to three otter groups on Kaboeri creek. From 13 January to 11 March 1978 I spent 46 days (340 hours 20 minutes) on the creek and recorded 140 direct sightings of 11 individuals for a total of 93 hours 22 minutes. Direct observations lasted from a hurried glimpse of a minute or less to 5 hours 7 minutes continuously (H ♂).

When reviewing the data on Fig. 38 one can immediately note the bias between the three groups observed. The H pair was observed for 14 hours 28 minutes in 5 sightings over a three day period indicating that each sighting was long, even after the H ♀ disappeared on 19 January. This in sharp contrast to the S group of 7 otters who was glimpsed several times a day but usually raced off into the forest after a few minutes or eluded my pursuit by boat by taking short-cuts overland, and re-entering the water further downstream. In 34 days I saw this group 91 times but observed it only for a total of 8 hours 23 minutes. The KI pair

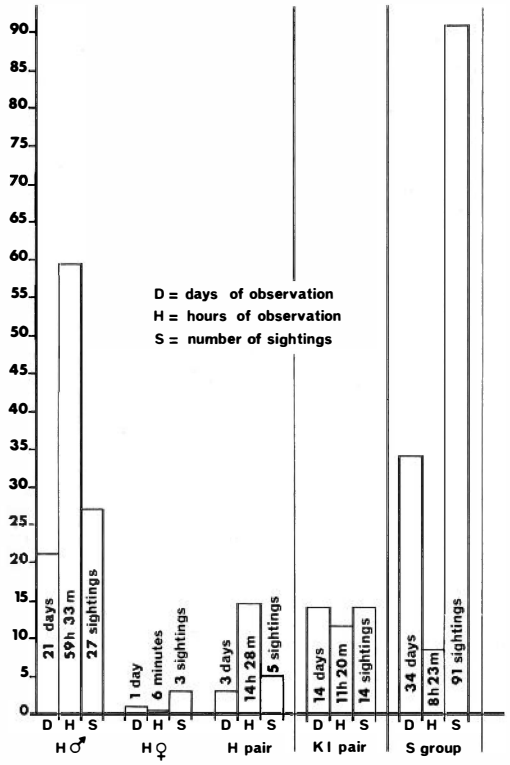


Fig. 38. — Number of days on which known individuals were observed on Kaboeri creek, with number of sightings and hours of observation, 13 January to 11 March 1978.

became rapidly habituated to my presence if I maintained a distance of 10 m but it lived near the entrance of the creek where viewing conditions were more difficult. It was observed on 14 days in 14 sightings for a total of 11 hours 23 minutes.

Therefore, the interpretation of the activity budget charts (Figs 39, 40) must be made with the knowledge that it is probably the H pair observed from January 13 to 19 that gives the best picture of an established pair's normal routine, including marking. When alone the H ♂ marked very little, if at all. The S group was too alarmed by my presence to do anything but swim away or go ashore so that the data are too fragmentary to be of any value.

3) Daytime activities

There appears to be no clear-cut pattern as to time of day or length of activity for any one activity. The otters divide their

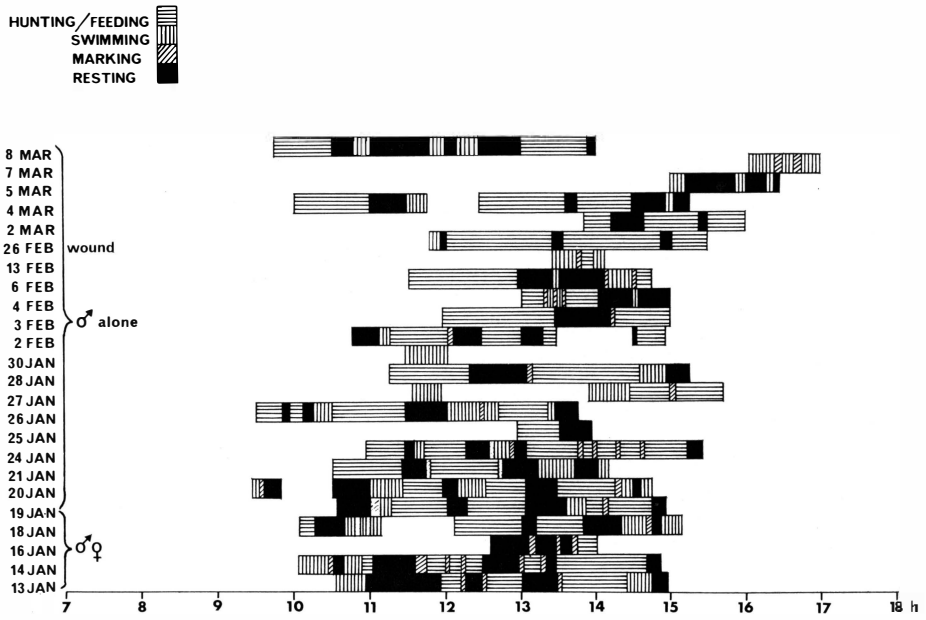


Fig. 39. — Activity budget of the H pair, 13 January to 8 March 1978.

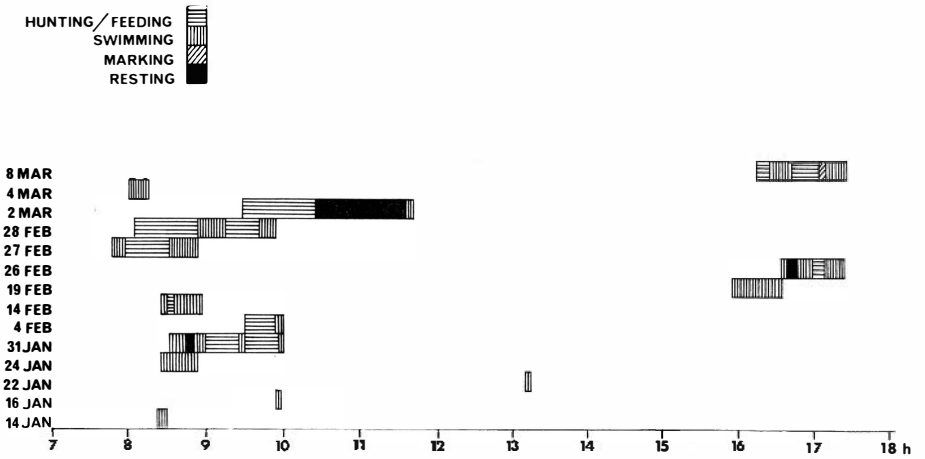


Fig. 40. — Activity budget of the KI pair, 14 January to 8 March 1978.

time almost equally between hunting (feeding) and resting ashore. They may swim without hunting from one fishing area to another or go to a rest site and also swim when patrolling their portion of the creek. When the ♂ H lost his mate he divided his time between resting and hunting as he no longer patrolled or marked a territory.

The KI pair had a larger home range which included the island at the entrance to the creek and at least 1.5 km of the creek itself. Both otters spent a large portion of the day swimming up and down and/or hunting in the relatively deep water of 3-6 m. They were observed resting ashore from 1030 to 1140, the longest time they were seen ashore while under observation. They were also observed marking a site once. They were a newly formed pair of subadults and only just establishing a territory on the creek, and their marking behavior may not have been as well developed as the H pair which were observed marking up to six times in one 4½ hour observation period. The KI female's nipples were not developped indicating that she had not yet had cubs and the pair virtually never groomed each other or rested in close contact like the older, multiparous H pair.

Mutual grooming takes up a significant portion of the resting period in a mated pair (cf. Pair Bonding) whereas in the subadult KI pair it was seen only eight times lasting only a few minutes. It usually precedes and follows a dozing period but may also take place spontaneously when the otters are resting briefly after finishing a fish ; one will turn to the other and nibble briefly before diving into the water. Rest periods, which occur at any time but usually follow a hunting sequence, may last up to 1½ hours, but more usually 50 minutes (29 observations of that length for H pair).

While hunting, otters swim abreast and close to the bank, and take the fish to a log or, less often, the edge of the bank and consume it immediately. The partner will continue to fish in the vicinity and wait for the other(s) to finish eating before resuming swimming up or downstream. Otters seem to take advantage of the tides during both fishing and patrolling, swimming in the direction of the tide and fishing usually at slack tide or low tide which may account for the fact that hunting and feeding activities are spread out so much during the daylight hours.

It was not possible to establish whether there was any appreciable difference between the proportion of time spent on different activities except as noted in passing above. Longer observations would be necessary to determine whether such factors as seasonality and breeding activity affect the daily activity pattern of individuals and groups.

D) Home Range and territory

1) Structure of campsites

When ashore, *Pteronura* use specific areas for comfort and territorial activities. On smaller rivers and creeks, a portion of the vegetation is cleared along the riverbank, usually measuring 8 m long and 7 m wide. Such areas have already been described by Schomburgk (1840) : " their feeding places are so devoid of vegetation, if we except the larger bushes and trees, that they cannot be mistaken, even if the number of scales and fish-bones did not point out the frequency of their visits. A complete path leads up to these places, which, in consequence of their ascending and descending single file, is hollowed out. " He goes on to add that " their haunts are easily known by a strong and disagreeable smell, in some instances so strong that we increased by all means in our power the speed of the canoes to get out of its precincts. "

This remarkably accurate description fails in only one detail — these areas are not used for feeding but only for marking, drying out, sleeping or resting and, sometimes, denning activities. Such areas were referred to as " campsites " by the Amerindians and *campoes* (camps) by the Bushnegros ; we called them campsites or sites. Campsites are used by family groups and are visited at regular intervals during the dry season.

The choice of location is dictated by a number of factors :

a) Visual location : sites are often visible at a distance, the cleared bank and smooth substrate clear of leaves contrasting sharply with the surrounding tangle of secondary undergrowth on either side (Fig. 41). River bends or islands are not particularly favored unless they are also used as a cross-over point.

b) Substrate : sites are usually above the high tide and high water level during all but the wettest months so that low lying portions of the river are avoided. The elevation is 50 cm to 2.5 m above the slack water line which means that the otters often clamber up the banks leaving deep scratch marks and trampling the earth down. The ground of the site is normally level with only a few large trees over 80 cm in diameter with perhaps a clump of smaller saplings ; bushes, grass and leaves are cleared and trampled by the otters and scratched away until the humus and roots are visible. Overhanging trees are present in nearly all the 227 sites measured ; of 167 sites measured on seven rivers, 125 (74.85 %) were under trees.

c) Forest type : the otters avoid areas of the creek which are prone to flooding during the dry season such as swamp forest or palm swamps with tall grasses and floating vegetation mats. In creek forest where " mokomoko " *(Montrichardia arborescens)*

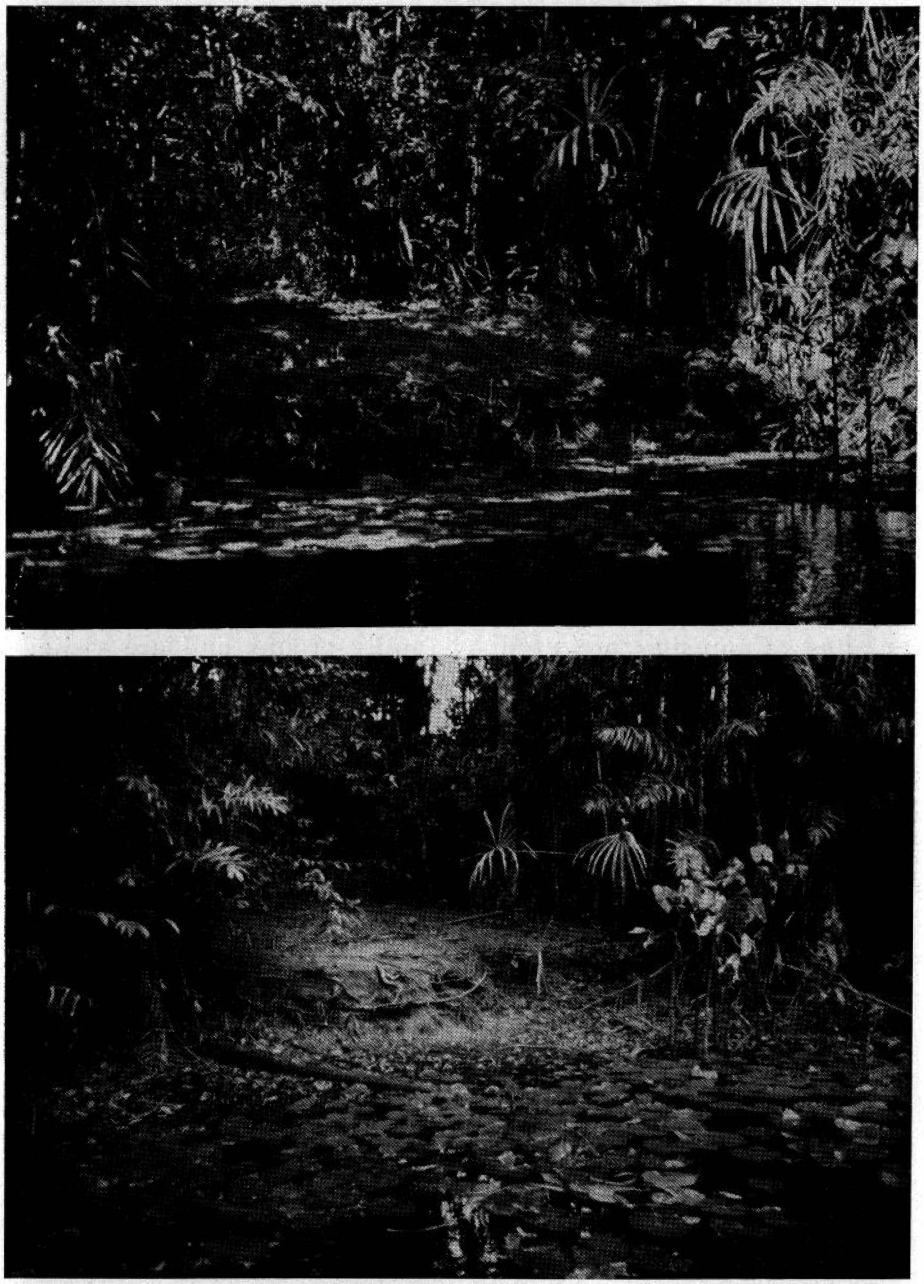


Fig. 41. — A camp site on upper Kaboeri creek (km 11.5). Abandoned (top) during the rainy season of 1977, the site is covered with encroaching vegetation. It was cleared (bottom) down to the bare ground in January 1978.

often borders the edges, the sites sometimes lie immediately behind this protective curtain, affording easy access through the thick stalks but not sufficiently thick to block the view of the river. Lilypads frequently were found in the shallows at the base of the sites on Kaboeri creek.

d) Accessibility : sites are often chosen for their accessibility to other areas. Small paths made and used by the otters may radiate from a site into the forest and they use this "back door" to reach a marshy pond in a low-lying area or as a short cut to cross back to the river. At the start and end of the rains, sites with back doors to flooded areas are used more often than those without them.

2) Size, Shape and Variation of the Sites

Even though there can be considerable variation in the size of a site, ranging from 1.5 m to 28 m in length (running parallel to the river) to 1 m to 14.7 m in width, the average size on three different rivers was remarkably similar : Upper Coesewijne river 8.12 m $\times$ 6.81 (11 sites) ; Kabo creek (Tibiti river) 12.25 m $\times$ 6.96 (16 sites), and Kaboeri creek 8.94 m $\times$ 5.99 (50 sites).

The width varies more than the depth as the otters tend to expand the sites in this direction rather than move further away from the river's edge. The latrine is usually located on the periphery, sometimes a short corridor leads to it. When otters return to large sites that have been abandonned for some time, the latrine may be central until all the leaves have been cleared away.

The shape of a site is usually rectangular or semi-circular ; the smaller sites being more circular in shape, becoming rectangular as they are expanded. A site usually starts as a resting area where a pair or family group go ashore and begin marking and/or defecating. Both adult males and females tear down the overhanging vegetation (see Olfactory Behavior), break all small saplings, scratch up the leaves, trample the substrate, start a latrine. While a number of sites may be started and visited several times in a few days they may be abandonned at this point or not visited for another season. On the whole, they are small, 2 m or 3 m in a diameter to begin with, being enlarged with each subsequent visit, as is the latrine (Fig. 42).

3. Seasonality, Upkeep and Deterioration

On Kaboeri creek where 50 sites were monitored at roughly monthly intervals, it was possible to establish that at least 23 could be considered perennial — they were visited again after the rainy season and cleared of the grass, fallen twigs and branches and leaves that had accumulated during three or four months' absence. This was particularly true of sites in good locations either from

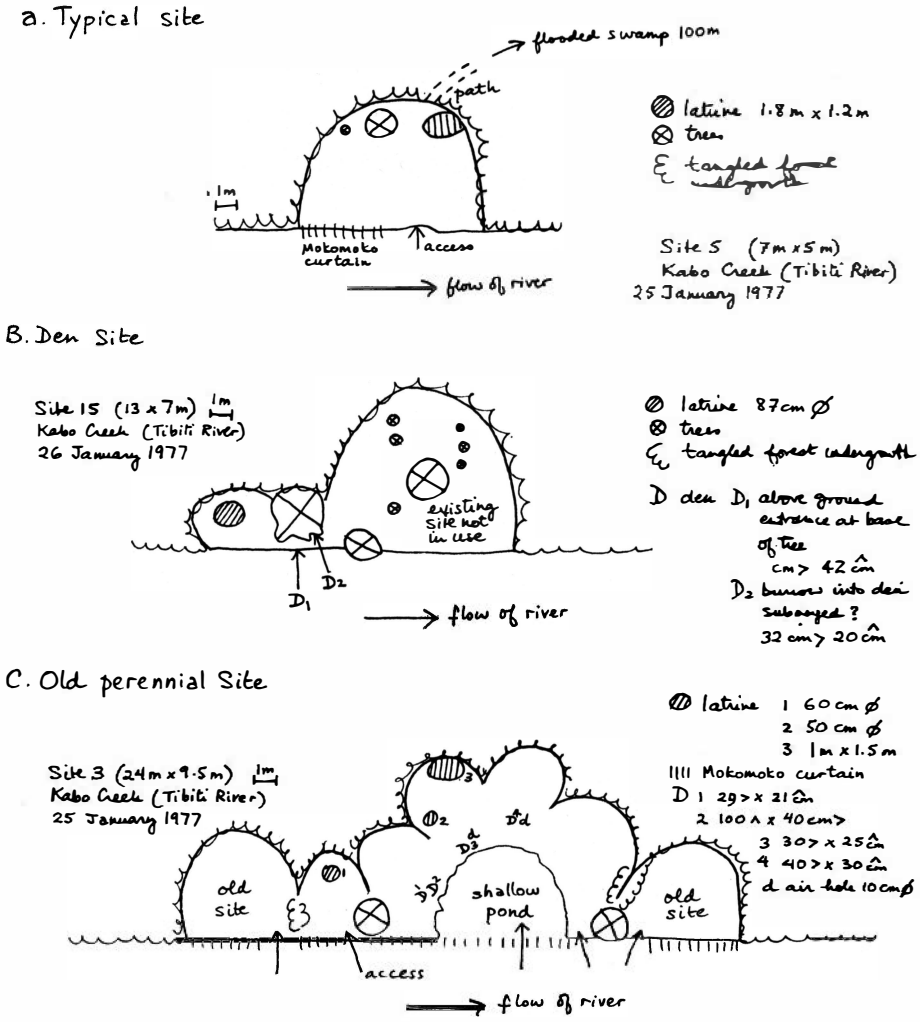


Fig. 42. — Comparison of various *Pteronura* campsites.

a territorial viewpoint or because they had backdoors into forest or cross-over points or because they were the only ones available in portions of the creek surrounded by low-lying areas unsuitable for site locations (Fig. 43).

For instance, the H pair on Kaboeri creek started sites at the Flag Tree (km 4.7) and Site 40 (km 3.7) in September 1977 and January 1978 and these were not visited again. Others sites were visited regularly : Sites 12 and 13 (km 3.6), in the center of the

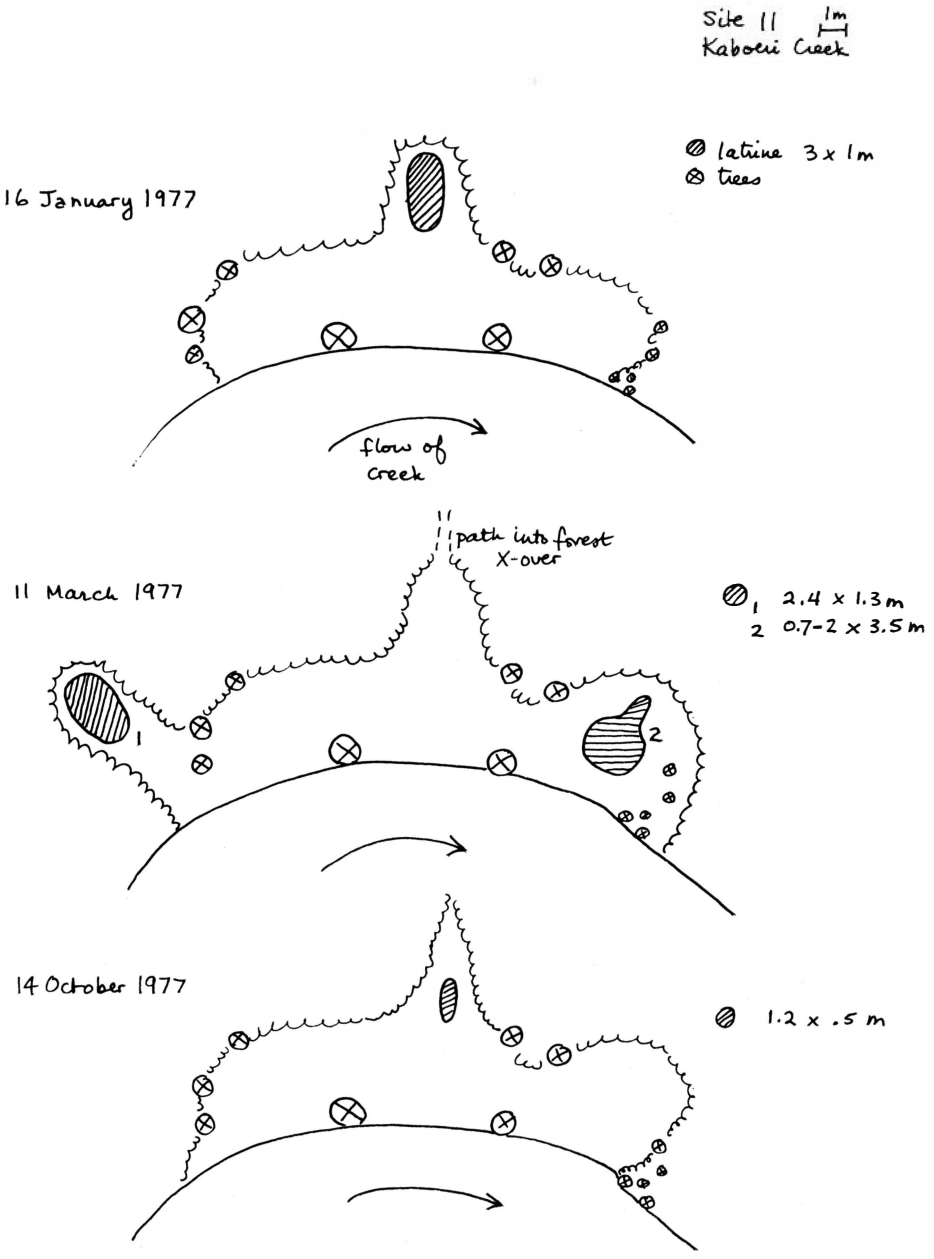


Fig. 43. — The evolution of a campsite from January to October 1977. The site was abandoned from 14 March to 21 September.

H pair territory in Jan.-April 1977 and September to January 1978 were in frequent use. Located at a territorial boundary, sites 2 and 3 (km 1.7) located well above the water line, were also visited frequently and expanded laterally, by the H pair in 1977 and then the S group in late 1977 and 1978.

During the rains, from mid-April to late August, the otters virtually abandon Kaboeri creek and many sites are flooded. Only the sites on high ground and/or those located as virtual islands in the center of low-lying flooded areas are occasionally visited. On upper Kaboeri creek contiguous sites 4B and 5D (km 10.5) were flanked by swampy areas and the next sites 2B and 4D were over a kilometer downstream at km 10.2, followed by another under-utilized portion of creek until km 7.8 to 8.2 with 6 sites. Site clumping may not only be dictated by the presence of long stretches of low-lying swamp followed by short stretches of high ground but also by the fact that such isolated portions become core areas in the home range and sites are expanded and new ones begun in the immediate vicinity on both sides of the bank.

Very old sites may be abandonned during a complete dry season — wet season cycle and only reactivated in alternate years. Site 4B (km 10.5) was such a site. When measured for the first time on 11 March 1977 it was abandonned and the grassy borders and broadleaf weeds virtually covered the 7 m $\times$ 5 m site. An old, central latrine (1.1 $\times$ 1.8 m) could still be recognized by the presence of dried scales and vertebrae on a bare patch. Mazama deer *(Mazama americana)* droppings were also present on the edge. (It should be noted in passing that such abandonned sites are sometimes used by other mammals. Droppings of capybara *(Hydrochaeris hydrochaeris),* tapir *(Tapirus terrestris),* margay or ocelot *(Leopardus tigrinus* or *L. pardalis)* were found on old otter sites). During the next rainy season, in May 1977, a new adjacent site 5D was cleared and the old one used with a peripheral latrine. In January 1978 the old site 4B had been again completely cleared of ground vegetation down to the yellowish sandy soil and was in use until the end of the study in March 1978 (Fig. 44).

4) Single spraints versus latrines

Most mustelids leave single scats on conspicuous objects at strategic points within the territory and, in the case of most *Lutra* species, these strategic points very often are landing places (pers. obs.). Another form of marking involves communal latrines which are used by the more social otter species such as *Aonyx, Amblonyx* and *Lutrogale,* but single scats may also be left by these species.

In Suriname, I found that *Pteronura* left single scats or spraints in only two types of habitats. The upper Coppename

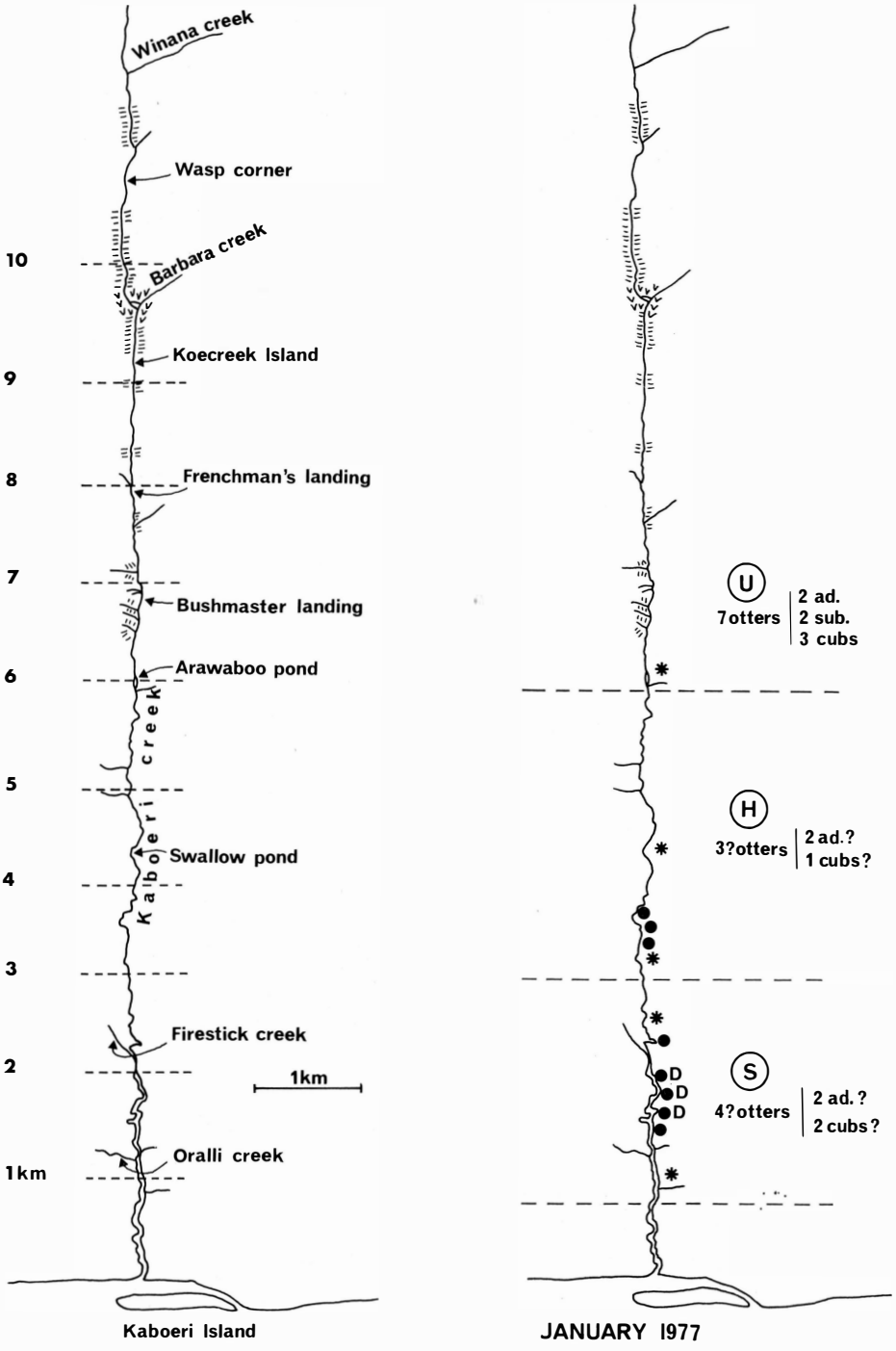


Fig. 44 a. — Observations on Kaboeri creek. January 1977 :
* sightings ; ● sites in use ; D den.

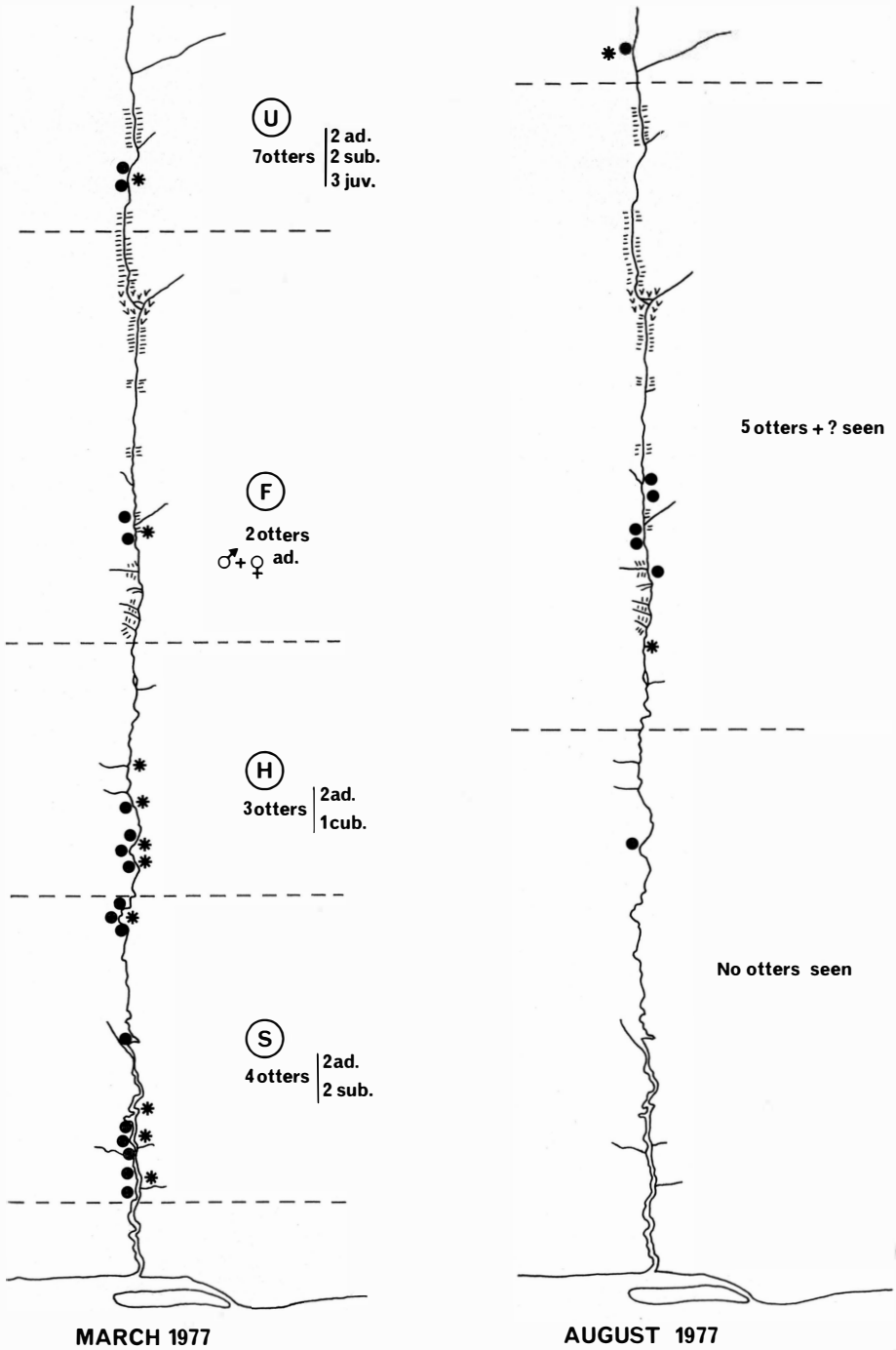


Fig. 44 b. — Observations on Kaboeri creek.
March (dry season) and August (rainy season) 1977.

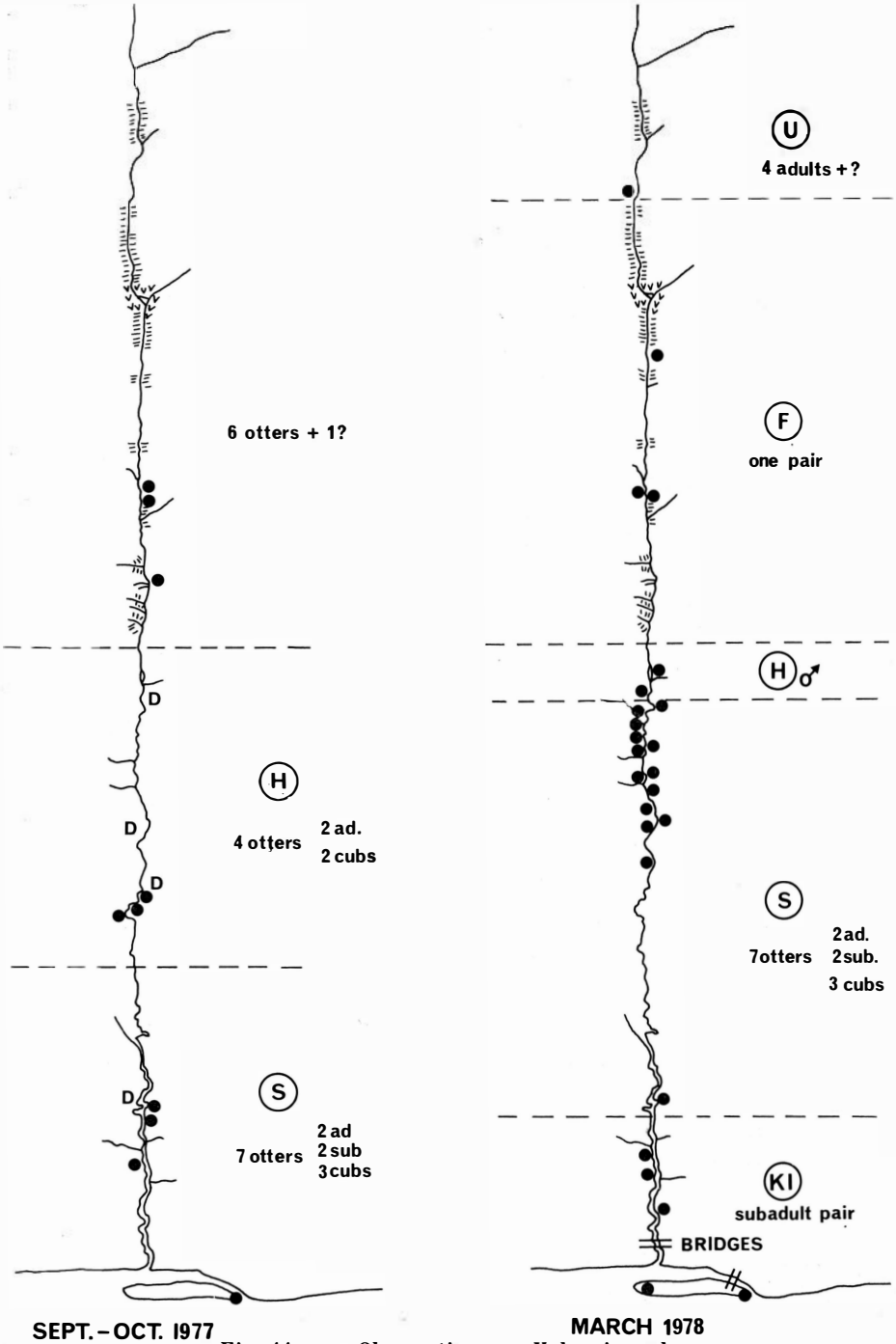


Fig. 44 c. — Observations on Kaboeri creek. September and October 1977, and March 1978.

Fig. 45. — Aerial view of the Hoof Falls — Raleigh Falls complex (Coppename river) during the dry season.

river in two plateau areas, the Hoof Falls-Raleigh Falls complex (Fig. 45) and about 20 km upstream, at Tonken Falls (Fig. 46). Small forest creeks with boulders and large fallen logs such as the Zuid river, Kabo creek (Corantijn river) and upper Tibiti river were another habitat where single scats predominated.

A) *The Falls areas*

The Raleigh and Tonken Falls system are plateaus where the broad Coppename river has spread, creating a multitude of small islands, sandbars, granite boulders, granite bedrock, small creeks, rapids and waterfalls. During the rainy season, many of the islands and boulders are covered by the deep, fast flowing waters and surging rapids. When the waters begin to recede in September-October, the fish and crabs are trapped in small pools on the sandbars and between the islands and between heaps of boulders. Both *Pteronura* and *Lutra,* as evidenced by tracks and spraints (scats), exploit these areas at this time.

Lutra tracks and spraint were also found, in 3 instances crossing *Pteronura* sites and tracks. The *Lutra* spraint is much smaller (2 g versus 7 g), 1 cm in diameter and 3 to 5 cm in length

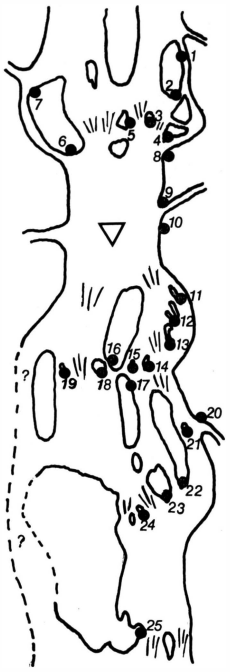


Fig. 46. — Single spraint sites at Tonken Falls Coppename river, during the dry season (26 September 1976). The sites are numbered from 1 to 25.

and can not be confused with the larger species. The fragments of crab exoskeleton and fish scales are also smaller indicating that the crabs are chewed more thoroughly and that smaller fish are taken. On a sandy beach a *Lutra* sand mound was seen — the sand had been scratched to form a circular mound and urine and scent were placed on top. *Pteronura* was never seen to do this, scenting broad areas and trampling the mud along the banks of communal sites instead.

Tonken Falls was surveyed on 26 September and 10 October 1976. This is a remote and uninhabited portion of the Coppename river which is infrequently visited by man and is of difficult access. The otters are therefore seldom disturbed. I found 29 sites and collected 43 of the 118 spraints seen. A site preference pattern is evident.

Small sandy beaches at the foot of boulders, often near rapids which are visible 50 m away are often chosen (72 %). The sandy portion may be less than 1 m in diameter and the individual spraints stand out against the background. The spraints are roughly cigar shaped 1.5-2 cm in diameter, 4-8 cm long and contain

mostly crab and fish (58 %) while spraints containing only fish or only crab occur in 21 % of the cases respectively. The crab's exoskeleton is rapidly bleached by the sun to a white or pale pink color and the dry whitish scat stands out even more against the yellow sand or dark grey boulder. Islands, whether sandbars or boulders are particularly favored (90 %), probably because they are the only sites available, the river being 600 m to 1.2 km wide at that point.

Usually 3 spraints were found per site (35 %) lying singly within a radius of 30-60 cm about 5-15 cm from each other. Grass tussocks may be present on the sandbars but the spraints are deposited on the sand about 1-1.5 m from the water's edge, usually about 50 cm above it (77 %) and/or on the highest point available (41 %). On larger islands, the spraints may be found near or under a tangle of overhanging bushes (52 %) but those on boulders, bedrock and sandy locations are in the open (48 %) and near the mainstream and/or rapids. The larger islands may be bordered by small creeks along slower stretches on more level ground. Two spraints were found on a log, an unusual location for Tonken and Raleigh Falls, but common in the Zuid river (44 %) and Kabo creek (Tables XI-XIV.)

The most interesting facts of this single spraint marking system are that 1) the spraints are not trampled into a communal latrine ; *Pteronura* or *Lutra* probably leave the water, turns around to defecate after smelling and inspecting the site and return to the water ; and 2) each site is within sight of the next one (76 %) so that all sites are strategically located spanning the river wherever possible. Because the river is so broad it may take 9-12 individual spraint sites to reach the opposite bank, the otters using each visual landmark at their disposal ; usually every boulder, sandy area or large islands with convenient hauling out spots. A transient otter traveling along such a wide river would follow the mainstream, perhaps going overland to avoid rapids, and could not fail to come across one or more of these single spraints along the way.

There are indications that at least some sites are visited regularly. One out of six sites marked on 26 September had three fresh spraints on 1 October when I returned.

At Raleigh Falls visited on 12 October 1976 the same " transect " phenomenon occurs : single spraints are used to join one far bank to another through a multiple visual scent post system. Again the majority of the 19 sites measured are within sight of each other (68 %) but here there are more islands (79 %) with overhanging vegetation (68 %) and fewer sandy patches (21 %) so that boulders are a favored location (63 %). Spraints are also

placed higher, between 50 cm-1 m above water (68 %), and this is not always the highest spot available (11 %). More single spraints (63 %) are found whereas on Tonken Falls five or more spraint were together in five locations (17 %).

The spraints contained fewer crabs here, perhaps because fewer were available or most had been taken already from small pools. Of the 22 spraints collected and analyzed, 7 (32 %) contained fish only, 9 (41 %) contained fish and crab and 6 contained only crabs (27 %).

No scenting or trampling evidence by *Pteronura* was found in the falls area and no sleeping or resting areas either. The otters probably sleep on islands in midstream which I could not reach — it would not be surprising to find communal latrines on sites that were used overnight if the individuals in a family group slept together.

I sighted few *Pteronura* at the falls. None at Tonken, one at Raleigh Falls, although three were seen repeatedly in October 1976 and a pair was sighted on the Adampada creek in a small falls complex on the upper Coppename. The otters were generally shyer there than in small forest creeks, probably because of the openness of the terrain and because they were not used to seeing human intruders.

B) *The forest creeks*

Single spraints were also found on boulders or logs along narrow forest creeks such as the upper Zuid river near the Kaiser mountains in central Suriname, the uper Tibiti river (Coppename river tributary) and Kabo creek (Corantijn river tributary). A single instance of a spraint on a log was recorded on the upper Maratakka river (Nickerie river tributary) and on Kaboeri creek, the main study are area (Table XIV).

On the Zuid river where 23 spraint sites were located, 10 (43 %) were on logs and 12 (52 %) on boulders (Table XV). Most of the boulders though were located in a white water falls complex area about 30 km downstream near the confluent with the Lucie river. The upper portion of the river is narrow (8-15 m wide), winding through the forest and very similar in appearance to the other rivers and creeks mentioned above. The banks are high and sheer making access to the otters difficult, which increases the probability of logs straddling the river or leaning against the bank and midstream boulders being used for marking. Eight

TABLE XI

Site analysis at Kabo Creek (Tibiti River), January 1977.

SITE	WIDTH (cm)	LENGTH (cm)	N SPRAINT SITES (Latrines)	SIZE SPRAINT SITE (cm)			N DENS on SITE	SIZE (cm)	
				WIDTH	LENGTH	LOCUS		WIDTH	LENGTH
1	7	9	1	100	220	P	—		
2	10	7	3	100	100	P	—		
				100	200	P			
				80	100	P/W			
3	30	5	3	60	60	Mi	4	29	21
				50	50	P		30	25
				100	100	P		100	40
								40	30
4	18	5	1	280	180	P	—		
5	7	5	1	120	180	P	—		
6	8	7	2	80	80	P	—		
				100	100	P/W			
7	17	7	5	100	200	P	—		
				100	150	Mi			
				50	50	Mi			
				100	100	P			
				80	80	M			
8	7	4	1	150	200	P	—		
9	9	7	3	100	200	P	—		
10	23	12	—	—	—	—	old, caved in		
11	5	6	1	50	50	Mi/W	—		
12	12	8	1	200	200	P	—		
13	8	11	1	180	100	P	—		
14	15	6.4	3	250	130	Mi	2 old		
				70	70	P			
				150	200	Mi			
15	8	7	1	87	87	P/W	2	32	20
								47	42
16	12	5	1	70	70	P	2	60	41
								45	38
	$\overline{X}$ = 12.25 Range = 5-23	$\overline{X}$ = 6.96 Range = 4-12	T = 28 $\overline{X}$ = 1.75/s Range = 0-5	$\overline{X}$ = 116.3 Range = 50-280	$\overline{X}$ = 116.32 Range = 50-200	16P 57.1 % 3P/W 10.7 % 1M 3.5 % 6M 21.4 % T = 28	10/4 si. 25 % sites have dens 2.5 d/si	$\overline{X}$ = 47.88 Range = 30-100	$\overline{X}$ = 32.13 Range = 20-42

Key : peripheral || - parallel T - total Mi - middle s, si - site $\overline{X}$ - median W - near water d - den

TABLE XII

Site analysis at Upper Coesewijne River, January 1977.

SITE	WIDTH (cm)	LENGTH (cm)	N SPRAINT SITES (Latrines)	SIZE SPRAINT SITE (cm)			N DENS on SITE	SIZE (cm)	
				WIDTH	LENGTH	LOCUS		WIDTH	LENGTH
1	7	5	2	100	300	P	—		
				150	200	P/W			
2	7.5	6	1	240	480	Mi	—		
3	9.2	7	4	40	100	P	1 (3)	48	26
				80	200	P		37	22
				120	300	Mi		30	40
				60	60	Mi			
4	6.8	5	1	100	30	P	1 (2)	40	40
								60	60
5	6.7	8	1	200	120	Mi	—		
6	9.2	7	3	120	300	Mi	1 (3)	40	35
				50	50	P		35	42
				300	500	P		32	45
7	5	4	1	200	100	Mi/W	1 (3)	20	10 airhole
								40	28
								18	18
8	14	8	1	120	540	Mi			
9	12	7	Old site - abandonned but new in Nov 1975						
10	7	10	1	80	200	P			
11	5	8	1	230	600	Mi	1 (2)	80	28
								37	25
	$\bar{X}$ = 8.12 Range = 5-14	$\bar{X}$ = 6.81 Range = 4-10	T = 16 $\bar{X}$ = 1.45/s Range = 0-4	$\bar{X}$ = 136.8 Range = 40-300	$\bar{X}$ = 255 Range = 30-540	7P 43.7 % 7M 43.7 % 1P/W 6.2 % 1Mi/W 6.2 % T = 16	5 (13) 45 % sites have dens 2.6 d/si	$\bar{X}$ = 39.77 Range = 18-80	$\bar{X}$ = 32.33 Range = 10-60

Key : P - peripheral || - parallel T - total Mi - middle s, si - site $\bar{X}$ - median W - near water d - den

TABLE XIII

Site analysis at Kaboeri creek, January to September 1977.

SITE	WIDTH (cm)	LENGTH (cm)	N SPRAINT SITES (Latrines)	SIZE/LOCUS SPRAINT SITE (cm)		
				WIDTH	LENGTH	LOCUS
1. 1B	7	6.5	1	120	220	P
2. 41	5.8	4.3	1	200	200	P/Mi
3. 1D	3.5	9.4	1	150	230	P
4. 42	3.8	7.2	1	190	190	P
5. 1X	—	—	—	—	—	—
6. 43	8.5	8.5	1	200	240	P
7. 1	7	7	1	100	100	P
8. 2	7	3	1	200	200	P
9. 3	8	7.5	1	220	300	P
10. 3C	2,6	2	1	100	180	P/Mi
11. 4	12	9	1	150	200	P
12. 5	1.5	.72	1	100	100	P
13. 6	2	3.5	1	200	200	Mi
14. 7	11	9	2	200/100	100/100	Mi/Mi
15. 44	2.5	6.2	1	250	250	P
16. 2C	3	7.2	1	130	360	P
17. 45	10	8.5	2	210/160	270/160	P/P
18. 8	6	4	4	250/250	250/250	P/P
				80/80	80/80	Mi/ Mi/W
19. 9	7	4	1	150	200	P
20. 10	7	3	1	100	300	P
21. 11	10	4	1	100	300	P
22. 47	10.1	6.1	1	140	90	P
23. 12	11	8	1	200	300	P
24. 13	20	13	1	210	400	P
25. 46	3	2	1	150	150	Mi
26. 40	10.2	9.3	1	190	240	P

27.	2D	25	11	3	220/75/240	220/75/160	P/P/P
28.	39	11.2	14.7	1	165	290	P/Mi
29.	49	2.2	1.1	1	110	110	P/Mi
30.	1C	11	9	1	160	270	P
31.	1D	21.6	3.6	1	340	160	P/Mi
32.	33	5	1.8	1	20	20	Mi
33.	34	9.5	1.7	3	140/100/290	170/100/210	P/P / P/W
34.	6D	7.2	6.7	2	160/120	240/210	P/W /P
35.	5B	16.5	7	2	220/200	170/170	Mi/W / P/W
36.	2X	6.3	6	1	220	210	Mi
37.	35	5.1	2.7	1	100	100	P
38.	36	12.1	3.8	1	290	110	P
39.	37	8	4.6	1	140	140	P/Mi
40.	38	7.7	6.4	1	183	178	P
41.	3D	14	3	2	110/330	110/110	P/ P/Mi
42.	4D	12.6	6.6	1	150	150	Mi
43.	2B	5.3	3.3	1	330	330	Mi
44.	5D	8.5	3.4	1	80	80	P
45.	4B	6.1	7	1	110	180	Mi
46.	3B	6.6	6	1	200	230	Mi
47.	14	16	8	3	100/80/50	200/80/50	P/P/P
48.	17	22	8	4	75/200 75/200	75/200 75/200	Mi/Mi W/W
49.	15	7	9	1	150	700	M/P
50.	16	4	5	1	170	170	M/P
51.	18	17	7.2	2	220/240	380/420	M/P /P
	$\overline{X}$	8.94	5.99	1.36/si	165.3	186.2	40P 58.9 %
	Range	1.5 - 22	.72 - 14.7	0-4	20-340	20-700	13Mi 19.1 %
							10P/Mi 14.7 %
							3P/W 4.4 %
							3Mi/W 4.4 %
							0W

Key : P pheripheral Mi - middle si - site $\overline{X}$ - median W - near water

TABLE XIV

Comparative analysis of Pteronura *sites and spraints along seven Suriname Rivers.*

	RALEIGH FALLS (Coppename R.) Oct 76 19 si.		TONKEN FALLS Oct 76 29 si. (Upper Coppename R)		MARA-TAKKA R. (Nickerie R.) Nov 76 18 si.		ZUID RIVER (Lucie R.) Jul 77 23 si.		KABOERI CREEK (Corantijn R.) Jan-Nov 77 51 si.		UP. COESE-WIJNE (Coppename R.) Jan 77 11 si		KABO CREEK (Tibiti R.) Jan 77 16 si.	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
1. *Location of site*														
< 10 m from rapids	4	21.0	5	17.3	—	—	—	—	—	—	—	—	—	—
< 5 m from rapids	8	42.1	21	72.4	—	—	5	21.8	—	—	—	—	—	—
> 5 m from water	10	52.6	21	72.4	10	55.5	17	73.9	5	9.8	—	—	9	56.2
< 5 m from water	17	36.8	7	24.2	8	44.4	1	4.3	6	11.8	11	100.0	7	43.8
2. *Dist. from next site*														
within 5 m	4	21.1	5	17.2	—	—	—	—	—	—	1	9.1	—	—
within 10 m	3	15.8	7	24.1	—	—	1	4.3	5	9.8	1	9.1	3	18.7
within sight	13	68.4	22	75.8	4	22.2	6	30.4	15	29.4	3	27.3	3	18.7
within 20 m	5	26.3	6	20.7	1	5.5	12	52.2	15	29.4	7	63.6	5	31.2
out of sight	6	31.6	4	13.8	14	77.8	16	69.6	77	52.9	7	63.6	13	81.2
3. *Type of site*														
Overhanging trees	13	68.4	15	51.7	17	83,3	10	43.5	44	86.3	10	90.9	16	100.0
Tress/low roots 50 cm ø	5	26.3	7	24.1	1	5.5	—	—	10	19.6	3	27.3	1	6.2
in open	6	31.2	14	48.3	4	22.2	13	56.5	3	5.9	—	—	1	6.2
in dip/crevice	—	—	—	—	—	—	—	—	—	—	—	—	—	—
4. *Location of spraint*														
sand	4	21.1	21	72.4	—	—	1	4.3	8	15.7	—	—	—	—
bare rock	5	26.3	8	27.6	—	—	—	—	—	—	—	—	—	—
boulder	12	63.2	2	6.9	—	—	12	52.2	—	—	—	—	—	—
sand/grass tussock	—	—	3	10.3	—	—	—	—	5	9.8	—	—	—	—
earth/leaves	1	5.3	7	24.1	17	94.4	—	—	51	100.0	11	100.0	16	100.0
log	—	—	1	3.4	1	5.5	10	43.5	10	19.6	2	18.2	—	—
island	15	78.9	26	89.6	—	—	10	43.5	1	1.9	—	—	—	—
mainland	3	15.8	3	10.3	17	94.4	12	52.2	50	98.0	11	100.0	16	100.0

5. *Elevation of spraint*														
ground level	3	15.8	1	3.4	10	55.5	1	4.3	39	76.5	7	63.6	13	81.2
> 50 cm above water	3	15.8	21	72.4	3	16.7	6	26.1	1	1.9	2	18.2	2	12.5
> 1 m above water	13	68.4	8	27.6	5	27.8	13	56.5	12	23.5	2	18.2	1	6.2
highest point avail.	2	10.5	12	41.4	—	—	11	47.9	—	—	—	—	—	—
6. *N of spraints on site*														
1	12	63.2	2	6.9	1	5.5	18	78.3	34	66.7	7	63.6	9	56.2
2	6	31.6	8	27.6	—	—	4	17.4	9	17.6	2	18.2	1	6.2
3	1	5.3	10	34.5	1	5.5	1	4.3	4	7.8	1	9.1	4	25.0
4	—	—	1	3.4	—	—	—	—	1	2.0	—	—	—	—
5	—	—	2	6.9	—	—	—	—	—	—	—	—	1	6.2
5+	—	—	5	17.2	—	—	—	—	—	—	—	—	—	—
Latrine-no single spraint	—	—	—	—	15	77.8	—	—	50	98.0	10	91.0	15	93.8
7. *Spraint distance from other spraint*														
> 1 m ø	5	26.3	21	72.4	2	11.1	3	13.0	13	25.5	1	9.1	3	18.7
< 1 m ø	1	5.3	4	13.8	11	61.1	1	4.3	39	76.5	6	54.5	8	50.0
over 5 m ø	—	—	2	6.9	3	16.7	—	—	1	2.0	2	18.2	4	25.0
8. *Other signs present*														
Tracks	3	15.8	1	3.4	7	38.9	1	4.3	9	17.6	2	18.2	3	18.7
Scratch marks	—	—	1	3.4	6	33.3	1	4.3	11	21.6	2	18.2	6	37.5
Food remains	2	10.5	1	3.4	—	—	1	4.3	—	—	—	—	—	—
9. *Contents of spraint*	(% of 22 spraints)		(% of 43 spraints)		(% of 16 spraints)		(% of 26 spraints)		(% of 40 latrines)		(% of 10 latrines)		(% of 15 latrines)	
Fish	7	31.8	9	20.9	16	100.0	6	23.1	40	100.0	10	100.0	15	100.0
Crabs and fish	9	40.9	25	58.1	—	—	10	35.7	—	—	—	—	—	—
Crab	6	27.3	9	20.9	—	—	10	35.7	—	—	—	—	—	—
10. *Spraint age*														
Fresh	3	13.6	7	16.3	6	37.5	6	23.1	14	35.0	5	50.0	10	66.6
Formed but dry	5	22.7	13	30.2	2	12.5	12	46.1	2	5.0	—	—	1	
Crumbled	14	63.6	19	44.2	15	93.7	8	30.8	24	60.0	9	90.0	9	60.0

Key : si. - sites — ø - diameter

TABLE XV

Pteronura *and* Lutra *spraint sites, Zuid river, 13-27 July 1977.*

LOCATION OF SPRAINT	*Lutra*		*Pteronura*		
log	2	8.7 %	8	34.8 %	
boulder	3	11.5 %	9	39.1 %	
sandbank	tracks only		1	4.3 %	T = 23

NUMBER OF SPRAINT(S)	*Lutra*		*Pteronura*		
one	5	15.1 %	13	39.4 %	
two	0		14	42.4 %	
three	0		1	3.0 %	T = 33

AGE AND COMPOSITION OF SPRAINT		*Old* (crumbling)	*Dry* (over 48 hrs.)	*Fresh* (24 hours)
Lutra	fish only	0	0	1
	fish/crab	0	1	1
	crab only	0	1	1
Pteronura	fish only	2	0	1
	fish/crab	2	5	3
	crab only	3	5	2

sites were found in this narrow portion of the river, three contained single *Lutra* spraints and five *Pteronura* spraints, with two sites containing two spraints each. Crabs remains were present in 8 of 10 spraints, 3 mixed with fish remains and of these two were *Lutra* (both fish and crabs). Both *Pteronura* and *Lutra* were seen three times and once respectively on the river. One communal latrine was found on a sandbank shaded by trees which had been used by a group of seven *Pteronura* for the night ; *Lutra* tracks were also present on this site.

The spraint was deposited on sloping logs 92 cm to 4.87 m from the water at an elevation of 42 cm to 1.26 m above the water. Logs, usually 40 cm to 80 cm in diameter, measured 78 cm to 1.34 m in circumference. The bark was still present on 5 logs. *Lutra* used logs twice, boulders once, also moving 1.6 to 1.8 m up the log and 82 cm to 1.2 m above the water.

I believe that the upper Zuid river is used jointly by *Pteronura* and *Lutra* during the rainy season when the lower portions of the river which are wider have a high water level with numerous white water stretches and rapids cascading through boulders leaving only isolated plateaus where the current is slower and where shallow hunting areas are available. *Pteronura* moves upstream at this time into the forest creek habitat which is probably exploited by *Lutra* year around. The smaller species seems to accommodate to the presence of the larger, each using

a single spraint marking system on logs and boulders, but never using the same one simultaneously. The much shyer *Lutra* appears to avoid the noisy *Pteronura* groups and encounters are probably rare.

5) Dens

Not all sites have dens and sites with dens are not necessarily perennial. On three rivers, the proportions of the number of dens to the number of sites varied :

Upper Coesewijne river :
45 % sites had dens (11 sites) (Table XII).

Kabo creek (Tibiti river) :
25 % sites had dens (16 sites) (Table XI).

Kaboeri creek (Jan-August 1977) :
16 % sites had dens (51 sites) (Table XIII).

The den consists of a tunnel leading to a single chamber which has been excavated into the riverbank. Up to three tunnels leading to the same chamber have been recorded and a chamber may be enlarged into a second chamber next to it (Figs. 47 & 48) to accommodate a group of 4 adults and three cubs together but

Fig. 47. — Four adult otters and three cubs occupied this double chambered den on Kaboeri creek. The two entrance tunnels were submerged at high tide.

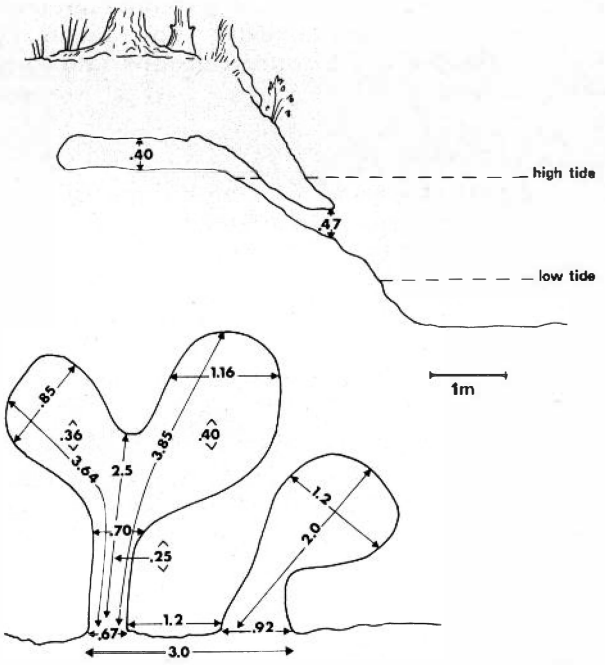


Fig. 48. — Den site 40 B on Kaboeri creek in 1977. It was used by a family of seven otters (4 adults and 3 cubs).

these variations are exceptional. The diameter of the tunnel opening is consistent with the approximate diameter of an adult otter in a crawling position, approximately 30-40 cm in diameter. Tunnel openings may partially cave in in looser sandy soils until they are quite wide, up to 1.50 m.

Upper Coesewijne river (5 dens, 13 holes)	39.77 cm (width) range = 18-80 cm	32.23 cm (height) range = 18-60 cm
Kabo creek (Tibiti river) (8 dens, 8 holes)	47.88 cm (width) range = 30-100 cm	32.13 cm (height) range = 20-42 cm
Kaboeri creek (Jan-Sept 1977) (8 dens, 14 holes)	57.14 cm (width) range = 32-150 cm	39.86 cm (height) range = 27-55 cm

The large variation between maximum and minimum sizes represent the difference between new den entrances (minimal size) and older dens (maximum size). The otters do not appear to enlarge existing holes originally excavated by other mammals but the sand or clay banks of the river are dotted with holes of

unknown origin which can be seen at low tide during the dry season. Many holes are probably the result of natural bank erosion, while others may be holes used by caiman or nocturnal fish such as Gymnotoids located under the roots of large trees close to the water's edge.

There appears to be no particular choice of soils in den excavation. Podsol and rough bleached sand or heavy clay are soils typical of marsh forest or xerophytic forests which are prime *Pteronura* habitats. While sandy soils cave in more often they are still used and the dens is repaired until it is abandonned.

It was possible to measure the tunnels and den chambers of 3 dens. The tunnel measuring 30 cm to 3.6 m in length leads up to the oval chamber which measures 1.2 m to 1.8 m in diameter and is 43 cm - 74 cm high. No bedding material was found inside, only a bare sandy floor worn smooth. No spraints and no separate latrine chambers were found. A small air hole 10-20 cm in diameter may be present if the overhanging tangle of roots in the roof does not offer sufficient ventilation. While the chamber floor is level, the tunnels leading to it may turn upwards or sideways at an angle of 35°-45°.

Two dens on the Maratakka and the Tibiti were excavated at the base of existing trees with entrances above ground ; both had a complementary submerged entrance.

Tunnels leading to the forest at the rear of the den, also called " backdoors ", were seen in 3 dens on Kaboeri creek and one on the upper Maratakka. Also, a female and her juvenile cubs were surprised in their den on the Coesewijne in February 1977 and both used the backdoor to escape into the forest.

Dens may have latrines above or adjacent to them which are used as long as the den is in use. The size of the latrine may be larger (1.5 m to 4.2 m in diameter) than a communal latrine of average size on a large site. Only the actual area used for the latrine is cleared and not the surrounding vegetation. It is usually the pungent smell of this latrine which attracts the observer to the den, which otherwise might pass unnoticed if it has submerged entrances. Fresh scratch marks on the banks may also be indications that a den is in use nearby.

New dens are excavated when the otters return to Kaboeri creek at the beginning of September and some of these are used until late February when the juveniles are two-thirds the size of their parents. Some dens appear to be temporary in nature and may be used once or twice for a period of a week and then abandonned permanently. Only two perennial dens were found on Kaboeri creek, both associated with larger sites located at km 7.9. and km 4.3 (Table XVI).

TABLE XVI

Dens in use on Kaboeri Creek 1977-1978,

SITE	ENTRANCE (S)		TUNNEL		CHAMBER		ENTR'CE SUBM'GD	SPRAINT SITE (m)	UNDER /ON LARGE SITE	LOCA-TION (km)	REMARKS
	WIDTH (cm)	HEIGHT (cm)	LENGTH (cm)	HEIGHT (cm)	HEIGHT (cm)	DIAM. (cm)					
1. 4	32	40					yes		yes	1.7	in use Jan-Mar 77 by S
	36	27					yes				
2. 5	35	35					no		no	1.75	in use Jan 77 only by S
3. 6	38	38					yes	3.52 × 2	no		in use Jan 77 only
4. 8	42	28					no		yes	3.5	in use Jan 77
	58	32					no				
5. 2 D	150	50					no		yes	4.3	Swallow Pond, in use Jan and Sept 77 by H
	65	55					no				
	72	50					no				
6. 5 B	80	40					no		yes	7.9	Frenchman's Landing, in use Mar and Oct 77
	60	40					no				
	57	48					no				
7. 17	35	35					no		yes	> 11	excavated Mar 77, in use by U
8. 18	40	40					no		yes	> 11	exc. Mar 77, in use by U
$\overline{X}$	57.14	39.86					3 yes		6 yes		
Range	32-150	27-55					11 no		2 no		

Dens not visited and/or flooded, Apr.-Sept. 1977.

9. 44	?	?					yes	2.5 ø	no	2.45	in use Oct 77 by S
10. 46	30	30					partly	1.5 ø	no	3.8	in use Oct 77 by H, 2 cubs seen here
11. 50	92	45					partly		no	4.2	in use Jan 78 by S
	67	47									
12. 57	33	35					no		yes	5.2	in use Mar 78 by S
13. 52	70	35	.70		43	1.6	no		no	4.5	in use Jan 78 by S near head site
14. 49	?	?					yes		no	4.1	in use Oct 77 by H, caved in
	32	32					yes				
15. 47	40	40			74	1.2	yes		no	3.6	in use Oct 77 by H
	32	32									
16. 45	56	47					no		no	2.9	in use early 78 by S
17. 61	35	70					partly		no	5.5	in use early 78
18. 70	43	20	.30	63		1.87		3.8 × 1.9	no	5.8	in use Sept 77 by H Arawaboo Pond
	55	20	.45	33					no		
	52	20	3.6						no		
19. 77 B	75	38	1.4			1.8	yes		no	11	in use early 78
20. 59 B	28	30								5.4	in use Mar 78 by S
21. 71	36	22					no		no	2.7	in use Jan 78 by S
						6.47	5 yes		13 no		
$\bar{X}$	48.5	35.19	1.29	48	58.5	1.62	4 no				
Range	28-92	20-70	0 3-3.6	33-63	43-74	1.2-1.9	3 part				
							8 yes		7 yes		
$\bar{X}$	52.53	37.37					15 no		15 no		
							3 part				

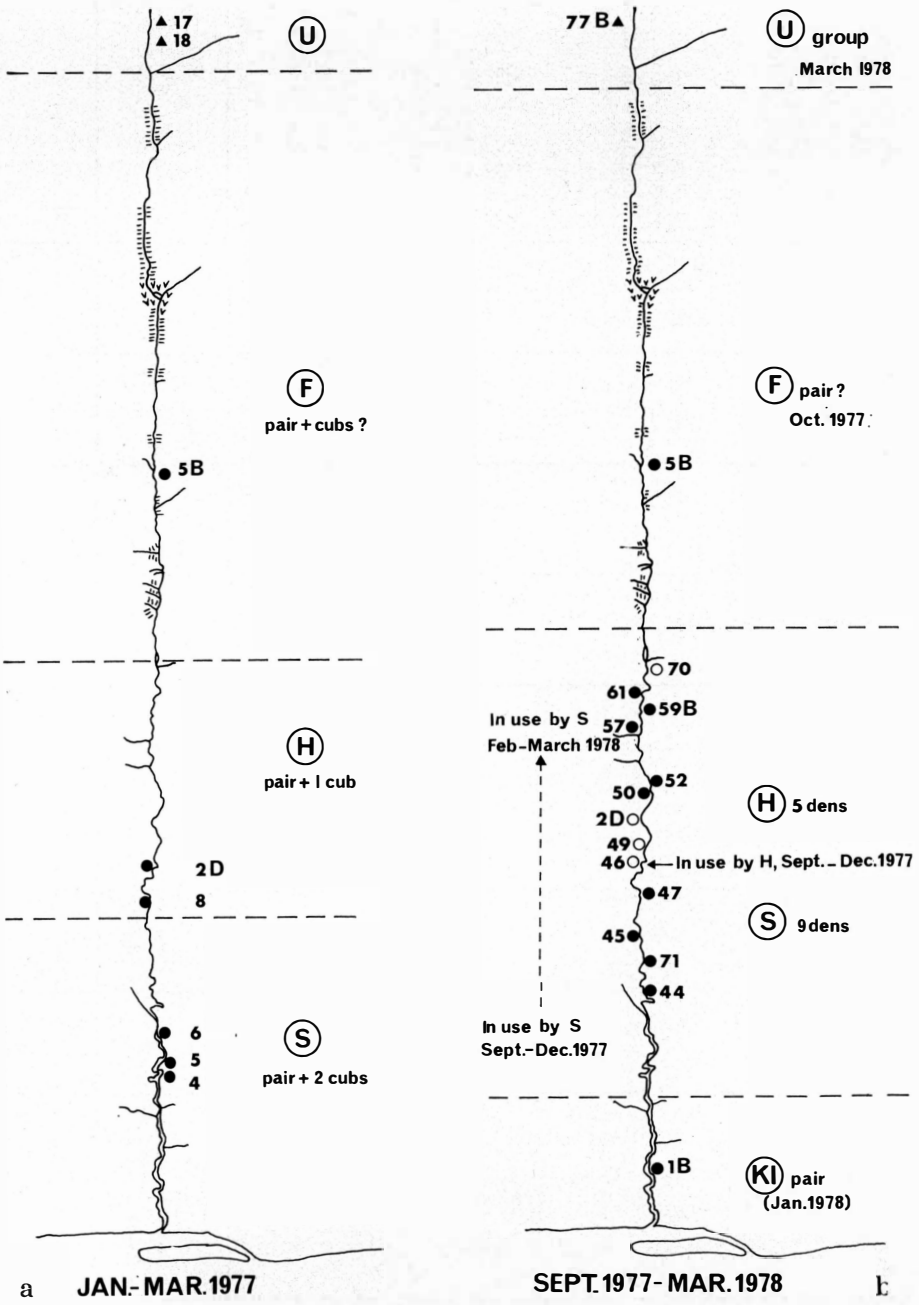


Fig. 49. — Dens observed in use on Kaboeri creek,

In early 1977 nine dens were in use (Fig. 49 a), while in late 1977-early 1978, 13 were used by three separate families with cubs. The S group of 4 adults and 3 cubs expanded its territory 4 km upstream when the pair living in that territory lost their two cubs and disbanded. They excavated or renovated five new dens when they settled in this new portion of their home range, using eight different dens in two months.

By March 1978, 21 dens had been located on Kaboeri creek (Fig. 49 b) ; 8 of the 26 riverbank entrances (31 %) were submerged, but three were visible or partly visible at low tide. The average size of the 30 den entrances which could be measured were 52.5 cm wide and 37.4 cm high.

6) Home Range

a) *Size in relation to habitat type*

To trace the movements of individual *Pteronura* in the dense, flooded forest during the rainy season proved an impossible task and most data were obtained by plotting movements during the dry season on Kaboeri creek.

The size of the home range can only be roughly estimated until more details are available on how far otters roam inland and up and down the larger rivers during the rains. One would like to speculate that the forest creeks on either side of larger rivers, particularly those with mosaic vegetation types like Kaboeri creek are the cores of much larger home ranges with no well defined boundaries. If Kaboeri creek which measures over 12 km in length is visited by most of the resident otters over its entirety and if the larger creeks radiating on either side are also explored, the home range is roughly 12 km long and 12 km wide. In the rainy season, the length of the excursions into the swamp forest and marsh forest might well be even greater than that.

b) *Kaboeri creek*

On Kaboeri creek, giant otters were identified individually 225 times during 77 days observation in 11 months of which a majority, 46, took place between 13 January and 11 March 1978. A number of different otters frequented this study area as residents, transients and newcomers indicating that the ranges were not occupied exclusively by an individual of a given sex but by a family group moving together. Otters within the center of their defended territory would immediately give the long-call if they heard an otter-like sound in the distance.

By January 1978, 23 otters were recognized individually of which 8 adults, 8 subadults and 7 cubs, and 6 others were not identified or not identifiable due to poor sighting conditions or the fact that they periscoped and did not reappear again. Of these,

probably 4 were transients and were glimpsed only occasionally, remaining a few days or weeks on the upstream portion of the creek.

Transients do not appear to pair up with residents or become integrated in family groups. For instance, in September 1977 when the otters were returning to their former haunts on the creek, group sizes were very different from those at other times of the year. It seems likely that transients were present but did not remain long. This tolerance of transients was not observed at other times during the dry season and even brief encounters were not seen. Perhaps this is due to the fact that, at that time, the sites had not been revisited yet and drenched with scent. Once this happens, the territorial boundaries are clearly established and transients become more discrete.

The transients either seemed to lack established dry season ranges or were so shy as to preclude proper identification. Some of these may have been 2 year-old subadults who recently left their family groups temporarily or permanently. All the sightings were of otters alone and single individuals were rare on Kaboeri creek. Their shyness would suppose them to be 1) newcomers and unused to a human observer or 2) a group member on a solitary foray, more unlikely, who felt insecure away from its group.

c) *Seasonal dynamics*

Availability of preferred prey species is certainly the governing factor in *Pteronura*'s seasonal movements. I speculate that giant otters can exhibit a wide variety of home range patterns, from exclusive territoriality during the dry season which coincides with cub rearing, through tolerance of transients at least during the transition to dry season, to lack of established ranges during the rainy season as the otters follow the spawning fish into the flooded forest. It is not yet known whether the sex and physiological condition of the resident otter play a further role in the defense of a portion of the home range, or lack of it, but it seems possible at it is characteristic of large carnivores and other mustelids.

TERRITORY

a) *Size and Structure*

Pair and groups of otters confined their activities during the dry season to well-defined areas of Kaboeri creek. While swimming or fishing, a pair or group would turn back and head the other way every time they reached a given point on the creek downstream and upstream. Even when I followed them from behind they would not trespass but would either swim back past the boat or go into the forest. I first observed these definite terri-

torial boundaries in March 1977 when a pair with their cub stayed on their boundary for an hour, appearing both nervous at my presence and undecided as to whether to continue downstream. When their cub attempted to do so they retrieved it and eventually headed back upstream to a den.

Territories appear to be spatio-temporal and keyed primarily to the preferred prey category of fish resting in shallow waters — each territory contains several stretches of good fishing areas where the otters fish each day. Territory size is variable depending on 1) the numbers of otters in residence along the creek ; 2) the type of habitat and 3) the number of good fishing areas available in a given portion of the creek.

b) *Patrol and maintenance*

Normally a pair of otters and their offspring of the past two years will clear and mark sites dotted along a 2 to 3 km section of the creek, even though they may wander over these borders at irregular intervals. Such uncharacteristic forays into neighboring territories may be done by only one individual in the group. While used to an observer within its territory, an otter spotted 4 or 5 km upstream from its normal haunt would be shy and unapproachable, disappearing into the forest or swamp as if it did not want to attract attention to itself.

At least a portion if not all the territory is patrolled each day by a pair starting shortly after dawn. The pair will swim steadily up or down one side of the creek, the direction chosen often coinciding with the movement of the tides, using this additional current to advantage. Stops may be made at preferred fishing areas or to eat a fish caught along the way. When approaching a territorial limit which may or may not be marked by a site, the pair or group turns back. As we have seen, all the sites are not visited and/or marked every day but they are patrolled as part of the normal activity pattern.

Territories may also be maintained from one year to the next. The H pair returned to the same portion of creek after the 1977 rainy season and so did the little known U group at km 10 and the S group at km 0 to 2.4. The maps show that four and later five groups of otters comprising 19 individuals in March 1978 were fairly evenly distributed along only 12km of Kaboeri creek, the largest S group of 7 holding the longest portions of creek.

Seasonal use of territories is more difficult to determine because sightings of known individuals become so difficult during the rains, and also because most of the sites are abandonned or flooded. I would speculate that the creek is visited only sporadically by its dry season residents and that territorial boundaries are not enforced at that time as evidenced by infrequent site marking.

Certain portions of Kaboeri's upstream creek are more difficult to delineate into territories because of the nature of the bank type. Reeds, marsh forest and palm swamps are not used for campsites along the banks so that existing sites are clumped close together in portions of xerophytic forest on higher ground. Between km 7 and km 11 there were only three areas suitable for sites : km 7.9-8.4 ; km 9.2-9.3 and km 10.5-10.6 These areas had 8 sites, 2 sites and 2 sites respectively with only marshy areas covered with floating vegetation in between. It is possible that the otters had sites behind the low-lying swamp areas in the forest or up the narrow forest creeks but this was not verified. Due to the difficulty of observation in this portion of the creek, the otters being shyer and impossible to follow when they hid in the swamps, I knew these two groups F (pair) and U (a group of seven) relatively little. The transients were observed for the most part in this upstream portion of Kaboeri. Perhaps they stayed up there because they too could elude the residents more easily by retreating into the swamps.

The " blank " areas of the creek where campsites did not occur because high banks were not available must be taken into consideration when estimating territory size and ultimately density or population level in a given area. If a territory is, say, a 2,5 km portion of the creek and contains at least two prime fishing areas, it does not follow that all territories will be the same size. Kaboeri creek presented special conditions : a) good fishing areas, b) a mosaic of habitats, some of them apparently unsuitable, c) human disturbance at the entrance of the creek. For these reasons, I am loath to speculate further on possible territory size in *Pteronura* or to even guess at the total population size of giant otters in Suriname.

c) *Invasion and expansion*

The S group, comprised of two adults and seven offspring, two born in late 1976 and three born in early September 1977 had maintained a territory on Kaboeri Island and used Kaboeri creek up to site 5 at km 2. When a bridge was built across the entrance of Kaboeri creek in October 1977 and then another across to Kaboeri Island, the S group began shifting their activities further and further upstream to km 3.4 by early January 1978. The H pair in this next territory had had two cubs in early October but had later lost them to an Amerindian poacher who wanted them as pets. Eventually the S group displaced the H pair who actively avoided them, running into the forest at their approach and on 19 January the female of the pair disappeared and was not seen again. The H male gave way to the S group and retreated to the top of his territory at km 5.8 to 6 on Arawaboo Pond, a prime fishing area. He used a very small resting site at km 5.8 which he did not mark and often slept hidden under bushes by the water-

side. The S group reached this area on the 8 February after centering their activities between km 4.5 and km 5.5 for 10 days. The H male hid in the forest each time the S group came to Arawaboo pond, usually every 2 to 4 days. Only once was the male H seen in his old territory at km 3.9 on March 8 a few days before the end of the study.

As soon as the S group moved upsteam, the subadult KI pair that had previously been seen on the Corantijn river 10 km upsteam, took up residence at the entrance to Kaboeri creek. They were first sighted at the entrance of the creek on 14 January and were very shy and were seen after that on 16, 24, 31 January and then regularly in February and early March using the first 2 km of the creek and Kaboeri Island.

Such a rapid takeover of available habitat would indicate that the increased river traffic due to the Western Suriname Development Project in Washabo and Apoera on the Corantijn river had a disturbing effect on the resident otter population who sought quieter and more remote portions of the creek. The rapid expansion of the S group territory may also be due to the fact that maturing cubs at the end of the dry season effectively doubled the number of otters in the group, and doubled their feeding requirements without immediately affecting the size of the corea area occupied, if the size of the territory was too small in the first place or was reduced through the avoidance of certain areas where human disturbance is high near the two bridges at the creek entrance. The subadult KI pair adjusted to the disturbance and exploited an undesirable portion of the creek where the fishing was difficult due to the deeper waters and where the human disturbance level was high.

d) *Discussion*

After analyzing home range and territoriality in *Pteronura* it would be useful to ask what density dependent factors control giant otter populations.

In his now classical study on animal community patterns, Elton (1949) stated that " competition for resources, space and prestige (sic) and intespecific competition, predators and parasites were the chief density dependent factors ". How does this apply to *Pteronura* which appears to have few, if any, natural enemies (man is not a natural enemy) and a low cub mortality ? Dispersal of subadults after the next litter has matured and eventual mortality of the adults on one hand and seasonal variations of extraneous factors affecting fish populations on the other are probably the principal mechanisms which directly regulate *Pteronura* density.

Schaller (1972) noted that territory size in lions appears to be correlated with food abundance during the leanest season. While

food abundance may determine *Pteronura* density, the social structure of giant otters, another large predator at the top of its food chain, with the strong pair bond and family groups, is quite different to that of the lion. The mortality rate is probably also high during the solitary dispersive phase, when the subadults are approaching 2-3 years of age. The population size appears to be regulated through the availability of territories which are linked to proper habitat and prey availability.

Pteronura appears to be a predator adapted to relatively narrow niche. It is dependent on fish that inhabit shallow waters and rest on the bottom for the most part and that migrate to flooded forest areas during the rainy season to spawn. The relatively narrow choice of prey species means that any predator is very vulnerable, should that fish population crash due to a natural phenomenon, pollution or overfishing by man.

I mentionned earlier (cf. Maintenance Activities) that a single pair of *Pteronura* requires 2200 to 2900 kg of fish per year and a family group of seven 7,500 to 10,200 kg. Hence the 19 to 23 otters residing on Kaboeri creek consume 20,400 - 24,800 kg to 27,700 - 33,500 kg of fish each year. Although it is impossible to estimate the fish production of the relatively narrow creek and its tributaries, this would appear to be near the carrying capacity. It must also be remembered that from April to August the otters are dispersed and do not hunt for weeks on end in the creek itself.

The carrying capacity of a habitat like Kaboeri creek has probably evolved in such a way that a stable population of otters is maintained so long as the environment and the fish population levels remain fairly constant. The building of two bridges provoked a marked shift in territory boundaries and, soon after, the disappearance of one adult female and her subadult offspring.

Thus, *Pteronura* appear to space themselves out by sight, scent and hearing. The territories encompass good fishing areas. This system can operate successfully only so long as the fishing areas are not depleted.

IV. — *COMPARISONS AND CONCLUSIONS*

A) Pteronura and other Lutrinae

Otter field studies, including this one, have two inherent limitations : a) a great deal of effort is required to find and observe otters, a fact which discourages many prospective field biologists and, b) a small sample size may affect the conclusions which can be drawn — the temptation to generalize from data based on few isolated individuals with, possibly, idiosyncratic behaviors, is strong.

Recently, the excellent field studies of Erlinge (1967 a and b) and Rowe-Rowe (1977) have begun to bridge the gap between our knowledge of otter behavior in the wild and in captivity. The existing otter literature has been reviewed in depth by Harris (1968) and shows the paucity of scientific information available as compared to anecdotal accounts of pet owners and early explorers and naturalists.

I will base my comparisons of *Pteronura* and the other Lutrinae largely on my own experience of captive zoo specimens based on 1363 hours of observation on *Lutra, Amblonyx, Aonyx, Lutrogale* and *Pteronura.* The genera can be divided into two categories : a) those showing a high degree of sociality with strong pair bonding *(Aonyx, Amblonyx, Lutrogale* and *Pteronura)* and b) the more solitary *Lutra* (cf. *Lutra enudris* section).

The Lutrinae have evolved a number of behavioral characteristics which are typical of the subfamily. Certain aspects of the repertoire, such as the use of the forepaws, vocalizations and agonistic interactions, when considered comparatively, can be identified as those showing the clearest evolutionary trends.

Particular attention was given to the study of the vocal repertoires and agonistic behavior patterns of three partially sympatric genera *Amblonyx, Lutrogale* and *Lutra* (Duplaix, 1969, 1971, 1972, 1975 and largely unpublished).

For instance, a systematic study of the vocal patterns provides useful criteria for defining and describing phylogenetic relationships. In addition to certain morphological distinctions (such as size, webbing and skull shape), each genus can be identified by the variations in its vocal repertoire. The presence or absence of certain specific vocalizations and their sequences readily distinguishes *Lutra* from *Lutrogale* and both of these from *Amblonyx.* (Sometimes classified as a subgeneus of *Lutra, Lutrogale* possesses closer behavioral and skeletal affinities to *Pteronura* and to *Amblonyx* and *Aonyx,* to a lesser extent, and should maintain its monotypic generic status). *Lutra,* a genus which encompasses both New World and Old World species, can be recognized by its unique generic vocalization : the staccato chuckle (New World) or the twitter (Old World) both given in a close contact, affiliative context between adults and mother to cubs. The contact call in *Lutra* is a one-syllabe chirp whereas in the four other genera including *Pteronura,* the sound is more of a bark with a nasal, guttural quality and the close contact sound is a humming-purr sound, interspersed with a falling ' coo '.

Interspecific and intergeneric differences in vocalizations arise mainly in these contact, summons and greeting calls, but similarities especially in threat and alarm vocalizations remain. The growl and the HAH ! with minor variations are common to all

the species studied. It is interesting to note that the widely dispersed "giant" otters, i.e. *Aonyx* (Africa), *Enhydra* (North Pacific) and *Pteronura* share more similarities in their vocal repertoires than sympatric species such as *Lutra lutra, Lutrogale perspicillata* and *Amblonyx cinerea.*

A comparative study of the agonistic behavior showed that overt fighting in aggressive encounters appears to be usually provoked by the response of the addressee. The response may be dependent on age, sex, breeding status and social rank, if any. *Lutra* males were particularly aggressive during the breeding season, often attacking without preliminary threats ; the females were aggressive towards other adult females and their offspring and towards males during a restricted postpartum period but full-fledged attacks were rare. In contrast, *Lutrogale* and *Amblonyx* have two separate male and female dominance orders reminiscent of certain social Canidae (Woolpy, 1968). The females maintain and regulate hierarchy within the family group through ritualized agonistic encounters. When the rare full-fledged attacks by females were observed, they had been stimulated by particular individuals (usually adults) or unfamiliar environmental conditions, e.g. when a newcomer was introduced to a group. While the top-ranking female is usually dominant over males in the group, it is the alpha male, often her consort, which initiates group movements and launches interspecific attacks during extra-territorial forays. The males play an important role during cub-rearing, and remain in the den with the female and cubs. All three genera exhibit a close pair-bond and travel in family groups.

When the other genera are compared to *Pteronura, Lutrogale perspicillata* immediately stands out as being the most closely convergent species. Morphologically it has the same heavy-bodied appearance with thickly webbed extremities and a tail which is slightly keeled along the edges. Its skull and baculum bear a closer resemblance to *Pteronura* than to any other lutrine species. Its social behavior and vocalizations are similar, including the harsh nasal snorts and whines ; and it too is a 'noisy' otter with a very varied repertoire of discrete social sounds. Unfortunately, data on its ecology in the wild are sparse. The preliminary findings of Wayre (1974) show that it travels in family groups in coastal swamps and mangroves, often venturing out to sea. In captivity it exhibits a high degree of pair-bonding and the male helps the female dig the cubbing den and remains with her during the rearing of the cubs (pers. obs.).

B) Conclusions

In Suriname, *Pteronura*'s annual life cycle and feeding ecology is closely linked and dependant upon the seasonal movements of the fish populations. The Characoids are *Pteronura*'s preferred

prey and the fish's reproductive biology is governed by the seasonal flooding associated with the long rainy season (April-July). The fish move into the flooded forest to spawn and the otters follow them there until the waters recede.

It has been determined that *Pteronura* is a diurnal and gregarious mustelid, living in well-established family groups and defending portions of its home range against conspecifics. A close pair-bonding was observed between adult males and females and the vocal repertoire of social sounds is complex, indicating the high degree of sociality of the species.

The birth season spreads over several months from August to October and a second litter may be born early in the following year if the first one fails. The cubs remain with the parents until the next litter of cubs is born and probably remain with the expanding family until the cubs have matured.

Both *Pteronura* and *Lutra* are well represented in Suriname, although the latter species is much shyer and difficult to observe. Both species are known to be sympatric on at least five major river systems. Size of prey, *Lutra*'s crepuscular habits and use of coastal swamp and high forest creek habitats, minimize competition or encounters between the two species.

The highest density of *Pteronura* was observed on Kaboeri creek, the Tibiti river and the upper Coesewijne river, all habitats associated with floodable swamp and marsh forest in black water creeks. This prime otter habitat occurs on a band across Suriname between 5°30" and 5°N.

RESUME

L'écologie et le comportement de la Loutre géante du Brésil *Pteronura brasiliensis* ont été étudiés de juillet 1977 à mars 1978 au Suriname.

L'espèce est diurne et grégaire, formant des groupes familiaux durables qui défendent certaines portions de leur domaine vital contre les incursions de leurs congénères.

Pteronura brasiliensis est piscivore. Les modalités de reproduction et les déplacements saisonniers des poissons Characoides qui forment l'essentiel de son régime ont une influence profonde sur l'écologie de cette loutre. Pendant la saison des pluies, par exemple, les *Pteronura* suivent leurs proies dans la forêt inondée, abandonnant temporairement leurs « bivouacs » et tanières habituels.

La reproduction a lieu d'août à octobre. Les jeunes loutres restent avec leurs parents quand naît la portée suivante, peut-être même jusqu'à leur propre maturité.

Le répertoire comportemental de *Pteronura brasiliensis* est décrit et comparé avec celui des *Lutra* solitaires.

Lutra enudris peut cohabiter avec *Pteronura* dans certains cours d'eau de Suriname. Ses mœurs solitaires, son activité surtout crépusculaire et la taille moyenne de ses proies, tout comme le fait qu'elle peut également habiter dans les marais côtiers et les petites rivières de la grande forêt, minimisent les chances d'une éventuelle compétition avec *Pteronura*.

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